Mating conflict in primates: infanticide, sexual harassment and female sexuality

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INTRODUCTION

In a variety of mammals and a few birds, newly immigrated or newly dominant males are known to attack and kill dependent infants (Hausfater & Hrdy, 1984; Parmigiani & vom Saal, 1994; van Schaik & Janson, 2000). Hrdy (1974) was the first to suggest that this bizarre behaviour was the product of sexual selection: by killing infants they did not sire, these males advanced the timing of the mother's next oestrus, and due to their new social position would have a reasonable probability of siring this female's next infant. Infanticide would therefore be one of the most dramatic expressions of sexual conflict (Smuts & Smuts, 1993; Gowaty, 1997, this volume).

Although this interpretation, and indeed the phenomenon itself, has been hotly debated for decades (e.g., Dolhinow, 1977; Bogess, 1984; Bartlett *et al.*, 1993; Sussman *et al.*, 1995), on balance, this hypothesis provides a far better fit with the observations on primates than any of the alternatives (cf. van Schaik, 2000a). First, several detailed studies showed that the males never attacked or killed their own offspring (Borries *et al.*, 1999; Soltis *et al.*, 2000), in accordance with the more anecdotal information compiled from all directly observed cases of infanticide in the wild (van Schaik, 2000a). Second, several large-scale studies have estimated that the time gained by the infanticidal male amounts to 25%, 26% and 32% of the mean interbirth interval (Crockett & Sekulic, 1984; Sommer, 1994; Borries, 1997). Third, in most cases (e.g. in 78% of 49 directly observed cases in the wild; van Schaik, 2000a), these males subsequently gained mating access to the female and had above-average chances of siring the next infant because of their dominant status. Because males rarely, if ever, suffer injuries during infanticidal attacks, and because there is no evidence that committing infanticide leads to reduced tenure length, one can safely conclude that, on average, infanticide is an adaptive male strategy.

The curious taxonomic concentration of observations of infanticide by males in primates, carnivores and sciurognath rodents can be explained by the fact that these radiations all share a peculiar life history feature. In all of them, females that lose their dependent offspring are ready to conceive sooner than they otherwise would– the key benefit to the male – due to the long period of infant dependence relative to the duration of gestation (van Schaik, 2000b).

Hrdy (1979) was also the first to argue that if we accept that infanticide by males is an adaptive phenomenon we should also ask about evolved counter-strategies. As she put it recently (Hrdy, 2000a): 'it should logically follow that infanticide must have acted as an important selection pressure shaping the behaviour and reproductive physiologies of mothers as well the protective responses by fathers and other relatives.' Soon after her proposal (Hrdy, 1979), female sexual behaviour became the focus of scrutiny from the perspective of infanticide reduction (e.g., Hrdy & Whitten, 1987; Small, 1993; van Schaik *et al.*, 1999), but association with protector males has received attention as well (van Schaik & Dunbar, 1990; Smuts & Smuts, 1993; cf. Wrangham, 1979).

In this chapter, we extend the work on female sexuality in primates in relation to the risk of infanticide. First, after reviewing the basic logic and empirical evidence for sexual counter-strategies against infanticide risk, we examine in more detail how female sexual behaviour can be effective in reducing attack tendencies by unlikely sires while still securing protection from more likely sires.

Second, we turn to sexual harassment[1], i.e. male aggression targeted against sexually active ('oestrous') females, and show how it can be viewed as an expression of mating conflict between the female and the dominant male. Because harassment is remarkably concentrated in catarrhine primates, we then examine sexual behaviour and physiology in that radiation relative to species vulnerable to infanticide in other primate radiations. We conclude that various features of catarrhine sexuality can plausibly be understood as responses to this harassment in the evolutionary arms race, although this topic requires much additional work.

Males as protectors

Before discussing aspects of female sexual behaviour as a counterstrategy against infanticide some attention to the association with likely sires is needed in order to explain why female sexual behaviour tends to lead to protection by one, or sometimes more, likely sires. Protection of infants by likely sires is made possible by the year-round male-female association found in virtually all primates in which females carry their infants (van Schaik & Kappeler, 1997). At least in multi-male groups, likely sires tend to be in close spatial proximity with infants (Janson, 1986; Paul *et al.*, 2000), and numerous reports indicate that these males actually defend the infants against attacks by other males (Borries *et al.*, 1999; review: van Schaik, 2000a).

Infanticide often happens when the former dominant male, the most likely sire of most infants even in multimale groups (reviews in Cowlishaw & Dunbar, 1991; Paul, 1997; van Noordwijk & van Schaik, this volume), is eliminated or incapacitated. Infanticidal attacks could have been provoked by his experimental removal, either in the wild (Sugiyama, 1966) or (quite frequently, and inadvertently) in captivity (e.g., Angst & Thommen, 1977), or by natural demographic processes (e.g., Steenbeek, 1996). In all these situations infanticide by the new male is commonly observed. Conversely, when one interprets the social context of all directly observed cases of infanticide in wild primates that occurred spontaneously, the great majority (85% of 55 cases: van Schaik, 2000a) is associated with a change in the dominant position in the group, which involves the ousting or weakening of the former dominant. Relative takeover rate (corrected for variation in interbirth interval) also explains much of the variation in infanticide rates in well-studied populations (Janson & van Schaik, 2000).

Thus, dominant males are effective protectors of infants as long as they are not ousted or incapacitated. Females should therefore be expected to mate preferentially with these powerful males whenever females can be confronted by males who are unlikely sires.

FEMALE SEXUAL BEHAVIOUR AS A COUNTER-STRATEGY TO INFANTICIDE

Theory

Hrdy (1974, 1979) hypothesized that female sexual behaviour in primate species vulnerable to infanticide has been modified to reduce the risk of infanticide by males. The basis for the argument is that primate males, like those of the majority of mammals, do not recognise their offspring (in itself possibly the product of female-driven evolution), and therefore must rely on indirect indicators of paternity probability. These indicators have been studied experimentally in rodents (vom Saal, 1984; Perrigo & vom Saal, 1994), but not in primates, where the indicators have to be pieced together by analysing individual cases (reviewed in van Schaik, 2000a). Primate males are thought to use rules of thumb such as the quality of their sexual experience with the female (i.e. mating frequency relative to her

[1] We follow the use of "harassment" as in Smuts & Smuts (1993), which differs from that in Clutton-Brock & Parker (1995).

attractivity [her 'stimulus value' to the male]) weighted for her mating frequency with other males, the interval between matings and birth, and perhaps the continuity of association between male and female. We assume that natural selection has favoured males that use those rules of thumb that yield the closest average match with the probability of paternity.

Conceptually, we can distinguish two kinds of matings by females that may reduce the risk of infanticide. First, by mating polyandrously in potentially fertile periods, females can reduce the concentration of paternity in the dominant male, and spread some of it to other males, so that long-term average paternity probabilities will be somewhat below 1 for the dominant and somewhat above 0 for the subordinates. Second, by mating during periods of non-fertility (e.g. during pregnancy; situation-dependent receptivity: Hrdy, 1979), a female may be able to manipulate the assessment by the various males of their paternity chances, although she obviously cannot change the actual paternity values allocated to the various males. This distinction is theoretically useful, but the various players are probably quite unaware of it, with males merely responding to visual, olfactory and behavioural stimuli emanating from the female that create variation in her attractivity (Snowdon, this volume; Zinner *et al.*, this volume).

If male behaviour depends on their estimate of paternity, this sexual behaviour can be effective. Hrdy (1979, 1997) reasoned that where males have a low, but non-zero probability, they would refrain from attacking the infant, whereas they would defend it when the estimate is higher.

Empirical evidence

The basic prediction is that females that are vulnerable to infanticide by males should be actively polyandrous whenever potentially infanticidal males are present in the mating pool (i.e. the sexually mature males in the social unit or nearby with whom the female can mate in principle). There is ample evidence that primate females in vulnerable species actively pursue polyandrous matings and that they often engage in matings when fertilization is unlikely or impossible (Small, 1993; Manson, 1995; summarised in van Schaik *et al.*, 1999). Indeed, females often target low-ranking or peripheral males reluctant to mate in the presence of dominant central males, especially during pregnancy (e.g., Watts, 1991; Wallis & Bettinger, 1993; Gust, 1994).

There are two sources of more direct empirical evidence to assess whether these derived features of primate sexual behaviour are indeed an evolutionary response to vulnerability to infanticide: (i) direct sexual responses by females to changes in group composition or male status; and (ii) broader comparisons of sexual behaviour between taxa that are or are not vulnerable to infanticide by males.

In species vulnerable to infanticide, females often respond to changes in the male cohort of a group with immediate proceptivity and effectively solicit matings with the new(-ly dominant) male (Struhsaker & Leland, 1985; Cords, 1988; Sommer *et al.*, 1992; Swedell, 2000), even showing rapid development of sexual swellings in species that have them (Stein, 1984; Colmenares & Gomendio, 1988; Zinner & Deschner, 2000). In various catarrhine primates in which multiple males temporarily enter a group ('male influx'), mating periods (duration of oestrus) are relatively longer compared to periods without male influxes (e.g., Cords, 1984, 1988; Takahata *et al.*, 1994). Similarly, in several species with both single male and multi-male groups, female mating periods are longer in multi-male groups (Brockman, 1999; Heistermann *et al.*, 2001).

Interspecific comparisons provide similar support: van Noordwijk & van Schaik (2000) found a clear trend toward more polyandrous mating among primate and carnivore species vulnerable to infanticide relative to those that are not vulnerable. Post-conception mating, while infrequently reported, was also concentrated in those orders of mammals

where infanticide is to be expected based on their life history. Within primates, post-conception matings are found predominantly, and perhaps exclusively, in species vulnerable to infanticide (van Schaik *et al.*, 1999). However, one prediction was not upheld: in most other mammals no systematic trend towards longer mating periods in species vulnerable to infanticide was apparent (van Noordwijk & van Schaik, 2000). We will later show that this prediction is only expected where males are able to force matings.

A different source of evidence for the effectiveness of sexual behaviour in reducing the risk of infanticide is the lower rate of infanticide in multi-male groups, when controlling for the effect of takeover of dominance (Janson & van Schaik, 2000). To some extent this reduction is obviously due to male protection because in multi-male groups defeated dominants tend to remain in the group, at least for a while (e.g., van Noordwijk & van Schaik, 1988; Perry, 1998; Borries, 2000). However, sexual strategies are implicated as well because we occasionally see protection of the infant by other resident males (e.g., Borries *et al.*, 1999), or absence of attacks by the new dominant who was a long-term resident and had mated before with the mothers (see below).

A problem

A remarkable aspect of infanticide is that – especially in multi-male groups – only a small to moderate proportion of the infants typically ends up getting killed. While this high probability of survival probably has multiple sources, it is reasonable to attribute at least some of it to the female's sexual behaviour. Yet, the latter's effectiveness is somewhat surprising because paternity is a constant-sum game, in that each infant can have only one sire and that the long-term average probabilities of fertilisation of all the players must add up to 1. A female therefore faces a considerable challenge. On the one hand, by raising the long-term probability of subordinate males through their mating behaviour, she reduces the risk of infanticide because these males are less likely to attack the infant when they become dominant. On the other hand, this behaviour must reduce the paternity probability of the dominant male, and hence make it less likely that the dominant will defend the infant against males entering from the outside (cf. Symons, 1982). It is therefore not immediately obvious that sexual behaviour could ever achieve an optimal balance and reduce overall risk.

Here, we will present a novel explanation for the effectiveness of sexual behaviour. Doing so, however, requires that we first determine the conditions in which natural selection favours infanticide by males (cf. van Schaik, 2000a).

When is infanticide favoured by natural selection?

In a species in which infanticide advances the female's next conception, and in a situation in which a male can be confident that $p = 0$ (i.e. he never mated with the female, where p is the probability of having sired the existing infant), infanticide is obviously an advantageous strategy, provided it can be committed at low cost. However, if the male has a mating history with the female, a more quantitative prediction is needed. In order to develop this prediction, we compare the expected mean number of offspring sired by a dominant male during his period of dominance (tenure) under two scenarios: with and without infanticide upon assuming the dominant position.

Denote the effective tenure period of a non-infanticidal dominant male as T, i.e. the period between the conception of the first infant sired during the new tenure to the end of the male's tenure. If the regular interbirth interval is t_n, and the interbirth interval following infanticide is t_i, the time gained by an infanticidal male is $t_n - t_i$. Thus, the effective tenure of an infanticidal male is $T + t_n - t_i$. Now we can calculate the benefit of the two strategies (B_n

and B_i, for non-infanticide and infanticide, respectively). These benefits in terms of expected number of infants are (*pace* van Schaik [2000a], which overlooked infants sired by non-infanticidal males before becoming dominant):

$$B_n = p + \frac{T}{t_n} P$$

$$B_i = -p + \frac{T + t_n - t_i}{t_n} P$$

where P is the probability of siring infants during tenure, assuming that this probability is constant regardless of whether the male commits infanticide. Then, the net benefit of committing infanticide is:

$$B_i - B_n = -p + \frac{T + t_n - t_i}{t_n} P - p - \frac{T}{t_n} P$$

$$= -2p + \frac{t_n - t_i}{t_n} P$$

Thus $B_i - B_n$ is positive (given that $t_n > t_i$) if

$$\frac{t_n - t_i}{t_n} P > 2p \qquad (1)$$

Inequality (1) ignores any costs to infanticide (see van Schaik [2000a] for discussion). In the average primate species, the maximum $(t_n - t_i)/t_n$ is around 0.5, which is attained when a newborn is killed. In this case $P > 4p$. As the infant gets older, P has to increase to make infanticide advantageous to the male. For the observed mean values of $(t_n - t_i)/t_n$, between 0.25 to 0.32 (see above), infanticide is advantageous if P is greater than approximately $7p$.

Optimum male decisions

Inequality (1) shows when infanticide is expected, but we cannot assume that males have perfect estimates of the relevant parameters. We must therefore translate these criteria into decision-making rules for males. Some cases are simple. First, if the newly dominant male never mated with the female, and $p = 0$, the rule is easy. Indeed, infanticide is commonly seen after a new male immigrant takes over a group (e.g., Steenbeek, 1996; van Schaik, 2000a). Second, if the male has a sexual history with the female but his estimate of p is very small, infant age matters because the benefits decrease as infants get older (cf. Crockett & Sekulic, 1984; Sommer, 1994; summarised in Fig. 2.1 in van Schaik, 2000a).

In multi-male groups, however, a male has generally mated with the female before, and optimum decision making may be more difficult. The male is forced to use indirect indicators based on his sexual history with the female (see above) to produce estimates that will tend to be highly imprecise, except when the male could monopolise most matings with sexually highly attractive females or when he could get only very few matings when she was not very attractive.

Frequent polyandrous mating during both periods of ovarian activity and periods of patent infertility (e.g. pregnancy) could have two consequences. First, it may lead to an increase in the estimated paternity probability (henceforth p'), especially if the males are not fully informed about the female mating activity with other males. Thus, especially by mating frequently at times of non-fertility, females may manage to increase p' of especially low-ranking males, producing a sum of these estimates greater than 1 (obviously, the actual paternity probabilities still add up to 1).

Second, frequent polyandry should lead to great uncertainty of each male's p'. One must assume that higher quantity of matings can compensate to some extent for lower quality (i.e. the female was less attractive). We suspect that non-dominant males have very imprecise estimates of their chances of paternity. In a situation of high uncertainty as to the value of p, it may be impossible to find optimum decision-making algorithms.

Table 8.1. *The payoffs of decisions made by newly dominant males with respect to infants, depending on whether the male had sired this infant or not.* (*see text for explication of variables*).

Decision:	Father	Not father
Kill	$-1+\frac{T+t_n-t_i}{t_n}P$	$\frac{T+t_n-t_i}{t_n}P$
Not kill	$1+\frac{T}{t_n}P$	$\frac{T}{t_n}P$

A newly dominant male may decide to choose the option that maximizes mean fitness. If uncertainty over the value of p approaches ignorance, his best guess may be that $p = 0.5$, and it is easy to show that not killing the infant is on average the best option (see Table 8.1). However, since a given male actually did or did not father the infant, in a case like this, a newly dominant male may actually maximise his fitness payoff by avoiding costly mistakes (cf. Resnik, 1987, p. 28), i.e. minimize the risk of losing a large portion of fitness (cf. risk avoidance in foraging: Stephens & Krebs, 1986).

A newly dominant male can make two kinds of mistakes: (i) he can kill an infant that he had actually sired before becoming dominant, thus losing one infant from his total number produced; and (ii) he can refrain from killing an infant that he did not sire, thus losing time to the next conception of the infant's mother. These two errors have different costs attached to them. Table 8.1 presents the payoffs of the two possible male decisions (kill vs not to kill), under two different conditions (male actually fathered the infant vs did not). The cost of the mistake, i.e. the male killing his own infant, relative to the optimum tactic of refraining from killing it, is the difference between killing it and not killing it:

$$C1 = -1+\frac{T+t_n-t_i}{t_n}P - 1 - \frac{T}{t_n}P$$

$$= -2+\frac{t_n-t_i}{t_n}P$$

Thus the cost of killing his own infant is in the range $-2 \le C1 \le -1$ (these are in infant units).

On the other hand, if the male did not sire the infant, the cost of not killing the infant (relative to the optimum tactic of killing it) is:

$$C2 = \frac{T}{t_n}P - \frac{T+t_n-t_i}{t_n}P = -\frac{t_n-t_i}{t_n}P$$

The cost of not killing another male's infant is in the range $-1 \le C2 \le 0$.

Committing the first error (killing one's own infant) has far greater costs ($C1$) than committing the second error (not killing some other male's infant; $C2$). Hence, if female mating tactics have confused paternity estimates to the point of near-ignorance, a newly dominant male will do better to avoid the more costly error, and should thus refrain from infanticide. This effect of deceptive female matings could explain why infanticide is not always seen in conditions where it might be expected.

We assume that the dominant males usually have less uncertainty concerning their decision whether to protect vs not to protect an infant, because their estimates of paternity will tend to be close to 1. However, if they also face considerable uncertainty verging on ignorance, they should also avoid making the costlier mistake. Table 8.2 provides the payoffs of the dominant male's decisions for the two possible states (father vs non-father). The costs of not protecting an infant that the male actually sired is:

$$C3 = -s-(s-c) = -2s+c,$$

(where s = probability of infant survival; and c = cost of protection, both expressed in infant units), whereas the cost of protecting an infant that he did not sire is:

Table 8.2. *The payoffs of decisions made by currently dominant males with respect to infants, depending on whether the male had sired this infant or not.*

Decision:	Father	Not father
Protect	$s - c$	$-c$
Not protect	$-s$	0

$$C4 = -c - 0 = -c\,.$$

For $s > c$ (a very reasonable assumption), the decision not to protect the infant when the dominant male is the actual sire is the costlier one. Thus, if a dominant male is so uncertain of his paternity as to be virtually ignorant of its value (i.e., if his estimate is close to 0.5), then his best decision is to protect the infant when it is at risk, up to a point. It also suggests, however, that males facing higher costs of protection, i.e. less powerful or injured males, are less likely to protect infants, or to protect with lesser intensity, even if they have mated extensively with the mother. As in the case of the newly dominant male, this approach leads to the same conclusion as the one that maximises his mean fitness (assuming that $s > c$).

Conclusions from the male decision model

The main conclusion from this analysis is that female polyandry and mating during non-fertile periods serve to raise the estimated paternity probability (p') values for all males involved, and making their sum exceed 1. Polyandry may also confuse p' to the point that the males' best course of action is to refrain from killing infants and to protect them if they have mated extensively, even if they actually did not sire them. Thus, female sexual behaviour may serve to overcome the constant-sum nature of the paternity game.

Unfortunately, developing convincing tests of these ideas is not easy, especially because incomplete infanticidal attacks by newly dominant males and the reduced rates of infanticide in multi-male species can have multiple sources, as noted above. Nonetheless, we believe it is meaningful to translate the conditions in which natural selection should favour one action over another into the actual decision-making processes of animals. However, if the interpretation advanced here is correct, a clear prediction follows. It is in the female's interest to keep individual males guessing as to the extent to which other males have also mated with her: the lower the perception of that frequency the higher a male's p', his estimate of his own paternity chances, should be. Hence, females should be likely to mate discreetly, especially with subordinate males. We will develop the same prediction from a consideration of mating conflict (see below).

To reach this conclusion we have assumed that the female can bias the values of these estimates in directions favourable to her, implying that natural selection was unable to equip males with better assessment rules than the ones they currently have. Thus, female sexuality may have been designed to withhold potentially useful information from males. Physiological work done from this perspective might be rewarding.

SEXUAL HARASSMENT AS AN EXPRESSION OF MATING CONFLICT

Mating conflict between the sexes is now recognised as an intrinsic part of sexual selection (Hammerstein & Parker, 1987). One aspect of it concerns intersexual conflict over the identity of each individual's mates. Especially in some mammals, this kind of mating conflict has found expression in sexual coercion of females by stronger males. Smuts & Smuts (1993) defined sexual coercion and considered two components: infanticide and sexual harassment. Many students of primate behaviour have reported harassment or aggressive restriction of movements of sexually active ('oestrous') females by males, especially high-ranking ones, sometimes to the

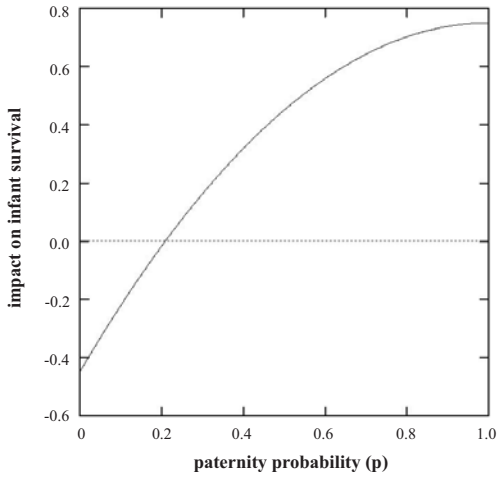

Fig. 8.1. The impact of the paternity (p) of a male on infant survival. The relationship has the form $g(p) = k - A(-1)^m (p-1)^m$; the parameters chosen are $k = 0.75$, $A = 1.2$, $m = 2$. As the male's paternity increases, the impact varies from attack to tolerance to protection. At $p = 0$, the intercept on the y-axis is ($k - A$), which is the maximum negative impact by a non-sire on the survival of the infant.

point that the female is injured or even killed (Smuts & Smuts, 1993; chimpanzees: Goodall, 1986, p. 452; Matsumoto-Oda & Oda, 1998; macaques: Chapais, 1983; Huffman, 1987, 1992; Manson, 1992, 1994; Soltis, 1999; hamadryas baboons: Kummer, 1995). Although infanticide is seen by some as an extreme form of harassment (Smuts & Smuts, 1993), the two are not often treated as being directly interrelated phenomena. Here, we develop a model to show that at least some of the sexual harassment in primates is directly linked to females' attempts to be polyandrous.

Theory

Assume a multi-male group of a primate species in which females are vulnerable to infanticide by males. One male is dominant and will guard a female when she is in oestrus, but other males are around and also interested in mating with the female. It is in the female's interest to dilute the paternity chances of the dominant male in order to reduce the risk of infanticide by mating polyandrously with other males in the group, or occasionally even in an adjacent group, in case one of them takes over top dominance or ousts the current dominant (Hrdy, 1979; Hrdy & Whitten, 1987; Small, 1993; van Schaik *et al.*, 1999; Soltis *et al.*, 2000; Heistermann *et al.*, 2001). One might expect that the dominant male would also benefit from reducing the infant's risk of infanticide. However, we will now show that the dominant male's probability of paternity that maximises his fitness is higher than that preferred by the female, and that he is therefore expected to attempt to prevent matings by the female with other males. Thus a male is not only in competition with other males, he may also have a conflict of interest with his mate(s).

A male's probability of paternity, p , is the long-term average proportion of infants sired by a male in similar conditions. We assume that the value of p is related to a male's assessment of it, although this relationship may be imprecise (see previous section). In general, a male's attitude toward the infant is a function of p , so that with increasing values of p , the male changes from attack (if given an opportunity to do so and if prospects for future mating access to the female exist), to indifference or tolerance, and finally to an increasingly strong tendency toward protection (Hrdy, 1979). We can represent the impact on infant survival of these changing attitudes as $g(p)$, with negative effects at low p and increasingly positive effects as p increases (see Fig. 8.1). We expect $g(p)$ to increase monotonically with p on domain [0, 1] and saturate at $p = 1$.

The function in Fig. 8.1 can be expressed as:

$$g(p) = k - A(-1)^m (p-1)^m \qquad (2)$$

where m (integer, $m > 1$) is a shape parameter that determines how fast $g(p)$ rises and how soon it saturates as p increases, and k and A are positive constants (such that $A > k$). The value of k is the maximum positive impact of the likely sire on the infant's survival, whereas A can be seen as the maximum negative impact of a non-sire (the Y-

intercept in Fig. 8.1 is at $k - A$). The assumption of $m > 1$ is critical for the result below, but in making it, we follow previous analyses of male parental care (Harada & Iwasa, 1996). It implies that as p increases, the costs of male protection efforts are also likely to rise due to increased competition with other activities or increased risk of injury, leading to a relative slowdown in investment in, and thus effectiveness of, protection (in other words, one must assume protection efforts to saturate).

The question is at what value of *the dominant male's* p (here called q to avoid confusion) the fitness of the dominant male and of the female are maximised. In general, female fitness, F_F, is maximised when the infant's survival is maximised, assuming there are no other major effects on fitness, such as variation in male intrinsic genetic quality or relatedness to the female. On the other hand, the dominant male's fitness, F_{DM}, is maximised when $q * F_F$ is maximised, whereas the fitness of a subordinate male (F_{SM}, or more precisely the highest ranking among them) is maximised when $(1-q) * F_F$ is maximised. We will now develop expressions for F_F, F_{DM} and F_{SM}.

We assume that infant survival is a function of q, but weighted for the dominant male's effective power $(1-\varepsilon)$, as well as a function of $(1-q)$, i.e. the strongest subordinate male's paternity, p, but weighted for his effective power. This yields:

$$F_F = g(q)(1-\varepsilon) + g(1-q)\varepsilon \qquad (3)$$

$$F_{DM} = q\{F_F\} = q\{g(q)(1-\varepsilon) + g(1-q)\varepsilon\} \qquad (4)$$

$$F_{SM} = (1-q)\{g(q)(1-\varepsilon) + g(1-q)\varepsilon\} \qquad (5)$$

The parameter ε estimates the maximum strength of the strongest other male in the group or the vicinity (i.e. within the female's potential pool of mates). This strength parameter is best interpreted as the likelihood that this male will successfully challenge the current dominant in the near future (and thus also protect the infant in the future), hence $0 \le \varepsilon < 1$. Its

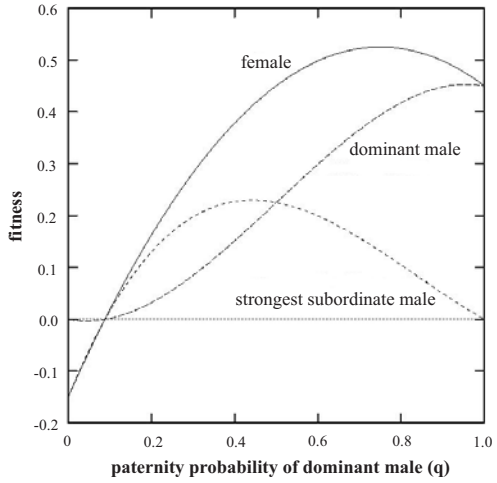

Fig. 8.2. The fitness of the female, dominant male and the strongest subordinate male as a function of the paternity q of the dominant male (Eq. 2-5). The optimal fitness for each of the three is at different values of q, which cannot be satisfied simultaneously, reflecting a conflict.

complement, $1-\varepsilon$, represents the probability that the dominant male will be able to withstand challenges to his dominant position, and hence also his ability to protect the infant against infanticidal attacks by any of these males (or yet others).

Figure 8.2 illustrates the resulting mating conflict: the dominant male's fitness is maximised at a higher value of q compared to the value of q at which the female's fitness is maximised. We did not find analytical solutions to Eqs.3-5 satisfying all values of m. However, for $m = 2$, the value of q at which the female's fitness is maximised ($q = \hat{q}_F$) is at $1-\varepsilon$; in other words, she is expected to favour matings by other males in proportion to their relative strength. Still assuming $m = 2$, F_{DM}, the dominant male's fitness, is maximized at

$$q = \hat{q}_{DM} = (1-\varepsilon)\left\{\frac{2}{3} + \frac{1}{3}\sqrt{4 + \frac{3k}{A(1-\varepsilon)^2}} - \frac{3}{(1-\varepsilon)}\right\}$$

or at $q = 1$, whichever is the smaller.

It can easily be shown that $\hat{q}_{DM}$ is greater than $1-\varepsilon$ (in other words, there is a conflict of interest between the female and the dominant male), provided

the factor $(k/A) > \varepsilon(1-\varepsilon)$. The factor $\varepsilon(1-\varepsilon)$ reaches its maximum value at $\varepsilon = 0.5$ which means that if $(k/A) > 0.25$ the conflict is guaranteed for all values of ε; for $(k/A) < 0.25$ the mating conflict might still exist but is not guaranteed, since it will depend on the value of ε. For values of $m > 2$, we found mating conflict in all numerical solutions that we attempted for realistic values of m, k and A (i.e. $\forall m \geq 2$, and k, A such that $(k/A) > 0.25$)[2].

Of course, this result raises the question as to the interpretation of $(k/A) > 0.25$. This inequality will often hold because protection is against infanticidal attacks; hence, if protection were totally effective, $k = A$. Since infanticide most often happens when the dominant male is eliminated or incapacitated, this implies that normally k is close to A, i.e. $k >> 0.25A$. Hence, for all realistic ranges of values of all three parameters, there will be a mating conflict between the dominant male in the group or neighbourhood and the fertile female.

As implied by Figure 8.2, a mating conflict exists between the female and the subordinate/ peripheral males as well, because the dominant male's paternity at her maximum fitness, $\hat{q}_F$, is higher than that of the best subordinate male (the graph shows his optimum in terms of the dominant male's paternity; his own optimum is the complement of that value). However, the behavioural expression of this conflict is usually preempted by mating competition between the dominant and the subordinate males, forcing the latter to mate much less than they would otherwise do. Hence, the subordinates never reach the zone in which females would prefer to mate less with them. Indeed, the subordinate males reach their optimum paternity, p, at a value much less than 1, because the dominant male is expected to attack infants obviously sired by them. On the other hand, when dominant males are not around, for instance because females are rather solitary, they too are expected to harass oestrous females.

In our equations we only incorporated the role of one subordinate male, the one most likely to succeed in challenging the dominant male in the near future. If only one clearly stronger, young subordinate male resides in the group, this approach is acceptable, because one expects females to recognise such males. For instance, male baboons about to rise in dominance rank have different behavioural styles and endocrine profiles from others of similar rank well before their actual rise (Virgin & Sapolsky, 1997). However, if there are more such males (and females recognise them as such), our treatment is conservative and mating conflict between the female and the dominant male is even more intense. For instance, if two males have a reasonable chance of upsetting the dominant male (i.e. with $\varepsilon > 0$), the female's fitness will maximise at $\hat{q}_F = 1 - 2\varepsilon$.

Predictions and evidence

A basic, albeit trivial, prediction is that, if no other males are in the mating pool, i.e. $\varepsilon = 0$, both the dominant male and the female will reach their optimum fitness at $q = 1$. Hence, in the absence of other males, no mating conflict is expected, and thus no harassment by the dominant male. When other males are present, however, various predictions can be made. We develop them here and also offer a preliminary evaluation of their fit with the primate literature.

1. Harassment by dominant males

Observations of harassment of oestrous females, especially by high-ranking males, inspired the development of the model. Its fundamental prediction is that the conflict of interest between the female and the dominant male may find expression in a behavioural conflict if the male has the means to coerce the female, e.g. by coercive mate guarding, and the female will try to escape in order to mate with other males (which, according to this model, she

[2] For the unrealistic case of $m = 1$ (see above), there is no mating conflict, with both sexes reaching their highest fitness at $q = 1$.

is likely to do)[3]. This is a strong prediction because it contrasts with the naive expectation that the males most likely to force matings will be non-preferred, and hence generally subordinate.

One might object that attacking the female instead of the rival male of a mating or consorting pair is simply the least risky option for a dominant male, and is also likely to prevent the female from mating with a third male while he is engaged in fighting. However, there is abundant evidence for harassment of fertile females by males when the female is not actually mating or even near another male (see Smuts & Smuts, 1993; and see below). Moreover, if dominant males are not near the fertile female, lower-ranking males are also expected to employ harassment. Thus, in both chimpanzees (*Pan troglodytes*) and orangutans (*Pongo pygmaeus*), possessive mate guarding and forced matings, respectively, by such non-dominant males are commonly observed (Tutin, 1979; Mitani, 1985; Goodall, 1986, pp. 457-64; Schürmann & van Hooff, 1986; Fox, 1998).

2. Female polyandry in relation to the number of males

The mating conflict model indicates that as the effective power of the dominant male $1-\varepsilon$ declines, the conflict of interest between the dominant male and the female will increase (see Fig. 8.3). One common source of the reduced power of the dominant is an increased number of males in the mating pool, because this probably increases the strength of the strongest among them and perhaps also because the larger number itself may wear out the dominant male, either directly or because coalitions are more likely (Bercovitch, 1989; Noë & Sluyter, 1990).

The model predicts that if the female wins the conflict, the concentration of paternity in the top-ranking male will decline as the number or strength of rivals increases. The female may achieve this outcome by mating more polyandrously during fertile cycles or by mating after conception.

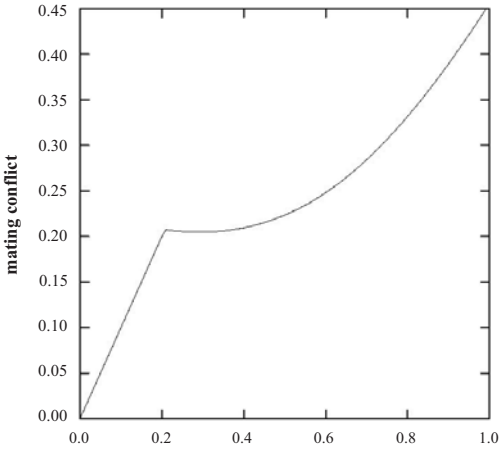

Fig. 8.3. The magnitude of the mating conflict ($\hat{q}_{DM} - \hat{q}_F$, see the text) between the dominant male and the female as a function of the strength of the strongest subordinate male (ε). The conflict between the dominant male and the female clearly increases with ε , albeit not monotonically.

The mating conflict model thus offers an amendment to the explanation for the distribution of paternities over the available males provided by the Priority-of-Access (PoA) model (Altmann, 1962). According to the PoA model, a dominant male excludes other males from mating as long as there is only one female near ovulation. Lack of absolute concentration of paternity in dominant males would be due to a reduction in male mating monopoly at times of overlap of female oestrous periods or high intruder pressure. The mating-conflict model claims that this pattern is due to active female polyandry, whereas PoA assumes females do not actively seek polyandry. PoA also assumes that male-male aggression serves only to monopolise access to females, and is therefore consistent with attacks on mating pairs, but not with male aggression targeted at the female in particular (see also van Noordwijk & van Schaik, this volume). To distinguish between the two models, detailed data on (changes in) male

[3] Note that harassment of mating pairs by juveniles (for example Drukker *et al.*, 1991) and females (Linn *et al.*, 1995) also occurs. Such harassment is of course not explained by the mating conflict model.

dominance relations as well as matings and their timing (i.e. the number of females sexually active simultaneously) are needed.

If challenger males from within the group are more likely to succeed than recent immigrants, as is often found (Henzi & Lucas, 1980; Cheney, 1983; van Noordwijk & van Schaik, 1985, 2001; Robinson, 1988; Perry, 1998), a subsidiary prediction follows: females may prefer to live in multi-male groups, all other things being equal because the 'insider' males pose less of an infanticide risk provided that they were granted a share of the matings. This idea has been suggested before but remains hard to test (cf. van Schaik, 1996; Nunn & van Schaik, 2000). However, our analysis here suggests that even the dominant male may find it in his interest to tolerate some unrelated subordinate males, because his optimum paternity may be slightly less than 1, assuming he can come close enough to this value in reality.

3. Female polyandry in relation to potential change of male dominance relations

The effective power of the dominant male may be reduced by increased strength of one or more of the subordinate males, increasing the risk of an effective challenge. If a female can recognise that the current top-ranking male is likely to be defeated before the birth of her infant, she should selectively decrease her matings with him. This scenario assumes that the top rank among males is acquired through challenge and not by succession, as in some macaque species with large groups and seasonal breeding (reviewed in van Noordwijk & van Schaik, this volume).

In many primate species females are known to attempt to break away from the monopolisation of the dominant males and actively attempt to mate with subordinate or peripheral males (Hrdy, 1981; Small, 1993). The primate literature contains a few reports that females are more actively polyandrous when the dominance situation among the high-ranking males is not stable (Samuels *et al.*, 1984; van Noordwijk, 1985; Janson, *fide* Manson, 1995; Manson *et al.*, 1997; Alberts *et al*., 2003) or when the single male in the group is weak (Agoramoorthy & Hsu, 2000).

A more refined prediction is that we expect females to attempt to mate preferentially with those subordinate or peripheral males most likely to successfully challenge the current dominant male in the future. Hence, oestrous females should not seek matings with other males than the dominant randomly but show distinct preferences, which should be linked to the target males' prospects for future dominance. In several populations young maturing males are known to rapidly rise in rank and take over top rank, surpassing several males over a period of only a few months (e.g., Cheney, 1983; van Noordwijk & van Schaik, 1985, 1988, 2001; Hamilton & Bulger, 1990; Virgin & Sapolsky, 1997; Soltis *et al.*, 2000). Since such challenges by maturing males are rather predictable, we expect the future top-ranking male (if already present in the group) to have a larger share of the matings than expected for his current dominance position. At least one study to date seems to confirm this point: Smith (1994) reports for a large captive group of rhesus macaques that high male siring success, attributed to female choice, preceded a rise to high dominance rank for young males.

4. Surreptitious mating with subordinate males

The non-zero value of p that maximizes the subordinate males' fitness leads to the prediction that it is in the interest of both the female and the subordinate male to mate as inconspicuously as possible in order to prevent the dominant male from adjusting his p estimate down, and withhold protection from the infant. We therefore expect that matings between females and subordinate males tend to take place out of sight of the dominant male, e.g. at the periphery or away from the group, and should less often be accompanied by calls. In order to distinguish this pattern from general mating competition, it should even happen if the dominant male is in visible contact but too far away to attack the pair effectively. We can further predict that inconspicuous mating

with subordinates is even found in species without effective male harassment of females.

Despite a serious lack of quantitative data, it has been noted for several species that matings between females and subordinate males tend to occur rather surreptitiously (*Pan troglodytes*: Tutin, 1979; Goodall, 1986; *Macaca fuscata*: Huffman, 1992; *M. mulatta*: Berard *et al.*, 1994; *M. arctoides*: Nieuwenhuijsen *et al.*, 1986; *M. sylvanus*: Paul, 1989). One study focusing on matings in concealed places noted that especially lower-ranking males *M. fascicularis* were involved in matings outside of visual contact with the rest of the group (Gygax, 1995), as predicted.

In many species females give a specific copulation call, to which other males do respond by looking at the pair (van Noordwijk, 1985) or even attacking them (Oda & Masataka, 1995). In at least one study a tendency was found for matings with subordinate males to be quiet (*M. thibetana*: Zhao, 1993), although another study found no effect of male identity on female calling tendency (*M. fascicularis*: van Noordwijk, 1985). Hence, renewed examination of the patterns in discreet matings may be worthwhile, also in species without effective male harassment (as long as infanticide by males poses a risk).

SEXUAL HARASSMENT AND REPRODUC-TIVE PHYSIOLOGY

The distribution of sexual harassment

The model presented above confirms the existence of a conflict of interest between the breeding female and the group's males. The conflict with the dominant male(s) is most likely to be expressed because this male (or males) will try to monopolise the female most of the time, thus preempting any conflict with the other males. The question, of course, is who wins this conflict? Whenever male harassment occurs, females can only win at serious costs. Coercive mate guarding makes it more difficult, and more costly, for the female to seek the matings with subordinate and peripheral males needed to achieve the distribution of p' values optimal to her. Harassment is more common where females are less powerful, both physically and socially (Smuts & Smuts, 1993). Giving in to coercion makes the female more vulnerable to infanticide, and if this risk is sufficiently increased, we expect that natural selection has produced physiological or behavioural tendencies in females to reduce the dominant male's monopolisation potential, provided that their costs do not exceed the gains of reduced infanticide rates.

Since it is not *a priori* clear what forms these female counter-strategies can take, we will first examine the taxonomic distribution of sexual harassment of sexually active ('oestrous') females in primates, building on existing reviews (especially Smuts & Smuts, 1993; Dixson, 1998), and then search for derived reproductive features in the taxa with harassment.

In order to capture the variation in male behaviours directed at sexually active or 'oestrous' females, we propose the following categories of sexual harassment (defined as aggression by sexually mature males against sexually active or 'oestrous' females):

(1) No sexual harassment, nor any attempts, reported.
(2) Sexual harassment attempts reported, but only in the direct mating context and mostly ineffective, i.e. the female wards off the male or counterattacks, and the male is unable to prevent the female from moving away or mating with others.
(3) Effective sexual harassment is observed in both the direct mating context and of oestrous females in general, as evidenced by coercive mate guarding and physical attacks on the oestrous female followed by submission. Male behaviours sometimes include bites that result in wounding or even death, forced matings, and attacks on

females when mating with other males.

The second category is needed because in several species (including also many non-primate mammals), males show aggression toward females in the mating context that is not accompanied by any attempts at coercive mate guarding. The presence of these behaviours suggests that aggression may be an integral component of mating in these species. The extent to which these attempts at harassment would constitute *de facto* harassment depends on the degree to which they stop females from achieving the preferred degree of polyandry. The literature is understandably vague on this, but it is our impression that females can still mate with other males. In any case, it is useful to keep this second category separate from the cases where males also attack oestrous females outside the direct mating context or force matings, the category of effective harassment.

For the present purpose, we limit our review to species vulnerable to infanticide. A species is considered vulnerable if infanticide by males is reported for it, or if it has a life history that makes the females of the species vulnerable to such attacks, or both (van Noordwijk & van Schaik, 2000; van Schaik, 2000b). The advantage of this definition is that we need not rely only on reports of infanticide, which tend to be rare. As required, all species known to have infanticide are also predicted by the life history measure to be vulnerable.

Although data on harassment are still very incomplete a few clear patterns emerge. Consistent with earlier compilations, we see no evidence for effective harassment in Lemuroidea (lemurs) or in Platyrrhini (New World primates), but many reports for the Catarrhini (Old World primates; Fig. 8.4). Examples of adult females being able to systematically elicit submission from adult males are most commonly found in lemurs, in several monomorphic New World primates and in the few pair-living Old World primates (Kappeler, 1993; Strier, 1994). In all these species, males attack rival males but we see at most attempts at harassment of

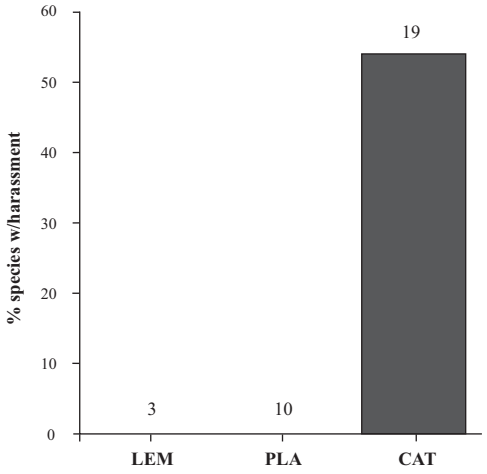

Fig. 8.4. The incidence of effective sexual harassment (which may include injury of females and forced matings) among primate species vulnerable to infanticide by males in three radiations (LEM = Lemuroidea; PLA = Platyrrhini - New World primates; CAT = Catarrhini - Old World primates). Based on literature review (starting with Smuts & Smuts, 1993), available from the authors upon request. Number of species with information indicated above columns.

females, e.g. in lemurs (e.g., Pereira & Weiss, 1991; Sauther, 1991; Brockman, 1999), and females often counter-attack and be able to choose their mates (Richard, 1992). Likewise, only in some New World primates do we see evidence of coalitions of males being required to inspect a female's sexual state (in *Saimiri oerstedi*, *Ateles*, *Lagothrix*: Boinski, 1987; Smuts & Smuts, 1993). Remarkably , effective sexual harassment is absent among New World primates, even the more dimorphic ones: for instance, female *Alouatta palliata* successfully rebuff attempts at forced matings by males (Jones, 1985).

Conversely, effective sexual harassment by males is reported for many Old World primate species. In this lineage, we also encounter many records of males generally harassing females, or females requiring coalitions in order to defend themselves against harassing males (Smuts, 1987; Smuts & Smuts, 1993). However, by no means all Old World primate species show sexual harassment by males.

Our sample is as yet too incomplete to allow analysis of the interspecific pattern in sexual harassment in

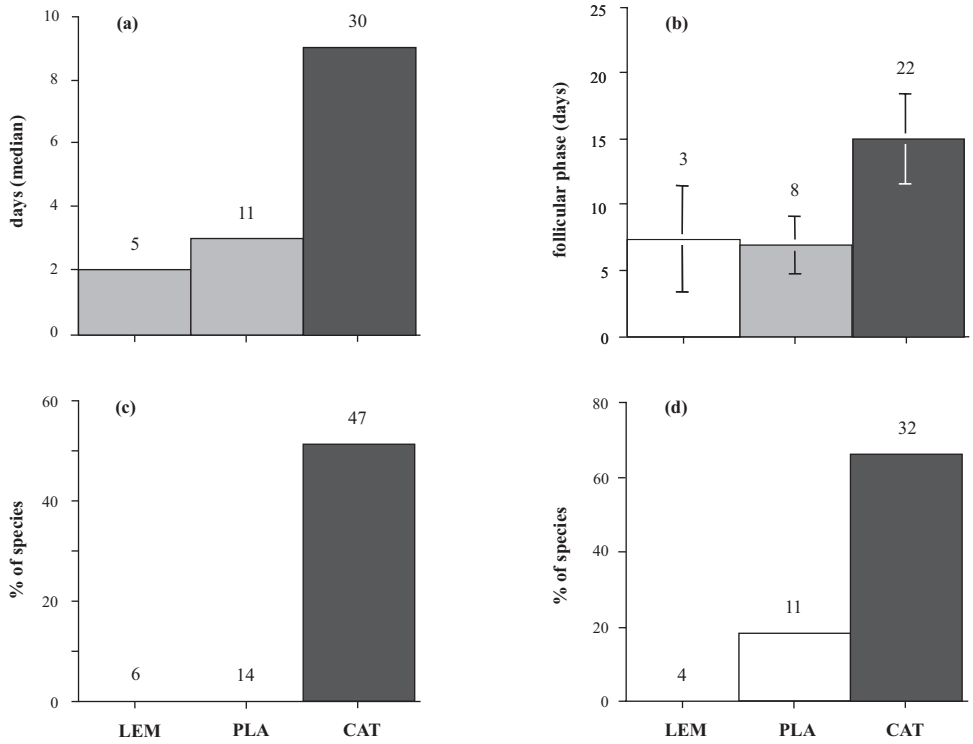

Fig. 8.5. Variation among species vulnerable to infanticide by males in three primate radiations (see Fig. 4 for abbreviations) in a variety of sexual features: (a) the median duration of the mating ('oestrous') period ($P < 0.001$); (b) the mean duration of the follicular phase (in days) of the ovarian cycle ($P < 0.01$); (c) the percentage of species showing exaggerated sexual swellings ($P < 0.001$); (d) the percentage of species with mating calls by females ($P < 0.01$). Tested with Kruskal-Wallis one-way Anova. Numbers of species indicated above columns. (a, c, and d based on data compiled in van Schaik *et al.*, 1999; b on data compiled by van Schaik *et al.*, 2000.)

relation to the known risk factors (larger male body size or weaponry, lack of female allies: Smuts & Smuts, 1993). Lemurs are largely monomorphic (Kappeler, 1991) and New World primates are far less dimorphic overall than Old World primates (e.g., van Schaik *et al.*, 2000). However, additional factors are probably involved because clearly dimorphic New World primate species and even some highly dimorphic Old World species (e.g. *Erythrocebus patas*) fail to produce clear evidence of sexual harassment. Hence, as yet unidentified additional factors are also involved in shaping interspecific variation in the occurrence and intensity of sexual harassment.

Female counter-strategies to male sexual harassment

Having found that effective sexual harassment of females by males is limited to Old World primates, we employ a two-step procedure to identify derived features of sexuality in Old World primates that possibly represent counter-strategies to the greater risk of sexual harassment. The first step is a systematic comparison of female sexuality in species vulnerable to infanticide in the three primate radiations compared above and see in which respect Old World primates stand out. The second step is to conduct comparisons within the Old World primates with variation in coercive abilities or infanticide risk.

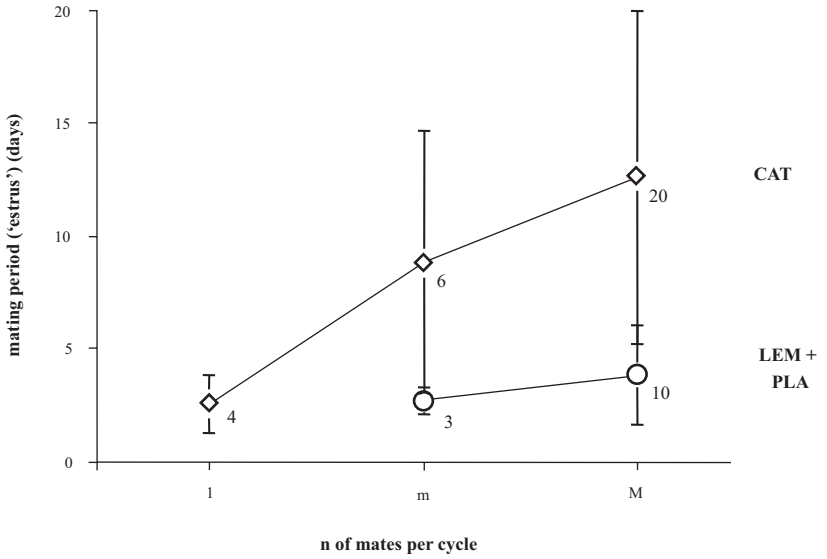

Fig. 8.6. Mean (± s.d.) duration of the mating ('oestrous') period in species vulnerable to infanticide by males in relation to the degree of female polyandry, in those vulnerable to male sexual harassment (CAT) and those not vulnerable (LEM and PLA). Degree of polyandry: 1- mating with a single male in > 90% of cycles; m- mating with multiple males in 10-50% of cycles; and M- mating with multiple males in more than 50% of the cycles (cf. van Noordwijk & van Schaik, 2000). Sample sizes (number of species) indicated at each point. Data on mating period taken from van Schaik *et al.* (1999). Rank correlation is significant ($P < 0.01$) for catarrhines.

The mating period ('oestrous' period, i.e. period between first and last mating) within an ovarian cycle is at least three times longer in the average Old World primate than in the other radiations (Fig. 8.5a). Moreover, mating period increases with the number of males that a females ends up mating with, in Old World primates but not in others (Fig. 8.6), consistent with the expectation that only in some Old World primates females would find it difficult to escape from the monopolisation of the dominant male in order to mate with other males.

The long mating periods in Old World primates are made possible by a change in the ovarian cycle, in that their follicular phases are about twice as long as in the other radiations (Fig. 8.5b). Comparisons within the Old World primates suggested that follicular phases are longer where the sexes are more dimorphic in body size or weaponry; specifically, we found evidence for correlated evolution between the length of the follicular phase and the degree of canine dimorphism (van Schaik *et al.*, 2000), suggesting that the factor explaining variation among radiations is also at work within the Old World primates lineage.

The long periods of sexual activity shown by Old World primate females require either that sperm remains viable in the female reproductive tract for long periods of time, or that ovulation is less tightly linked to the visual, olfactory or behavioural signals than usually assumed, or both (cf. Martin, 1992). There is no work in support of the former possibility, but recent work has supported the second idea. Nunn (1999) and van Schaik *et al.* (2000) review endocrinological work showing that ovulation is only poorly linked to these signals and thus should be rather unpredictable for males. Recent work by Heistermann *et al.* (2001) on hanuman langurs confirmed this prediction, showing that ovulation can take place with approximately equal probability at any time in the variable period of female sexual activity and that males do not recognise the female's time of ovulation, both in terms of behaviour and of the degree to which paternity is concentrated in the dominant.

If unpredictable timing of ovulation was favoured

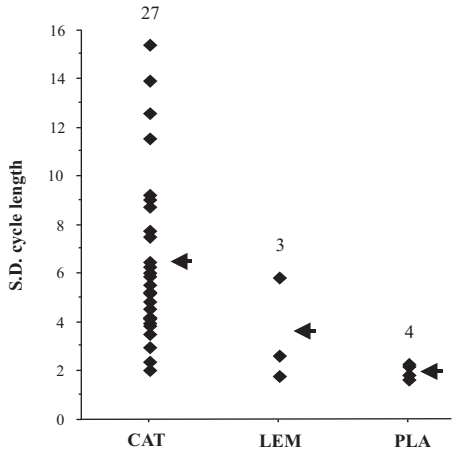

Fig. 8.7. The standard deviation of the length of the ovarian cycle in species vulnerable to infanticide in three primate radiations (see Fig. 8.4). Number of species indicated above columns. Arrows indicate medians. Tested with Kruskal-Wallis one-way Anova ($P < 0.01$).

by natural selection because it allowed the female to have longer mating periods of variable length, then there should be less need for it among the species that, while vulnerable to infanticide, are not vulnerable to male sexual harassment, i.e. lemurs and New World primates. There are as yet no detailed studies of the kind done on langurs for any of these species. However, we can get an indication of the extent to which ovulation is unpredictable by examining the variability in the duration of the follicular phase of the ovarian cycle (in most species, males can recognize when the luteal phase is well under way; e.g., Dixson, 1998). Data on variation in follicular phase length are scarce, but because the variability in the follicular phase exceeds that in the luteal phase (on average by about a factor of two: see compilation in van Schaik *et al.*, 2000), variability in the total duration of the ovarian cycle may provide a rough indication of unpredictable ovulation. Figure 8.7 shows that the standard deviation of the length of the ovarian cycle in our sample (based on Hayssen *et al.*, 1993 and a compilation by K. Hodges & U. Moehle, unpubl.) is indeed higher for Old World primates than it is for the two other radiations (including only species vulnerable to infanticide). The differences among them are significant (Kruskal-Wallis test, $H [2] = 11.37$; $P < 0.01$), and in the expected direction.

Old World primates differ from the other radiations in two more aspects of sexual behaviour: sexual swellings and copulation calls. The first has generated much interest from Darwin (1876) on (e.g., Dixson, 1983; Hrdy, 1997; Nunn, 1999): females of several species have exaggerated sexual swellings (Fig. 8.5c). Among Old World primates these swellings are found only in species that are actually or potentially polyandrous (cf. Clutton-Brock & Harvey, 1976), and among them predominantly in non-seasonal breeders (van Schaik *et al.*, 1999). The restriction to Old World primates and the predominance among non-seasonal breeders is consistent with the hypothesis that these swellings are needed where the risk of harassment by dominant males is particularly serious (females in seasonal breeders can move more freely from male to male because they tend to be sexually active simultaneously). Thus, as argued by Nunn's (1999) graded-signal hypothesis, sexual swellings function not only to attract the dominant male(s) during their maximum size (when the probability of ovulation is highest), but through their exaggeration they can also attract lower-ranking or peripheral males when the dominant males are less attracted due to the costs to these males of mate guarding for too long. For further discussion of exaggerated swellings see Zinner *et al.* (this volume).

Second, we find that females mating calls are more common among Old World primates (Fig. 8.5d). Mating calls are given during or after ejaculation. They are not to be confused with 'oestrous calls' given when the female is receptive before actually mating (generally interpreted as alerting all males within hearing distance to her condition), or with 'distress' calls given by female northern elephant seals or chickens when mounted by a subordinate male or at a time the female is not receptive, often followed by interference by a higher-ranking male (Cox & LeBoeuf, 1977; Pizzari &

Birkhead, 2000). Mating calls may alert other males that the female has mated, and may thus attract them (O'Connell & Cowlishaw, 1994; van Schaik *et al.*, 1999). Mating calls may be a graded signal whose quality varies throughout the cycle (Semple & McComb, 2000) and thus somehow indicates the probability of ovulation, much like swellings (their distribution across species largely mirrors that of swellings: van Schaik *et al.*, 1999). Females may also use them tactically, calling only or more often with particular males than with others (see above). More detailed field studies and comparisons between species, including several New World primates, may help us determine whether their function is, as proposed here, linked to the reduction of male sexual harassment.

Thus we found strong evidence for a link between the distribution of physiological, morphological and behavioural characterstics of female sexuality with the occurrence of harassment by males who are physically stronger.

Lineage differences in sexuality

The significant differences between radiations in various features serve to show the existence of a grade shift. Explaining grade shifts is inherently difficult because many factors have changed in parallel. For instance, among Old World primates, we see, relative to the two other radiations, the presence of terrestrial adaptations, larger mean body size (relative to extant species in the other lineages), larger mean group size, a general reduction in reliance on olfactory communication, greater tendencies toward folivory (relative to New World primates), etc. It is of course entirely possible that one or a combination of these factors facilitated the evolution of longer follicular phases or exaggerated swellings in Old World primates. However, the variation *within* the lineage, with respect to the duration of follicular phases in relation to male harassment potential, to the duration of mating period in relation to potential for polyandry, and to the conditions in which exaggerated swellings occur, suggests that subsequent evolution within the lineage in these traits did correlate with variation in harassment potential. Thus, variation within the lineage is in the same direction as that between the lineages. We therefore believe that the idea that the combination of male harassment and infanticide risk facilitated the evolution of these derived sexual features is a viable working hypothesis, worthy of further evaluation.

DISCUSSION AND PROSPECTS

It should be stressed that we do not propose that primate sexuality is molded by infanticide risk alone: there are numerous selective factors on what is perhaps the behaviour most tightly linked to fitness and thus most directly responsive to natural selection (Dixson, 1998). Birkhead & Kappeler (this volume) discuss additional hypotheses for female polyandry in primates, but these are not necessarily incompatible with the infanticide avoidance function.

Nonetheless, the aim of this chapter has been to evaluate Hrdy's (1979) predictions concerning the impact of infanticide risk on sexual behaviour and reproductive physiology in primates. The original predictions are upheld but a link to sexual harassment can also be added to the list. Our preliminary exploration suggests that harassment has impacted female reproductive behaviour and physiology but as always, the role of comparative work is best regarded as complementary to focused observational or experimental studies. The studies used to evaluate the hypotheses were not designed with these ideas in mind, and confounding factors can therefore rarely be excluded. We therefore make the following suggestions for future work.

More detailed studies of female sexual behavior could incorporate the role of social dynamics in the optimal balance between paternity concentration in dominants and dilution or manipulation of its

assessment. For example, if new dominants are always recent immigrants, very little paternity dilution is expected, but if new dominants are always long-term residens, much more paternity dilution is expected. Strong tests would correct for the expectation based on the Priority-of-Access model. As to male decision making it will be difficult to improve on the behavioural monitoring of Borries *et al.* (1999) on hanuman langurs, although additional work on different species would be worthwhile. With respect to mating conflict, detailed studies such as those of Gygax (1995) on the tendency of particular individuals or pairs to engage in matings in concealed locations or on the females' tendency to give copulation calls can be conducted.

Future work on female reproductive physiology could focus on three issues. First, detailed work on the sexual behaviour of females in species in the different radiations along the lines of the study by Heistermann *et al.* (2001) is needed, where social and sexual behaviour, female ovarian state and paternity are all recorded simultaneously. Second, we should study (if necessary by experimental manipulation) the impact of male representation in the social unit on female reproductive physiology and behaviour in species of different lineages. Third, more fine-grained comparative work on the relationship between sexual harassment and possible coercion indicators in Old World primates, as well as detailed studies of highly dimorphic New World primates, may help us understand the distribution of male sexual harassment in relation to female reproductive physiology.

SUMMARY & CONCLUSIONS

We explored the hypothesis that the vulnerability of females to infanticide by males has affected female sexual behaviour and given rise to sexual harassment in many primates. After establishing the adaptive nature of infanticidal behaviour for males who attack infants they did not father, we briefly reviewed sexual counter-strategies by females (polyandrous mating, mating during pregnancy). We then addressed two main issues. First, because paternity distribution is a constant-sum game, a female faces a considerable challenge. We argued that the female's sexual behaviour serves to produce paternity estimates among the various males that add up to more than 1. Moreover, paternity uncertainty may force males into avoiding the costliest mistakes, making them refrain from attacking infants they probably did not sire and making them protect those they may have sired. Second, we proposed an explanation that links infanticide with the common observation that high-ranking males often harass oestrous females. We developed a model that shows that a mating conflict exists between the female and the dominant male(s), and examined several detailed predictions about mating behaviour. Mating conflict can find expression in harassment if males can coerce females. This model led to several predictions, and a preliminary evaluation showed a good fit with existing data on primate sexual behaviour. We also noted that effective sexual harassment among primates is probably limited to Old World primates, in which it may have produced an arms race, leading to further changes in female sexual behaviour and physiology in this lineage, including longer mating periods, longer follicular phases with more unpredictable ovulation, exaggerated sexual swellings and perhaps more extensive female copulation vocalisations.

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