Reproductive Strategies of the Orang-Utan: New Data and a Reconsideration of Existing Sociosexual Models

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Recent field data indicate that MacKinnon's model of the orang-utan's sexual and agonistic activity needs to be revised. In this model, male reproductive activity is concentrated in an extended phase of subadulthood and in early adulthood. According to this model, the role of older adult males is primarily that of range guardian, and in that role they would ensure that the offspring they had generated earlier would have safe access to food resources. This study presents cases suggesting that subadult males, even though sexually active, may have low reproductive success. In previous studies adult males were shown to display less sexual initiative than subadult males. In this study an adult male was at times involved in frequent mating activity in response to proceptive activity of females in the course of consortship. This adult male proved to be a successful breeder, thus refuting the hypothesis of adult male sterility. The female is most likely to conceive through cooperative mating in lengthy consortships with the dominant resident adult male. We hypothesize that the extended subadult phase represents a submissive strategy, allowing subadult males to remain in the home range of adult males but with minimal reproductive success.

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INTRODUCTION

It is only quite recently that the behavior of wild orang-utans has been studied extensively. From 1967 to 1981, six major field studies, each consisting of more than 1000 observation hr, were carried out (Horr, 1972; Rodman, 1973; MacKinnon, 1974; Rijksen, 1978; Gladikas, 1978; Schürmann, 1981). These studies revealed three remarkable characteristics which, in combination, distinguish the orang-utan from the other primates. These characteristics are as follows.

(1) Solitary Nature. The dispersed nature of orang-utan society and the low frequency of interaction have led field-workers to regard the orang-utan as basically solitary. The average group size is between 1.8 (MacKinnon, 1974) and 1.9 (Rijksen, 1978). The social unit encountered most frequently is a female with her offspring. The next most important relationship is the consortship: a male and a female ranging together for several days, weeks, or even months (Rijksen, 1978). Groups of 5 to 8 animals sometimes occur (MacKinnon, 1974; Rijksen, 1978), and one group of 15 animals has been reported (MacKinnon, 1979).

(2) Marked Sexual Dimorphism. There is extreme sexual dimorphism in orang-utans (Fig. 1). The fully grown adult male is twice the weight of an adult female (Napier and Napier, 1967; Eckhardt, 1975). This contrast is enhanced by other features: the adult male's long hair, gular pouch, and cheek-flanges (Rijksen, 1978). Among primates, sexual dimorphism in body weight is greater only in the hamadryas baboon and the bonnet macaque (Clutton-Brock *et al.,* 1977), both of which are terrestrial species living in social groups with a marked dominance hierarchy (Jolly, 1982). Sexual size dimorphism in social primates has usually been explained as the phylogenetic result of the male role in group defense against predators (deVore and Washburn, 1963; Altmann and Altmann, 1970), but this role certainly is totally absent in orang-utans (Rijksen, 1978). Male orang-utans have never been observed to provide protection against predators. Crook and Gartlan (1966) have discussed factors in several primate societies enhancing intrasexual selection and producing sexual dimorphism in size, increased male size being preadaptive to the male's defensive role. Male competition does occur in orang-utans but has been observed very rarely (Rijksen, 1978; Galdikas, 1978). Does this male intrasexual selection fully account for the development of such marked size dimorphism in a large arboreal animal with a solitary life-style (cf. Trivers, 1972; Leutenegger and Kelly, 1977; Leutenegger, 1978)?

(3) Extended Phase of Subadulthood. In orang-utan society two types of potentially fertile males can be distinguished: the adult male and the subadult male. The adult male has fully developed secondary characteristics (big body, long hair, gular pouch, cheek callosities), and he is able to per-

Fig. 1. Sexual dimorphism in the orang-utan. The young adult female Yet (left) (10-11 years) approaches the adult male Jon (18-26 years), who is feeding on durian fruit. Note the difference in body size.

form the far-carrying long call (MacKinnon, 1971). The subadult male has not yet developed these features (Fig. 2). Whereas the general body growth of the male is a gradual process (Brandes, 1931b), his typical display features can develop comparatively rapidly at some point between 9 and 20 years of age. In captivity cheek-flanges can grow considerably within a few weeks (Brandes, 1929) and develop from nothing to fully grown within 6 months (Aulmann, 1932), at an age as young as 9 years (Seitz, 1969a) or as old as 18.5 years (Jones, 1968). Age estimates for subadult males in the wild vary from 4 to 5 years (Horr, 1977) and from 8 years (Rijksen, 1978) to 15 years (MacKinnon, 1974; Rijksen, 1978; Galdikas, 1978) and to 18-20 years (Jones, 1968; our own estimate, below). Brandes (1939) has suggested that the quality of the males' food and their physical condition may influence this development. It is our conviction that social factors may also have a strong influence, e.g., the absence of a dominant adult male. This conviction has been popular among zoo people for some time. The subadult male is physiologically mature. This has been proved in zoos where reproduction has been successful even at the age of 8 years (Seitz, 1969b). Why, then, is the development of secondary sexual characteristics in a physiologically mature male delayed for

Fig. 2. Subadult male Doba (11–12 years) without cheek-flanges.

an estimated period of 5 to 10 years? Recent field data may shed some light on the functional aspects of this question.

MODELS OF THE SOCIOSEXUAL ORGANIZATION

The above-mentioned characteristics of orang-utans have puzzled primatologists trying to understand their evolutionary development. We outline two models for the sociosexual organization of the orang-utan, one by Rodman (1973) and one by MacKinnon (1979), and reconsider these on the basis of recent data.

Rodman's Model

Even in an animal with a notoriously solitary life-style we expect at least some courtship and mating behavior. Such behavior, however, was surprisingly scarce in the first field studies of orang-utans, despite the comparatively large number of observation hours (cf. Schümann, 1982). Horr (1975) in 1450 hr of observation, did not observe any sexual behavior; Rodman (1979)

reported only one copulation by an adult male in 1640 hr of observation. From his data, Rodman inferred a model for the male sexual strategy in which he predicted that adult males are in intense competition for receptive females. The greatest reproductive success is achieved by the most dominant resident adult male, whose home range overlaps with the ranges of several females (Rodman, 1973). Rodman thus emphasized male intrasexual selection based on male competition for access to several dispersed females.

MacKinnon's Model

One year later MacKinnon (1974) described 11 copulations which he observed in 1500 hr of observation. He called all these copulations "rapes," because of their forcible and sometimes violent character. These rapes were performed exclusively by subadult males. MacKinnon did not observe any sexual activity at all by adult males. This led him to develop a model (MacKinnon, 1979) that deviates from Rodman's model. MacKinnon declared Rodman's model to be sound for the sexual strategy of high-status resident males, but he rejected it as an oversimplification for the other classes of males. MacKinnon suggested that males adopt different reproductive strategies at different stages in the life cycle. He surmised that the stage of greatest sexual activity and the stage of greatest agonistic activity of the male are out of phase (MacKinnon, 1979, p. 267). MacKinnon (p. 271) concluded, "The breeding strategy of the male orang-utan can be divided into two parts. As a young adult he consorts with as many potentially receptive females as possible to make the maximum genetic contribution to the population. As an older male he consolidates and protects his contribution. The two parts overlap in his period of physical peak as a prime adult. As he grows older he becomes larger and more frightening, which makes consorting more difficult but enhances his effectiveness as range guardian." A schematic presentation of his model is given in Fig. 3 (after MacKinnon, 1979, p. 268).

On the basis of his field data and of data from zoo observations, MacKinnon concluded that subadult males (R1) and young adult males (R2) are sexually active and that old adult males are nonreproductive and even "impotent," although they nevertheless display agonistic and calling behavior (A3) (MacKinnon, 1979).

In summary we can say that Rodman's theory is the more parsimonious one. Since MacKinnon's field study (1968–1971), three more studies on feral orang-utans have been carried out (Rijksen, 1978; Galdikas, 1978; Schürmann, 1981). These studies provided detailed data that provoke questions about the empirical facts underlying MacKinnon's theory and the tenability of its sociobiological implications. In order to answer these questions, we present-some of our own observations on a Sumatran orang-utan population.
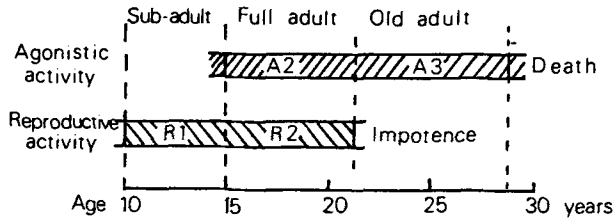
Sub-adult | Full adult | Old adult

Agonistic activity

A2 A3 Death

Reproductive activity

R1 R2 Impotence

Age 10   15   20   25   30 years

Fig. 3. Schematic presentation of the sociosexual phases in the life of a male orang-utan as proposed by MacKinnon (1979, p. 268).

THE KETAMBE FIELD OBSERVATIONS

Over a period of 4 years, a wild orang-utan population (*Pongo pygmaeus abelii*) was studied in Ketambe in the Gunung Leuser Reserve in Sumatra. This population consisted of 34 animals, 17 of which were followed in longitudinal focal-animal studies over a series of full days (2–40). The field data involved 4200 hrs of observation by the first author and 5800 hr by Indonesian students engaged in the project. During the study, three types of mating were distinguished:

(i)   uncooperative copulations [cf. "rapes" of MacKinnon (1974)], forcibly initiated by males and resisted by struggling and screaming females;

(ii) cooperative copulations initiated by males with nonresisting females; and

(iii) cooperative copulations initiated by females with cooperating males.

Two types of social contacts were distinguished: (i) the consortship, a relationship of synchronous activity lasting for several days or weeks (cf. MacKinnon, 1971; Rodman, 1973); and (ii) the short encounter, lasting less than 1 day, often less than 1 hr [Galdikas (1978) reports an average of 2.75 hr for 15 such nonconsort encounters].

Two types of sexually mature males were distinguished: (i) the adult male and (ii) the subadult male (cf. Rodman, 1973; MacKinnon, 1974; Rijksen, 1978; Galdikas, 1978).

Two age classes of sexually mature females were distinguished: (i) the young or adolescent female without offspring and (ii) the older female with offspring (cf. Shürmann, 1981, 1982).

These different classifications occur in specific combinations, which seem to follow a general pattern. The data concerning the copulations observed during 4 years of study are presented in Tables I and II. Even though the number of copulations ($N = 88$) is larger than in any other orang-utan

Table I. Number of Observed Matings of Orang-
Utans of Different Age/Sex Classes (Ketambe,
1975–1979)

Copulations	Subadult males	Adult males	Total
Cooperative			
All	17	48	65
Young females	17	47	64
Older females with offspring	0	1	1
Uncooperative			
All	21	2	23
Young females	6	1	7
Older females with offspring	15	1	16
Total	38	50	88

field study to date [Rodman (1973) $N = 1$ copulation; MacKinnon (1974), $N = 11$; Rijksen (1978), $N = 5$; Galdikas (1981), $N = 37$], it should be realized that these copulations occurred in a small number of relationships ($N = 17$, cf. Table II); 52% occurred in one relationship. One should, therefore, be cautious in generalizing. However, there are two very clear differences between our data and the data published by MacKinnon (1974, 1979). First, our data show that a relatively large proportion of the copulations is performed by one adult male in the population. Second, our results indicate a preponderance of cooperative copulations in the total mating activity of the adult male. Of all the copulations observed in this study, 74% (65/88) were cooperative. [Only the field study of Galdikas (1978) on Bornean orangutans shows a similar degree of cooperation, namely, 65%.] All 65 of the observed cooperative copulations by adult and subadult males occurred during consortship (Table I). Most forced copulations took place in a nonconsort context. Of the observed 23 rapes, only 3 occurred during a consortship, whereas 7 occurred during short encounters between a male and a female and 13 were initiated by subadult resident males in a complex social situation when a female was in consort with the resident adult male and stayed too far away from him. The three rapes during consortship were rather exceptional situations; two occurred when a subadult male changed consort partners, and one when an older female (Bel) ignored the adult male's (Jon) frequent "male presenting" (Schürmann, 1981) during a lengthy consortship (Fig. 4).

In the relationship between females and subadult males it was always the male that took the initiative, both in "rapes" ($N = 21$) and in cooperative copulations ($N = 17$). All 47 copulations of the adult male with young females (Fig. 5) were initiated by the female and were generally preced-

Table II. Number of Matings in the Observed Male/Female Combinations (Ketambe, 1975-1979)[a]

Females: name, class, age (years)	Males: name, class, and age (years)						Total matings observed
	Jon, AM, 20-28	Zet, AM, 30-40	Boris, SM, 17-19	Roba, SM, 14-16	Doba, SM, 13-15	Bobbie, SM, 13-14	
Bell, FO, 18-19	1C	–	–	–	11U	1U	1C 12U
Rim, FO, 19-21	1U	–	2U	–	1U	–	4U
Yet, YF, 12-13	46C	1U	5C 1U	1U	5C 1U	2C	58C 4U
Sina, YF, 10-12	1C	–	1C	–	3C	1C	6C
Pluis, YF, 9-11	–	–	1U	–	–	–	–
Anti, YF, 9-11	–	–	–	–	–	2U	2U
	48C 1U	1U	6C 4U	1U	8C 13U	3C 3U	65C 23U

[a]AM, adult male; SM, subadult male; FO, female with offspring, YF, young female; C, cooperative copulation; U, uncooperative copulation. The estimated age ranges in 1978 are given.

Fig. 4. Subadult male Doba (left) (12–13 years) rapes adult female Bel (17–18 years) in dorsoventral position. Bel is uttering mating squeals.

Fig. 5. Female Yet (12–13 years) initiates a copulation with adult male Jon (20–28 years) in ventroventral position.

ed by elaborate female proceptive behavior (Schürmann, 1982). During two
consortship periods, lasting 15–17 and 20–22 days, when the adult male Jon
consorted with the nulliparous female Yet, there were 42 copulations, all of
which were initiated by the female. One of these copulations resulted in con-
ception and the birth of a male infant (Yop). For this same male three con-
sortship periods were observed, of 7 + , 9 + , and 10 days, respectively, during
which he consorted with an older female (Bel) with offspring. In this case
it was the male that initiated the two observed copulations, after the female
had shown a modest form of proceptive behavior: one copulation proceed-
ed cooperatively; the other did not. Conception occurred, but according to
our calculations, the copulation that caused conception must have taken place
during a period in which no observations were made of this female. The three
reported consortship periods preceded this interval. Female Bel was again
found in consort with Jon 3 days before she gave birth to a female infant,
Bonnie (Fig. 6). Bel was not seen having any consort relationships with other
males, so we have little reason to doubt that Jon is also the father of the
second offspring recorded in this population.

   Reports on recent fieldwork in the same study area mention a third
young female (Sina) that was sired by Jon in January 1981 and consortships
of Jon with a fourth young female (Pluis) in 1982 (Sugardjito, personal com-
munication, 1982).

   In the 3 years of this study which preceded these conceptions, several
subadult males — at least four — were observed to copulate with the female
Yet (12 cooperative copulations and 7 rapes). None of these 22 copulations
is known to have resulted in conception.

   Clear pregnancy swellings of the labia had never been observed before
but were clearly visible during both known pregnancies within a few weeks
of conception (Fig. 7). Female Bel had a very distinct swelling when she was
observed 6 weeks after the calculated conception date, and female Yet's swell-
ing was apparent at 3 weeks. A note of caution is in order, however: an ear-
ly miscarriage could have occurred without the observer's seeing it. A female's
abdomen appears to expand no more during pregnancy, even in the eighth
month, than it does on a rich foraging day.

   Female Yet was already menstruating in 1972 (Rijksen, 1978), but a
successful conception did not occur until 1978. During 72 days in the year,
before Yet's conception, 14 copulations of Yet with subadult males were
recorded (2 rapes and 12 cooperative copulations); extrapolated, this would
mean about 70 copulations in 1 year. Even if we assume that the female was
at the peak of her attractiveness in this last year and that the number of
copulations may have increased gradually, we still estimate that Yet engaged
in some 130–210 copulations with subadult males during the 5 years before
conception.

Fig. 6. Female Bel (18–19 years) with her female infant Bonnie (2 days old).

a

Fig. 7. Labia of female Yet in 1978 (12–13 years): (a) normal situation, not pregnant; (b) swelling in the fourth month of pregnancy; (c) slightly deflated swelling in the seventh month of pregnancy.

b

c

It seems more than pure chance that during 60 ovulatory cycles not one of these copulations with subadult males resulted in conception. Tutin (1980) calculated that adolescent sterility lasts for an average of 26 months in wild chimpanzees. Even if such a period of adolescent sterility also occurs in orangutans, it can only partly explain the long interval between menarche and the first conception. If such a state of affairs is representative, this indicates that adult male orang-utans have far more reproductive success than subadult males.

The observations of Rijksen (1978), and Schürmann (1981, 1982) leave no doubt that young females often consort with both subadult and adult males. Generally, however, they prefer consortships with bigger and older subadult males and, ultimately, with the biggest one, the most dominant (alpha) male. The observations made by Galdikas (1979) and Schürmann (1982) leave no doubt that the adult male is actively selected by the female, not only to consort with, but also to mate with. These field data differ from those of MacKinnon in that they attribute a greater role to the reproductive function of the adult male.

RECONSIDERATION OF MACKINNON'S MODEL IN VIEW OF NEW FIELD DATA

In MacKinnon's (1979) model (Fig. 3), R1 represents the period of reproductive activity of the subadult male, and R2 the period of reproductive activity of the fully adult male. Thereafter the adult male is supposed to cease reproduction; MacKinnon (1979) called this the impotence period. The *age* estimates made by MacKinnon were 10 to 15 years for subadult males and 15 to 21 years for adult males. These ranges are certainly not as limited as he proposed. Subadult males can be much older than 15 years, and adult males older than 30 years. Four subadult males in Ketambe were estimated by Rijksen (1978) in 1973 to be 8 to 14 years old. These same males were still subadults in 1979 (first author's observation). Consequently, their ages in 1979 must have ranged from 14 to 20 years. Some zoo-born male orangutans did not develop cheek-flanges until they were about 18 years old (Brandes, 1931a; Ulmer, 1958; Jones, 1968). These data from the field and those from zoos (see above) indicate that there is great variability in the transition ages of the subadult male, subadulthood starting at 8 to 10 years and continuing up to 20 years or more.

The sexual activity of males in period R1 is in accordance with our own observations (Table I). When Jon was first observed in 1971, he was already fully adult (Rijksen, 1978). At that time he was estimated to be over 13 years of age, but in view of the possible age ranges of subadult males he could

have been as old as 21 years. However, no sexual activity by Jon was observed during the period from 1971 till 1977 (Rijksen, 1978; Schürmann, 1981, i.e., in at least 6 years of full adulthood during which he was observed regularly. So the reproductive activity of the fully adult male, i.e., during R2, can be very low or absent. In Jon's older adult phase, between 1977 and 1979, when according to the foregoing estimate, he was at least 19 and at most 29 years old, 50 copulations were observed. According to MacKinnon, this phase would be after the R2, i.e., in the impotence phase. It appears that adult males are as much involved in sexual activity as subadult males, although probably much less regularly. Nevertheless, MacKinnon's statement that subadult males are more sexually active than adult males is in agreement with our data, where 47 of the 50 copulations involving adult males were initiated not by the male but by the female.

Even later, in 1981, Jon sired a third female, Sina; and in 1982 he consorted with a fourth female, Pluis (Sugardjito, personal communication, 1982). These data indicate that Jon, when aged about 19 to 29 years, had just about reached his peak both in reproduction and in dominance; and this phase was still continuing in 1982, when he must have been 24 to 32 years old. Another male, Zet, judged to be much older than Jon on the basis of general appearance and shrinking cheek-flanges, was observed to rape a female. Another even older male, Mozes, with completely worn canines and several open pulpae, that was estimated to be about 40 years old, was observed in consort with an old female (Mif) in the month before he died. Several orang-utans in zoos live until they are over 40 and some even till they are more than 50 (Jones, 1976). The Ketambe field data provide evidence of at least one potent adult male aged between 24 and 32 years.

Agonistic activity of both subadult and adult males is rarely seen in the wild, but the few observed interactions (Rijksen, 1978; Galdikas, 1978) and indirect evidence — missing or stiff fingers and scars (Galdikas, 1978) — indicate that the agonistic activity of subadult males is less frequent and less intense than that of adult males. Nevertheless, it is sufficiently frequent to permit recognition of a dominance hierarchy among subadult males. In this dominance hierarchy, the older and bigger individuals can generally displace the younger and smaller ones (Rijksen, 1978; Schürmann, 1982). Really impressive agonistic activity of males with displays and long calls starts, however, only in full adulthood. For several years, the adult male Jon was in conflict with two higher-ranking adult males, Gorm and Mozes, in his home range. In this period, which would correspond to MacKinnon's A2, he stepped up his agonistic activity and gradually enhanced his status as well. In the A3 phase, at the age of about 20 to 28 years, Jon had become the most dominant adult male in the study area. Our observations indicate that male agonistic activity starts in subadulthood and gradually increases to reach a plateau somewhere during full adulthood.

IMPLICATIONS OF MACKINNON'S THEORY

The supposition by MacKinnon (1979) that there is an impotent adult male that safeguards the reproductive opportunities of his male offspring logically implies female migration and male kin selection. The adult male can consolidate and enhance his genetic contribution only if sons remain within his home range and if he is tolerant toward his sons and their sexual activities. If males do not migrate, we would expect female migration to be responsible for outbreeding. This phenomenon has been reported for chimpanzees (Goodall *et al.,* 1979; Pusey, 1979), but it is rare in other primate societies. There is no field study that provides any evidence of female migration of orang-utans. On the contrary, most recent field studies (Rodman, 1973; Rijksen, 1978; Galdikas, 1978), including MacKinnon's (1974), report males wandering more often than females, which is suggestive of male migration. If the sons do not migrate, they will start competing reproductively with their father when they become sexually active. According to MacKinnon's model, this could occur as soon as the adult male reaches the age of 21 years, namely, when the first son, which a male would have had in his R1 phase, reaches the R1 phase himself at the age of 10 years. If MacKinnon were right, and the father refrained from further reproductive efforts in favor of the subadult males, this would make sense only if he were selectively tolerant toward his own sons.

An adult male is generally intolerant and mildly aggressive toward subadult males and chases them away, particularly when he is in consort with a female (Rijksen, 1978; Galdikas, 1978; Schümann, 1982). If there is selective tolerance, it must be so subtle as to have escaped our attention and that of other field-workers. In contrast, adult males are very aggressive toward each other. Fierce chases have been observed, and several other studies (Rijksen, 1978; Galdikas, 1978) contain reports of fights and resultant wounds and scars. There is certainly no tolerance between adult males. In MacKinnon's model, the first son can be an adult male at the age of 15 years, when his father is only 26 years old. When males reach that age—and they do become much older (see above)—they will, according to MacKinnon's model, inevitably come into conflict with their own sons. Another reason why offspring consolidation is nearly impossible is that the adult male cannot possibly control the other individuals in the dispersed orang-utan population in his home range in the tropical rain forest.

From a sociobiological point of view, MacKinnon's argument that an adult male becomes impotent and still displays in favor of his offspring is the one which needs to be examined most critically. One's future fitness benefits more from one's own reproduction than from the reproduction of one's offspring (Wilson, 1975). In sexual reproduction, having one offspring of one's own is twice as effective in spreading one's genes as having

one's offspring produce one grandchild. We must assume very strong
ecological and social selective pressures if we are to accept the evolution of
such an aberrant sociosexual structure. Neither in the field nor in the literature
could we discover evidence of forces that could have caused such a develop-
ment. MacKinnon's model implies in essence a one-sided altruism—in the
reproductive sphere—on the part of a parent toward his offspring. The reverse
one-sided altruism, where a child refrains from reproduction in favor of his
parents, has been noted repeatedly (van Hooff, 1981). But it is very im-
probable that a parent would refrain from breeding in favor of his offspring.

DISCUSSION

The Sociosexual Model

In contrast to the view of MacKinnon, our data do not show a clear-
cut phase difference in male sexual and agonistic activity. The differences
between subadult male and adult male strategies are to be sought not so much
in the frequencies of their sexual and agonistic activities as in the pattern
of their actions: "rape and flight" versus "wait and fight."
In the sociobiological framework of mating-system theory the ultimate
consequences of behavior are far more important than their mere frequen-
cies (cf. Wilson, 1975; Emlen and Oring, 1977). We should therefore con-
sider those ultimate consequences: the reproductive success or the fitness and
the agonistic success or dominance position (Trivers, 1972), which result from
sexual and agonistic activity.
We conclude that in orang-utans these two variables, reproductive suc-
cess and high rank, are chronologically related. In his sociosexual develop-
ment, the subadult male obtains a gradually increasing dominance position.
As a young adult he competes with other adults until he is the highest-ranking
male in his home range. Initially the subadult has low reproductive success,
but this increases when he reaches a high rank as an adult. We conclude that
a high rank is a precondition for reproductive success and that reproductive
success does not precede agonistic success, as implied by MacKinnon's model,
but that agonistic activity and the resulting high rank precede reproductive
success. Because of his dominant position, the adult male can monopolize
the consortship with a receptive female for as long a period as is necessary
to inseminate her. On her part, the female offers the adult male the possibility
of controlling other males' access to her at her crucial (receptive) periods by
tolerating or even seeking his presence. In this way the dominant adult male
is able to monopolize the available receptive females in sequence (see above).

Outside the consortship, the adult male cannot control his females and the latter may copulate with other males; so we cannot speak of a strict form of polygyny. We can describe this mating system as a modified form of female defence polygyny. Normally this consists of males controlling access to females directly, which they can usually do by virtue of female gregariousness (Emlen and Oring, 1977; van Schaik and van Hooff, 1983). In the case of the orang-utan, the females are dispersed in space and in time. The most appropriate name is a *dispersed harem,* a term proposed by Nadler (1981).

Adult Male Mating Strategy

The mating strategy of the adult male is to attract with his locator call (the "long call") as many potentially receptive females as he can into his home range, from which he repels other adult males. The adult male consorts and mates with the female that has approached him. With young females he adopts a passive waiting attitude, leaving the initiative for copulation and the action to the female. The only action of the adult male — besides the long call — is "male presenting" toward the female (Schürmann, 1981). This passive attitude and male presenting can be interpreted only as a result of epigamic selection. Toward older females, however, the adult male may behave differently. Probably because they do not shy at him so easily, it is not necessary for him to adopt such a passive attitude. The male may make a greater contribution to the behavioral synchronization of the consort relationship with older females that have offspring than he does in consortship with young females. The adult male may take the initiative in mating but, again, in reaction to some proceptive behavior by the female.

Subadult Male Mating Strategy

Subordinate males, including all subadult males, are forced to end their consortship when the female makes contact with the resident adult male. The mating system of subadult males follows two patterns. (1) *Consortships with young females,* which may but need not, include cooperative mating, can be profitable to the male as an investment in future relationships that may prove productive when he reaches full adulthood. (2) *Rapes,* although not yet shown to be successful, occur regularly and may yield occasional profit. As the profit is low, so are the costs, and so rape is an easy secondary strategy adopted by males whenever the alternative of cooperative consort copulations proves impossible. It is to be expected that rapes are attempted particularly with older and strange females, when males or females are straying outside their usual range.

The intolerance between adult males explains, in the ultimate sense, the developmental strategy in which the maturing of adult display characteristics is inhibited and postponed. Lacking secondary sexual characteristics, physiologically mature males may be able to roam around in the home range of a resident adult male without provoking severe aggression.

Female Mating Strategy

Orang-utan females do not show any visible estrus swelling or other observable indications of ovulation. For the observer, and probably also for the orang-utan male, it is only changes in the female's (proceptive) behavior which indicate her cycle stage and receptive period. The evolutionary development of this concealed ovulation must be the result of epigamic selection (cf. Mayr, 1972): females without ovulation indications had a greater reproductive success than females with ovulation indications. There is a tremendous difference between the parental investment of the orang-utan male and that of the female. The female carries the fetus and raises the offspring for about 6 years, whereas the male simply inseminates the female. Because of this difference in parental investment, it is necessary for the female to be much more selective in her partner choice than the male. Concealed ovulation enables the female to adopt a sexual strategy in which she can best avoid mating with unwanted partners and approach preferred partners at the right time (Burley, 1979). The occurrence of concealed ovulation thus implies that mate selection is a female prerogative, and this provides an additional explanation for the development of orang-utan sexual dimorphism.

The Evolution of Sexual Dimorphism in Orang-Utans

Natural selection could have had only a minor influence on the development of size dimorphism (cf. Mayr, 1972). The bigger body of the adult male is clearly less adaptive for an arboreal life-style. The constraint on the adult male's body size by ecological disadvantages must be lessened by reproductive advantages (Clutton-Brock et al., 1977), viz., access to more females. Male group defense (see above) is not applicable to orang-utans. The most probable explanation for the male's physical secondary sexual characteristics is that they have evolved as a result of intrasexual selection (Trivers, 1972; Crook, 1972), i.e., the competition between males for females or for home ranges with sufficient resources to support a dispersed harem. On the other hand, the big body, long hair, cheek-flanges, and inflated gular pouch, features which seem designed to threaten and impress an opponent, may also attract females and, therefore, result partly from epigamic selection. Female

epigamic selection deserves more credit than it has received hitherto for the explanation of sexual dimorphism in the orang-utan.

CONCLUSION

Our final conclusion, then, is that the most plausible model for the sociosexual organization of orang-utans is an elaboration of the *prima facie* model originally proposed by Rodman (1973). In this model the major reproductive role was ascribed to the adult male. The complex and less parsimonious model developed later by MacKinnon (1979) must be rejected on the basis of data from recent field studies. There appears to be no reason to accept that the major reproductive activity of males is concentrated in an extended phase of subadulthood and that the adult male loses his reproductive capacity at an age as low as approximately 21 years — after which he functions mainly as a range guardian, protecting the resources for his previously begotten offspring. Instead, it appears that an adult male can be involved in long-lasting consortships with frequent and intensive sexual interaction and proven reproductive success.

Extended male subadulthood can be seen as a strategy allowing male animals to roam in the home range of fully matured males, to attempt consortship and (as a secondary reproductive approach) rapes. The reproductive success of these approaches is determined largely by female choice, i.e., her preference for the adult male fully adorned with secondary sexual characteristics.

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