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Review Article

Intrasexual Selection and Male Mating Strategies in Baboons and Macaques

Leo Berenstain[1] **and Ted D. Wade**[2]

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If baboon and macaque mating systems constitute a form of female defense polygyny, male mating strategies should be intrasexually selected and should vary in predictable ways with female defensibility, and demographic factors which affect the numbers of competing males per estrous female in populations. Substantial behavioral evidence exists for intrasexual selection of male mating strategies in baboons and macaques. Limited evidence also offers tentative support for theory-based predictions about the relationship between male mating strategy and female defensibility. Although male dominance rank generally predicts mating success, there are a number of factors which tend to increase the success of subordinate males above that expected from a simple dominance-based model of priority of access to mates.

KEY WORDS: sexual selection; mate choice; dominance theory; interference competition; baboons; macaques.

INTRODUCTION

In most species females make a substantially greater investment in gametes and offspring than do males (Trivers, 1972). As a result, female reproductive success is limited more by ecological factors such as the avail-

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[1] Graduate Group in Ecology, c/o Department of Anthropology, University of California, Davis, Davis, California 95616.

[2] Primate Laboratory for Behavioral Studies, Department of Psychiatry, University of Colorado Medical Center, Denver, Colorado 80000.

ability of energy and nutrients, while male reproductive success is limited more by mate availability. Females are consequently selected for greater mating selectivity and males for more intense mate competition (Darwin, 1871; Fisher, 1930; Williams, 1966). In his theory of sexual selection Darwin (1871) proposed that these selective forces produce male traits which enhance success in excluding rivals from potential mates (*intrasexual selection*) and attracting females (*intersexual* or *epigamic selection)*. The intensity of sexual selection on males is greatest in polygynous species, in which the amount of variance in male reproductive success associated with mate competition is relatively high (Bateman, 1948; Borgia, 1979).

Predicted consequences of polygyny and sexual selection include (1) increased sexual dimorphism in behavior, size, weaponry, and/or display dress and (2) increased male mortality after puberty, resulting in skewed adult sex ratios. Extensive work on the ecology of mating systems in diverse nonprimate taxa has shown that both polygyny and its predicted correlates evolve when either females or resources crucial to female reproductive success are defensible (i.e., monopolizable) by a portion of the male population (Orians, 1969; Selander, 1972; Jarman, 1974; LeBoeuf, 1974; Bradbury and Vehrencamp, 1977; Emlen and Oring, 1977; Blum and Blum, 1979; Wells, 1977; Wittenberger, 1979; Berry and Shine, 1980). Much of the variance in primate sexual dimorphism and demographic patterns is accounted for by a mating system in a manner consistent with sexual selection theory (Crook, 1972; Clutton-Brock and Harvey, 1977; Leutenegger, 1978; Harcourt, 1981). There is substantial agreement that the mating system of polygynous one-male primate groups is a form of female-defense polygyny in which individual males obtain exclusive mating access to groups of females by excluding rivals from social groups and perhaps ensure female acceptance by defending the home range (Goss-Custard *et al.*, 1972; Crook, 1972; Struhsaker and Leland, 1979; Bradbury and Vehrencamp, 1977; Harcourt, 1981).

It has been suggested that multimale primate groups exhibit another form of female-defense polygyny in which males defend females only near the time of ovulation (Harcourt, 1981). Since female defense is expected to generate intrasexual selection for male traits enhancing success in interference competition, the behavior and morphology of male baboons, macaques, and other species typically occurring in multimale groups should reflect such selection. Access to estrous females should be decided at least in part by agonistic interactions among males, and male success in mate competition should be correlated with success in other competitive contexts. Note that we use the terms "estrus" and "estrous" to refer specifically to the period of heightened female attractivity, receptivity, and proceptivity occurring at about the time of ovulation and that the sexual behavior of primate females, especially macaques, may peak also at other points in the menstrual cycle (Loy, 1970; Rowell, 1972). Morphologically, baboons and macaques appear intrasexually selected, closely resembling one-male species in both degree and forms of sexual dimorphism. However, it is perhaps especially in multimale groups, where females may have a greater capacity to exercise mate choice, that the results of male mate competition are complicated by the fact that estrous females are not passive resources but active organisms having genetic interests that may conflict with those of males (Rowell, 1972; Saayman, 1975; Bernstein, 1976; Wittenberger, 1979). Female choice could strongly affect the success with which males use agonistic means to gain exclusive access to potential mates. Some authors have correctly emphasized the potential importance of female choice in multimale groups and have also raised serious questions about the strength of existing evidence for intrasexually selected male behavior in baboons and macaques (Rowell, 1972; Bernstein, 1976; Duvall *et al.*, 1976; Saayman, 1975; Seyfarth, 1978a, b). These genera comprise most of the primate species typically occurring in true multimale groups (*sensu* Eisenberg *et al.*, 1972), and their social behavior has been studied in far greater detail than that of other multimale species. In this paper we evaluate the extent to which mating strategies of male baboons and macaques are consistent with some general predictions from sexual selection theory and with alternative explanations.

PREDICTIONS FROM SEXUAL SELECTION THEORY

If baboon and macaque mating systems constitute a form of female defense polygyny and male behavior in mating contexts is intrasexually selected, males should engage in interference competition for access to estrous females and male dominance rank should predict mating success (Bernstein, 1976). Variation in these outcomes should also be partially explained by sexual selection theory. According to theory, the intensity of intrasexual selection in female defense systems depends on the degree of female defensibility, i.e., the extent to which individual males can monopolize matings with ovulating females through competitive interactions with rivals and/or active sequestering of females that seek other mates (Bradbury and Vehrencamp, 1977; Emlen and Oring, 1977). (Note that competitive interactions may involve covert avoidance as well as overt avoidance and confrontation and may, thus, often be difficult to detect.) We suggest that in primates female defensibility should be largely a function of (a) a population's mean number of males per estrous female, (b) the degree of female agreement with or acquiescence to male mate choice, and

(c) the extent to which females' activities can be monitored by males. When the number of males competing for each estrous female increases the energetic costs and injury risks of defending a female increase, and when female disagreement with male mate choice increases, the energetic cost of sequestering a female increases. Thus, female defensibility is inversely related to both parameters. When females are relatively cohesive in space or when they inhabit relatively open areas, their defensibility is enhanced because males can monitor their locations and activities fairly closely (see Trivers, 1972; Stephenson, 1975).

The first parameter can be estimated roughly from reports in the literature, since it is a straightforward function of (1) the numbers of breeding males and females per group, (2) the degree of breeding seasonality, and (3) the degree of synchrony in females' cycling within suitable breeding periods. The effect of factor 1 on parameter *a* (above) is straightforward; factors 2 and 3 affect parameter *a* by determining the mean number of females simultaneously in estrus. Since female baboons and macaques cycle independently within suitable breeding periods (Rowell, 1972), differences in factors 1 and 2 alone will determine differences in female defensibility for a given degree of female agreement (parameter *b).* When these two factors interact so as to increase female defensibility, male intrasexual competition will yield greater payoffs and the intensity of intrasexual selection will increase. Variation in parameter *a* should thus predict some variation in male competition and the mating advantages of dominance. A corollary of this hypothesis is that, as female defensibility decreases and males become less able to monopolize a large number of mates, males should respond in a compensatory manner by becoming more selective in mate choice, i.e., by attempting to increase the mean quality of mates (Hausfater, 1975; and see below).

Parameter *b,* on the other hand, is extremely difficult both to predict from theory and to estimate for baboons and macaques. When both sexes actively select mates, their relative contributions to observed outcomes are usually unclear (Wittenberger, 1979). This situation is further complicated by the theoretical interdependence of mating strategies of the sexes (Borgia, 1979; Wittenberger, 1979). While the benefits of intrasexual competition will depend in part on female choice, as suggested by parameter *b,* the level of intrasexual selection will conversely influence female choice. As intrasexual selection increases, females are more strongly selected to favor the winners of intrasexual competition, and if winners are at least as fit as rivals in other respects, females should evolve a net preference for those males, enhancing intrasexual competition (Fisher, 1930). However, since females should and often do select mates for attributes other than competitive ability (Wittenberger, 1979; and see below), an absence of female preference for winners or even a female preference for losers does not indicate an absence of intrasexual selection on males. Both the difficulty of predicting outcomes involving interactors with conflicting interests and the insufficient development of theory about female choice have seriously limited the evolutionary understanding of mating systems (Borgia, 1979; Wittenberger, 1979).

In the following sections we assess the evidence for intrasexual selection of male behavior in baboons and macaques and examine its consonance with alternative explanations, given the current state of sexual selection theory. We attempt to test several predictions discussed above: (1) males compete for access to ovulating females by fighting and threatening rivals, sequestering females, initiating consortships, and transferring among social groups; (2) a positive correlation exists between male dominance rank and reproductive success; (3) female defensibility partly determines the degree of dominance advantage in mating both among and within taxa; and (4) males respond to decreasing female defensibility by increasing the selectivity of their mate choice. Unfortunately, the multiple variables affecting these outcomes are often intercorrelated, and there are insufficient data to permit statistical control of these intercorrelations (e.g., Clutton-Brock and Harvey, 1977). Therefore, we must rely on qualitative evaluation of the effects of intercorrelations among factors, despite the serious limitations inherent in this approach.

INTRASEXUALLY SELECTED MALE BEHAVIOR

Intermale Aggression

Though the absence of overt intermale aggression over estrous females does not imply the absence of intrasexual competition (see above), its presence clearly indicates intrasexual competition. If such competition is widespread in a taxon, it can be considered strong evidence for intrasexual selection. In several macaque species intermale fights or threats are more frequent or intense during the mating season than at other times (Carpenter, 1942; Kaufmann, 1967; Wilson and Boelkins, 1970; Norikoshi and Koyama, 1975; Dittus, 1977; Enomoto, 1981). At least some contests are clearly for access to estrous females (Lindburg, 1971; Stephenson, 1975; Dittus, 1977; Enomoto, 1981) and lead to serious wounds (Vandenburgh and Vessey, 1968; Wilson and Boelkins, 1970; Dittus, 1977; Enomoto, 1981). Teas *et al.* (1978) also noted increased male aggression during the mating season but did not specify the recipients' sexes. In all three adequately studied multimale baboon species, fights may increase in frequency or intensity and produce more numerous or more serious wounds when they occur for access to estrous females or in the presence of estrous females (Hall and DeVore, 1965; Paterson, 1973; Hausfater, 1975; Packer, 1979a, b; Ransom, 1981; S. Smith, personal communication). Packer (1979a) noted that escalated fighting, leading to wounding and takeovers of consorts, occurred most often on those days on which female consorts were most likely to ovulate. Harding (1980) also reported escalated fighting over estrous females, and serious wounding occurred in one such fight. These data parallel those from other multimale cercopithecids. In multimale groups of *Presbytis entellus* dominant males exclude subordinates from the group during the mating season (Bishop, 1979; Boggess, 1980). Intermale aggression over females is also seen in *Colobus badius* (Struhsaker, 1975).

The intrasexual selection hypothesis appears to be the only plausible explanation of these data on intermale aggression. While it is conceivable that such aggression is sometimes an artifact of temporarily decreased interindividual distances between males attracted to the same female, males associate peacefully in other contexts (e.g., Sade, 1972; Ransom, 1981). It is also unlikely that a "resource" such as individual distance, which can be easily obtained by both males via one's avoidance of the other, should lead to escalated fights (Popp and DeVore, 1979).

Male Initiative in Sexual Relations

In some species with one-male groups, males are intrasexually selected to obtain long-term exclusive access to groups of females, and they consequently experience little or no immediate competition for estrous females and little or no selection to initiate copulations (Harcourt, 1981). When multiple adult males coexist in groups, however, competition for mates occurs primarily when females are at peak estrus, and males are selected to initiate consortships with estrous females. Such male initiative is widely reported in baboons and macaques [baboons (Hall and DeVore, 1965; Hausfater, 1975; Seyfarth, 1978a; Packer, 1979a); macaques (Simonds, 1965; Tokuda, 1961-1962; Conaway and Koford, 1965; Kaufmann, 1965; Sugiyama, 1971; Lindburg, 1971; Enomoto, 1974; Stephenson, 1975; Baxter and Fedigan, 1979)]. In *Presbytis entellus,* a species having both one-male and multimale groups, males show more sexual initiative in multimale groups than in one-male groups (Bishop, 1979). Though it is possible that females prefer males that initiate consortships, females of these species also initiate consortships (e.g., Rowell, 1972; Seyfarth, 1978a; Lindburg, 1971; Stephenson, 1975), and it is unclear why females should prefer such males unless male initiative were already intrasexually selected.

Sequestering of Females

Intrasexual selection has generated various forms of male sequestering behavior in diverse taxa (Wilson, 1975; Blum and Blum, 1979; Wells, 1977; Berry and Shine, 1980; Lott, 1981). In all multimale baboon and macaque species studied to date it is primarily the male that maintains proximity to a mate during consortship [e.g., baboons (Hausfater, 1975; Packer, 1979a); macaques (Tokuda, 1961-1962; Kaufmann, 1965; Stephenson, 1975; Taub, 1980; Glick, 1980)]. Active sequestering is also seen. Male baboons herd estrous but not pregnant females away from extratroop males (Cheney and Seyfarth, 1977; Packer, 1979a). Consorting males of both genera often herd or chase females away from within-group males [baboons (Hausfater, 1975; Packer, 1979a, b; Ransom, 1981); macaques (Carpenter, 1942; Tokuda, 1961-1962; Lindburg, 1971; Sugiyama, 1971; Stephenson, 1975; Kurland, 1977; Dittus, 1977; Enomoto, 1978, 1981)], as may males attempting to initiate consortships (Tokuda, 1961-1962; Enomoto, 1978, 1981). In *Macaca fuscata* (Tokuda, 1961-1962; Kurland, 1977; Enomoto, 1981), *Macaca mulatta* (Carpenter, 1942), and captive *Macaca radiata* (Glick, 1980; personal observation), such chases may be violent, resulting in females being bitten and injured, and may facilitate female compliance. Saayman (1970) also reported that estrous chacma *(Papio ursinus)* females sometimes fled from approaching males but eventually halted and fear-grimaced as the males copulated with them. In *Papio anubis,* females that attempt to provoke changes in consort may be attacked by their consorts (Ransom, 1981). Male sequestering behavior is easily explained by sexual selection theory, and to our knowledge no alternative evolutionary explanation has yet been offered.

Harrassment of Consortships

Disruption of rivals' mating activity is almost certainly intrasexually selected behavior. Such disruption by males is frequent and effective in some nonprimate vertebrates having either male dominance hierarchies or leks (Geist, 1971; Wiley, 1974; LeBoeuf, 1974; Sinclair, 1977; Lott, 1981). Adult male harrassment has been seen in captive macaques [(Hanby *et al.,* 1971; Gouzoules, 1974); rhesus (personal observation)] and in many wild and semi-free-ranging baboon and macaque groups (e.g., Hall and DeVore, 1965; Neville, 1968; Lindburg, 1971; and see below). Rowell (1972) stated that harrassment was ineffective in preventing copulations, but effective harrassment was reported in a study of captive macaques (Hanby *et al.,* 1971) and in additional field studies [baboons (Hausfater, 1975; Packer, 1977, 1979a, b; Ransom, 1981); macaques (Stephenson, 1975)]. Of particular note is Packer's (1977) observation that adult male olive baboons were most likely to join alliances if the opponent was consorting with an estrous female and that such alliances often effect takeovers of females (see also Hall and DeVore, 1965; Paterson, 1973; Ransom, 1981). Packer (1979a) further demonstrated that harrassments were targeted only at consortships involving males that were truly competing genetically with the intruder: transferred males never harrassed the consortships of adult natal males (i.e., males born in their current group), which invariably consorted with young infertile females.

Breeding Dispersal

Males of many mammalian species disperse from their natal groups or ranges prior to breeding and on one or more occasions after breeding in adopted groups or ranges (Greenwood, 1980). There is evidence that natal dispersal in *Papio anubis* is intersexually selected by female inbreeding avoidance (see below) but that subsequent breeding dispersal is intrasexually selected (Packer, 1979a). In this and other baboon and macaque species, breeding dispersers appear to maximize their access to mates by transferring to groups in which more mates are available (Harcourt, 1978). This occurs both when males experience reduced mating success due to intrasexual competition (Dittus, 1977) and when they are high in dominance and breeding rank in their current groups (Lindburg, 1969; Hausfater, 1975; Norikoshi and Koyama, 1975; Sugiyama, 1976; Packer, 1979a). If female choice were the primary determinant of male breeding dispersal, only males experiencing poor or decreased mating success, as do natal males (Packer, 1979a), would be expected to transfer. Drickamer and Vessey (1973) reported that males transferred to groups with higher female-to-male ratios than their groups of origin, and Packer (1979a) showed that nonnatal but not natal males transferred into groups containing more available estrous females. Male-female ratios in groups did not affect male transfer in Cayo Santiago rhesus macaques (Koford, 1966; Boelkins and Wilson, 1972), but these studies did not distinguish natal from nonnatal males, nor did they monitor the changing availability of estrous females. Some macaque males maintain a long-term membership in one troop but transfer briefly to neighboring troops during the mating season (Lindburg, 1969; Dittus, 1974), a pattern suggesting attempts to maximize access to a population's females. There are additional reports of male dispersal peaking during the mating season (Koford, 1966; Neville, 1968; Vandenburgh, 1967; Boelkins and Wilson, 1972), but these support only the general hypothesis that male dispersal is somehow related to mating success.

Is Variation in Female Defensibility Related to Variation in Form or Intensity of Mate Competition?

Popp and DeVore (1979) defined the variables affecting two competitors' readiness to enter into or escalate aggressive encounters: (1) the net expected benefit of access to a contested resource, (2) the competitors' respective competitive abilities, (3) the probabilities of access to the resource through aggression or alternative strategies, and (4) the expected effects of the encounter on relatives. As the number of males per estrous female decreases (see Predictions from Sexual Selection Theory), the per-female costs of female defense decline, enhancing the per-female net benefit of mating access. This should increase the tendency of males to escalate competitive encounters over estrous females. However, the effect of variable 2 on escalated encounters should be related to female defensibility in a way that counteracts this tendency. The more males there are in a group, the greater the potential for them to form coalitions which may to some extent offset the effect of individual differences in competitive ability on mate competition. As competitive asymmetries are reduced by coalition formation, males will be readier to escalate encounters and will engage in more harrassment of and fighting with rivals. If the effect of increasing number of males per estrous female on competitive asymmetries is great enough, it could produce an inverse relation between female defensibility and frequency of escalated encounters, regardless of the effect of female defensibility on variable 1 (above). That social experience may have heightened importance for intrasexual competition in groups with many competing males is suggested by the positive relation found between the number of adult males in captive groups of rhesus macaques and the degree of delay in young males' sexual maturation (Rose *et al.*, 1978). The very limited data on baboons in Table I also suggest that the above factors may be interacting in the hypothesized manner. Female defensibility appears inversely related to level of overt intermale competition. In both groups having high female defensibility, the level of overt competition was low; of those groups having moderate female defensibility, overt competition was high in one, moderate in two, and low in two; and the one group with low female defensibility showed high overt competition. [Packer (1979a) did not discuss differences among four groups in overt competition.] Males often formed coalitions to harass consorting males in the group having the lowest female defensibility (Hall and DeVore, 1965). From Packer's (1977) report, however, it seems likely that males formed such coalitions in two groups with high female defensibility as well as in two with low defensibility, although it is not known to what extent the groups varied in this respect.

Table I. Female Defensibility and Male Mating Strategy in Baboons[a]

Papio sp.	$\bar{X}$ adult (♂♂/♀♀)	Sex ratio	Female defensibility	Overt competition	Selectivity	Male rank/RS[b]	Study
ursinus	3/12	1:4	High	Low	Low	Very high	Hall & DeVore (1965)
ursinus	2/8	1:4	High	Low		Very high	Seyfarth (1978a)
ursinus	3/30	1:10	Mod	Low		Low (negative)	Saayman (1971)
ursinus	8/22	1:2.8	Mod	Mod	Low	Very high	S. Smith (pers. commun.)
cynocephalus	8/13	1:1.6	Mod	Mod	High	Mod	Hausfater (1975)
anubis	3-5[c]/12	1:4	High	$\bar{X}$ = high	Low	$\bar{X}$ = high	Packer (1979a, b)
anubis	5-8[c]/12	1:2.4	Mod		Low		Packer (1979a, b)
anubis	9-11/13	1:1.4	Low		High		Packer (1979a. b)
anuhis	10-12/15	1:1.5	Low		Low		Packer (1979a, b)
anubis	7/17	1:2.4	Mod	High		Mod	Ramsom (1981)
anubis	5/12	1:2.4	Mod[d]	Low		High	Hall & DeVore (1965)
anubis	6/7	1:1.2	Low[d]	High		Mod	Hall & DeVore (1965)

[a] Female defensibility for each group has been classified as high, moderate (mod), or low according to the probable mean number of males competing for each estrous female as judged by the numbers of breeding males and females. All else equal, defensibility is inversely related to sex ratio and absolute numbers of males and females. The rationale for these effects is discussed in the text. Since baboons are primarily nonseasonal breeders whose females cycle independently, only the number of females in a group systematically affects the mean number of females simultaneously in estrus. Only some of the groups are classified as to mating indices on the basis of quantitative data. The evidence on the basis of which we have classified groups according to dominance advantage is also discussed in the text.

[b] RS, reproductive success.

[c] Higher figure includes natal adult males.

[d] Breeding somewhat seasonal.

If there is indeed a conflict-generating reduction in competitive asymmetries in groups with low female defensibility, this demonstrates that the intensity of intrasexual selection need bear no direct relation to the frequency or intensity of overt intermale conflict, as is sometimes supposed (Rowell, 1972; Saayman, 1975; Bernstein, 1976). Intrasexual selection generally favors male traits which create and augment advantageous competitive asymmetries. Especially when a species' existing forms of combat are extremely dangerous, as they are for male baboons and macaques, individuals may be strongly selected to avoid rivals that possess such traits. The selection of traits which so reliably predict advantage in combat that rivals are selected to avoid combat is as surely intrasexual selection as is the selection of traits which are often used in actual combat (Struhsaker, 1969). It should also be noted that the reciprocal altruism of coalition-forming male baboons (Packer, 1977, 1979a) can itself be viewed as intrasexually selected. The intrasexual selection of cooperative behavior is perhaps strongest when traits such as size and canine development, which enhance individual competitive ability, can no longer respond to intrasexual selection.

We were unable to classify most groups of macaques effectively according to frequency or intensity of overt intermale competition for mates, perhaps because they seem to vary less than baboon groups in this respect. However, the fact that macaques generally show less intermale aggression and greater proportionate use of male-to-female aggression than do baboons (references in Intermale Aggression) is consistent with their more seasonal mating and with the apparently greater degree of female influence on consortships and male troop membership in macaques (Lindburg, 1969; Stephenson, 1975; Kurland, 1977; Packer and Pusey, 1979; Takahata, 1980). By increasing the number of females simultaneously in estrus, a greater seasonality tends to decrease the number of males competing for each estrous female. This in turn reduces the advantage to males forming coalitions and diminishes the males' tendency to escalate encounters over estrous females. The extensive coalition formation in mating competition seen in some baboons has not been reported for macaques. Additionally, increased female influence should produce a concomitant decline in variable 3 (above), the mean probability of a male's gaining access to an estrous female via aggression, so long as female mate preferences do not always coincide with male preferences. This reduction in female defensibility should further relax selection on males to engage in dangerous escalated conflicts with rivals. This combination of selective forces may partly explain why male macaques tend to focus their attacks, harassments, and chases on their own consorts and rivals' consorts rather than on rivals.

Variation in Popp and DeVore's (1979) fourth variable may explain some of the variation in intermale aggression among macaque species. Male

Barbary macaques (*Macaca sylvanus*) appear more closely related to other males and females of the same group than are males of other macaque species (Taub, 1980), except perhaps bonnet macaques (Wade, 1979). Hence, their lower intermale and male-female aggression levels may be due in part to kin selection. Wild bonnet males have also been reported to be less aggressive toward one another than are males of other macaques (Simonds, 1965; Rahaman and Parthasarathy, 1969; Sugiyama, 1971; Koyama, 1973), and Wade (1979) has attributed this to kin selection. Captive bonnet males may be extremely aggressive to potential mates (Glick, 1980; personal observation), but only chasing of females has been reported in wild groups (Simonds, 1965; Rahaman and Parthasarathy, 1969).

MALE DOMINANCE RANK AND REPRODUCTIVE SUCCESS

Heritable interindividual differences are found in traits which affect success in interference competition (DeFries, 1980). Such differences form the basis for the evolution of dominance relations in diverse taxa (Wilson, 1975; Popp and DeVore, 1979). Far from being artifacts of captivity (Gartlan, 1968; Rowell, 1972, 1974), linear or near-linear dominance hierarchies are the rule in wild and semi-free-ranging baboons and macaques (e.g., Hausfater, 1975; Angst, 1975; Loy, 1975; Deag, 1977; Wade, 1978; Wheatley, 1978; Packer, 1979b; Busse and Hamilton, 1981). If dominance relations reflect individuals' relative competitive abilities—both intrinsic abilities and those dependent on social context—and male competition for mates is strong, implying intrasexual selection, priority of access to mates should be correlated positively with dominance rank (Altmann, 1962). In the following section we discuss further the relation between dominance theory and intrasexual selection, attempting to clarify some issues about which great controversy has persisted in the primate literature (Gartlan, 1968; Rowell, 1972, 1974; Bernstein, 1976; Deag, 1977; Wade, 1978; Popp and DeVore, 1979; Harding, 1980). We then evaluate the evidence pertaining to a correlation between male rank and reproductive success in baboons and macaques.

Dominance Theory and Intrasexual Selection

According to Rowell (1972), the idea that male behavior contributing to dominance relationships is in part intrasexually selected implies that behavioral dominance is a unitary trait. If dominance is favored by selection, asks Rowell, then why do animals that behave subordinately continue to exist? But Deag (1977) showed that it is the tendency to attempt to dominate competitors, rather than dominance per se, that should be favored by selection. Dominance is not an individual trait but an aspect of social relationships that is affected by numerous behavioral and morphological traits (Hinde, 1979), including the behavioral tendencies to compete for resources *and* to dominate potential competitors even when resources are not immediately at stake (personal observation of macaques). In ecological settings in which interference competition is at least occasionally advantageous to individuals and where either heritable or nonheritable differences in competitive ability exist, a strategy of active interference with resource acquisition by competitively inferior conspecifics will be an evolutionarily stable strategy (Dawkins, 1980). If other traits conferring competitive advantages on individuals that actively compete are to some degree heritable, these traits will evolve concurrently with the above behavioral strategy. The strategy will be effective only insofar as individuals' perceptions of their own and others' competitive abilities are accurate (Dawkins and Krebs, 1978). Assuming at least minimal accuracy of assessment, the adoption of the strategy by group-living individuals should produce a dominance hierarchy. Depending upon circumstances it may also be advantageous for an individual to compete for resources not only directly but also indirectly by asserting dominance over potential competitors, in effect training them to anticipate losing competitive interactions with the individual and to permit uncontested access to valued resources by that individual.

This model of dominance relations explains interactions in which a dominant individual clearly goes out of its way to supplant a subordinate in the absence of any contested resource (e.g., deWaal, 1977; Ransom, 1981; personal observation of *Macaca mulatta, M. nemestrina,* and *M. radiata*). Thus, it is not entirely an illegitimate reification of the concept of dominance rank to say that individuals of some species compete indirectly for resources by competing directly for rank (cf. Popp and DeVore, 1979). To say that individuals compete for rank is, of course, only a shorthand way of saying that they attempt to dominate as many group members as possible.

The outcomes of competitive interactions are determined largely by dominance relationships, which reflect relatively enduring differences in abilities, but they are also affected by more transient differences in competitive abilities and by fluctuations in the expected net benefits associated with interactions (Popp and DeVore, 1979; Packer, 1979b). The latter factors may either reinforce or offset existing dominance relationships in a given interaction, but they are theoretically and perhaps empirically separable from the more enduring interindividual differences which determine dominance relationships (cf. Deag, 1977; Popp and DeVore, 1979). It is not surprising, then, that access to mates by male primates is not necessarily determined solely by dominance relationships (e.g., Suarez and Ackerman, 1971).

Two major points relevant to our discussion of male dominance rank and reproductive success follow from this dominance model: (1) if intrasexual competition affects mating success, the latter will be positively correlated with dominance rank, since dominance relations reflect relatively enduring differences in competitive abilities; and (2) even in the absence of countervailing female preference (see below), the relation between male rank and mating success will often be imperfect because numerous factors other than dominance relationships affect the outcomes of competitive interactions.

Male dominance rank and mating frequency are closely related in elephant seals (LeBoeuf, 1974), several ungulate species (Geist, 1971; Sinclair, 1977; Lott, 1981), and some primates (see below). Several authors have argued that mating frequency, especially in a 1- or 2-year study period, may be a poor predictor of lifetime reproductive success, which is presumed to be of ultimate relevance for sexual selection (Hausfater, 1975; Stephenson, 1975; Bernstein, 1976; Saunders and Hausfater, 1978). It is true that sexual selection favors not those individuals that mate most often or even those that obtain the most mates but rather those that optimize the trade-off between (a) quantity of mates per unit time and (b) mate quality (Fisher, 1930; Borgia, 1979). It is not strictly true, however, that a nonpositive relation between male rank profile (*sensu* Hausfater, 1975) and lifetime reproductive success negates the hypothesis that male mating strategies have been intrasexually selected. When factors other than rank contribute to male reproductive success, males that are at a disadvantage based on these factors might be selected to compensate by occupying higher ranks for greater durations than rivals. Sexual selection would favor this conditional strategy (*sensu* Dawkins, 1980) even if males that adopted it did not thereby achieve greater lifetime reproductive success than those with poorer lifetime rank profiles. It has also been argued that because male rank may be closely related to age, there may be little variation in male lifetime rank profiles, weakening intrasexual selection (Hausfater, 1975). But consider a system in which male rank alone determines mating success and competitive ability is so strongly related to age that all males have both equal lifetime rank profiles and equal reproductive success. Any male that failed to compete for rank would be strongly disfavored by selection; thus, intrasexual selection would maintain male competitive behavior.

To summarize, we have hypothesized that intrasexual selection promotes both direct competition for mates and indirect competition for mates via competition for rank. The most general resulting prediction about the relation between male rank and reproductive success is that males which compete for mates and for rank have higher reproductive success than males which do not compete but are equivalent in all other respects. The prediction that males with better rank profiles have higher reproductive success is a special case of the general prediction and makes the limiting assumption that rank profile is independent of other factors which promote advantages in mating. Since it is impossible either to determine the validity of this assumption or to test the general prediction for baboons and macaques, we shall proceed to evaluate evidence pertaining to the special case, keeping in mind that its limiting assumption may eventually prove invalid for these taxa. We consider the special case to be supported by any data indicating that high male rank increases (a) the quantity of mating opportunities per unit time or (b) mate quality. We also discuss additional predictions (Predictions from Sexual Selection Theory) about the manner in which variations in female defensibility affects male mating strategies.

Effect of Male Rank on Quantity of Mating Opportunities

Numerous studies of wild and captive baboons and macaques have indicated a positive relation between male rank and frequency of mounts, ejaculations, or consortships [baboons (Hausfater, 1975; Seyfarth, 1978a; Packer, 1979b; Busse and Hamilton, 1981; S. Smith, personal communication); macaques (Carpenter, 1942; Tokuda, 1961-1962; Conaway and Koford, 1965; Kaufmann, 1965; Southwick and Siddiqui, 1967; Lindburg, 1971; Hanby *et al.*, 1971; Angst, 1975; Dittus, 1977; Wheatley, 1978; Glick, 1980; see also Struhsaker, 1967, 1975, and Keverne *et al.*, 1978, for other cercopithecid genera)]. A few studies have not found such a relation (Loy, 1971; Sugiyama, 1971; Eaton, 1974; Enomoto, 1974). Drickamer's (1974a) analysis indicated that some positive correlations might be artifacts of the greater visibility of dominant males in field studies. This caveat does not apply to several studies, however (Hausfater, 1975; Seyfarth, 1978a; Packer, 1979b; S. Smith, personal communication), and it is noteworthy that only one study has reported a negative association between rank and mating activity (Saayman, 1971). Furthermore, Drickamer's correlation for observability bias affected the statistical significance but not the direction of differences among high-ranking, mid-ranking, and low-ranking males in mean numbers of consorts, matings, and copulations, all of which were predicted perfectly by rank.

According to theory (Predictions from Sexual Selection Theory), dominant (i.e., high-ranking) males should have the greatest capacity to monopolize mating opportunities when female defensibility is high. Within each genus groups with especially high female defensibility do tend to show

Table II. Female Defensibility and Male Mating Strategy in Macaques[a]

Adult (♂♂/♀♀)	Sex ratio	Female defensibility	Selectivity	Correlation consorts' ranks	Male rank/RS[b]	Study
Free-ranging *Macaca mulatta,* Cayo Santiago						
2/6	1:3	High	Low	Low	Very high	Carpenter (1942)[c]
2/4	1:2	High	Low	Low	Very high	Carpenter (1942)[c]
8/18	1:2.3	Mod	–	–	High	Carpenter (1942)[c]
9/14	1:1.6	Mod	–	–	High	Carpenter (1942)[c]
11/21	1:1.9	Low	Low	Low	Low	Loy (1971)
12/31	1:2.6	Low	–	–	Mod	Conaway & Koford (1965)[c]
13/31	1:2.4	Low	Mod	Mod	Mod	Kaufmann (1965)[c]
Captive *M. mulatta*						
2/28	1:14	High	Low	Low	Very high	Smith (1980)
4/28	1:7	Mod	Low	Low	High	Smith (1980)
4/28	1:7	Mod	–	–	High	Smith (1980)
2/38	1:19	Mod	–	–	Low	Smith (1980)
4/38	1:9.5	Low	–	–	Low	Smith (1980)
8/39	1:5	Low	–	–	Low	Duvall *et al.* (1976)
Wild *M. fuscata*						
6/11	1:1.8	High	–	–	Very high	Tokuda (1961-1962)[c]
8/16	1:2	High	–	–	High	Hayashi [see Nozawa (1972)][c]
8/21	1:2.6	Mod	–	–	High	Enomoto (1974)
8/30	1:5	Mod	High	High	Mod	Stephenson (1975)
13/21	1:1.6	Mod	–	–	High	Hayashi [see Nozawa (1972)[c]

16/21	1:1.3	Low	High	High	Mod[e]	Stephenson (1975)
12/43	1:2	Low	–	–	Low	Kawai [see Nozawa (1972)[c]
17/42	1:2.5	Low	High	Mod	Mod	Stephenson (1975)
			Captive *M. fuscata*			
13/20	1:1.6	Mod	–	–	Mod	Hanby *et al.* (1971)
18/36	1:2	Low	–	Low	Low	Eaton (1974)
N = 150	–	Low	High	Low	–	Fedigan & Gouzoules (1978)
			Captive *M. radiata*			
2/6	1:3	High	Low	Low	Very high	Pers. observ.
6/21	1:3.5	Low	High	High	Mod	Glick (1980)
7/28	1:4	Low	High	High	Mod	Samuels (1982)

[a] The procedure is the same as in Table I, footnote *a*. In estimating female defensibility we have given slightly greater weight to the number of females per group than we did for baboons, since this parameter should have a greater impact on the number of females simultaneously in estrus in seasonal breeders such as macaques. Note that classification categories (high, low, etc.) are relative and specific to species × condition groupings. Note also that, in classifying groups as to dominance advantage, we have not relied solely on rank correlation coefficients concerning rank and mating activity in those groups for which such data exist. Groups in which the alpha male almost entirely monopolizes matings often have lower rank correlations than do groups in which the alpha male is less successful (see Nozawa, 1972). This is due to a leveling of the very low mating indices of subordinate males in the former groups. We consider dominance advantage to be greater in the former than the latter groups, regardless of differences in correlation coefficients.

[b] RS, reproductive success.

[c] Quantitative analysis given by Nozawa (1972).

[d] When three natal males were excluded from the analysis.

[e] Mod because two very old high-ranking males appeared sexually impotent; otherwise high. These males continued to gain access to estrous females because of their high ranks.

the strongest relationship between male rank and mating success (Tables I and II). Strong support for our prediction comes from Nozawa (1972), whose graphical presentation of rhesus and Japanese macaque mating patterns showed that alpha males are more able to monopolize estrous females when there are relatively few breeding males in a group. Packer (1979b) noted that in groups in which males coalesced to harass consorting rivals, the reciprocal nature of such coalitions tends to reduce the correlation between rank and priority of access to estrous females. This observation is consistent with our prediction, because more frequent male coalitions should occur in groups with low female defensibility (see Intermale Aggression). Samuels (1982) also reports that the correlation between rank and mating success in captive bonnet macaques is reduced when dominance relationships are unstable. Unstable dominance relationships are an effect of reduced competitive asymmetries, just as frequent coalitions are a cause of reduced asymmetries.

Dominant males should also become more selective in their mating behavior (e.g., mate choice, timing of consortship and harassment, etc.) when female defensibility is low (Predictions from Sexual Selection Theory). Unfortunately, the data on selectivity within each genus are spotty and insufficiently comparable to permit even a tentative assessment of this hypothesis. It is suggestive, however, that reports of very low selectivity in macaques are from large groups with low female defensibility (Stephenson, 1975; Fedigan and Gouzoules, 1978; Wolfe, 1979; but see Small and Smith, 1982).

Macaques appear to differ from baboons in two ways that should reduce female defensibility and consequently reduce the effect of male rank on mating success and increase male selectivity in macaques: (a) macaques breed more seasonally, and (b) the timing of ovulation appears to be less precisely cued by female morphological and physiological changes in macaques (Hendrickx and Kraemer, 1969; Hausfater, 1975; Czaja *et al.*, 1975; Seyfarth, 1978a). Greater seasonality should increase the mean number of females simultaneously in estrus, and reduced precision of ovulation cues should increase the time and energy a male must spend in consortship to ensure fertilization of his consort. In fairly large groups of comparable size and sex ratio, somewhat stronger correlations between male rank and reproductive success and less selectivity may exist in baboons than in macaques (Loy, 1971; Stephenson, 1975; Packer, 1979b; S. Smith, personal communication), but there is no evidence for such a contrast in smaller groups (Tables I and II). Though greater selectivity has been reported in macaques, it has been for group sizes beyond the range of baboon group sizes for which comparable data exist.

In either genus there are too few groups which differ in habitat cover but are comparable in other aspects of female defensibility to permit even a preliminary assessment of the effect of this variable. Observations of captive rhesus macaques, however, suggest that increased habitat cover raises the number of copulations obtained by subordinate males (Stephenson, 1975).

Effect of Male Rank on Mate Quality

For males, mate quality is a function of (a) the probability that a mate will conceive and (b) the probability that a mate will produce offspring having high fitness. The relevant attributes of female baboons and macaques include (1) phase of estrus, (2) dominance rank, (3) age, (4) age of most recent offspring, and (5) genetic relatedness to the male. Below, we discuss the effects of these attributes on male mate choice.

1. Phase of Estrus. A number of studies have shown that dominant males consort with females closer to the probable time of ovulation than do subordinate males [baboons (Hall and DeVore, 1965; Saayman, 1970; Hausfater, 1975; Packer, 1979b; Ransom, 1981; Busse and Hamilton, 1981; S. Smith, personal communication); macaques (Stephenson, 1975; Samuels *et al.*, 1980; Glick, 1980)]. Dominant males also establish more or longer consortships, increasing the probability of mating with ovulating females [baboons (Seyfarth, 1978a); macaques (Tokuda, 1961-1962; Southwick *et al.*, 1965; Lindburg, 1971; Sugiyama, 1971; Missakian and Varley, 1977; Fedigan and Gouzoules, 1978; Dittus, 1979; Glick, 1980; Samuels, 1982)]. Smith's (1981) electrophoretic work demonstrated a strong relationship between male rank and actual reproductive success over three breeding seasons in six large captive groups of rhesus macaques. In another captive rhesus group Duvall *et al.* (1976) found a relation between male rank and reproductive success in only 2 of 3 years; in 1 year newly introduced low-ranking males reproduced as well as the alpha male, but they also increased their reproductive rates the following year after rising in rank.

A female preference for dominant males could also account for these data (Bernstein, 1976). That intermale competition at least in part explains them is suggested by reports that dominant males (1) engage in more frequent or more effective harassment of consortships than do subordinates [macaques (Tokuda, 1961-1962; Kaufmann, 1965; Hanby *et al.*, 1971; Stephenson, 1975)], (2) may take over subordinate males' consorts at peak estrus without even being challenged (Saayman, 1971; Ransom, 1981), (3) actively sequester their consorts from rivals (see Intermale Aggression), and (4) by their presence inhibit the mating activity of subordinates [baboons (Hausfater, 1975); macaques (Dittus, 1974; Stephenson, 1975; Perachio *et al.*, 1973; personal observation of *Macaca nemestrina* and *M. radiata;* Keverne *et al.*, 1978, for *Miopithecus talapoin*)]. The widespread nature of these and other forms of male competition for estrous females makes it highly unlikely that they are neutral or maladaptive rather than intrasexually selected.

2. *Female Rank.* Female dominance rank predicts reproductive success in macaques due to its effects on fertility and infant mortality (Drickamer, 1974b; Hird *et al.*, 1975; Sade *et al.*, 1976; Wilson *et al.*, 1978; Dittus, 1979; Silk *et al.*, 1981; see also Dunbar and Dunbar, 1977, for *Theropithecus gelada*). This relationship probably also exists in baboons, though it has not yet been documented (Altmann, 1980). When group females are not maximally defensible, therefore, selection should favor males that mate with dominant females, since by so doing they will raise not only their own and their sons' reproductive success but also that of their daughters, which will socially inherit matrilineal rank [baboons (Lee and Oliver, 1979; Altmann, 1980); macaques (Koyama, 1967; Sade, 1972; Missakian, 1972; Loy, 1975)]. Dominant males do often tend to mate selectively with dominant females [baboons (Hall and DeVore, 1965; Seyfarth, 1978a); macaques (Simonds, 1965; Stephenson, 1975; Kurland, 1977; Wolfe, 1979; Samuels *et al.*, 1980; Samuels, 1982)]. Lindburg (1971) observed selective association between dominant males and females in the mating season, and males sometimes rejected low-ranking females' attempts to initiate consort relations. Kaufmann (1967) reported that during the mating season dominant males increased both their amount of association and their selectivity of association with dominant females more than did subordinate males, but Loy (1971) found no correlation between the ranks of consorts in another Cayo Santiago group, and Small and Smith (1982) also found no correlation in captive rhesus groups. In two Japanese macaque troops dominant males not only consorted selectively with dominant females, while subordinate males consorted with subordinate females, but also selectively harassed matings of dominant females (Stephenson, 1975). Similar patterns have not been reported in captive Japanese macaques (Eaton, 1974; Fedigan and Gouzoules, 1978). While Hall and DeVore (1965) noted that an alpha-male chacma baboon ignored the peak estrous phases of the two lowest-ranking females, which instead copulated with subordinate males, Packer (1979b) found no association between ranks of consorts in olive baboons. Though there was no general relation between the ranks of consorts in another chacma group because the dominant male did most of the mating, two of the subordinate male's three consortships were with low-ranking females that came into estrus at the same time as a higher-ranking female, which consorted with the dominant male (Seyfarth, 1978a).

If a correlation between the ranks of mates is partly a function of relatively high selectivity in males and if male selectivity depends on female defensibility in the manner hypothesized in Predictions from Sexual Selection Theory, then the degree of correlation between mates' ranks should be predicted by female defensibility. In Cayo Santiago rhesus macaques (Table II), the only group reported to show such a correlation had low female defensibility (Kaufmann, 1965), but so did another group which showed no correlation (Loy, 1971). The captive rhesus groups yielding no correlation had high and moderate female defensibility, respectively (Smith, 1981; Small and Smith, 1982). Of the three wild Japanese macaque groups showing a correlation, two had low and one had moderate female defensibility (Stephenson, 1975), but both captive groups showing no correlation also had low defensibility. Thus, there is no evidence for a relation between female defensibility and male choice for dominant females in macaques.

The frequent association found above between ranks of mates could be due to female choice (Bernstein, 1976). There is some evidence that (1) females prefer dominant males as mates [baboons (Hausfater, 1975; Seyfarth, 1978a, b); macaques (Lindburg, 1971; Stephenson, 1975; Dittus, 1979)], (2) mate competition occurs among females [baboons (Hall, 1962; Rowell, 1967; but see Hausfater, 1975); macaques (Southwick *et al.*, 1965; Lindburg, 1971; Perachio *et al.*, 1973; Wade, 1976; Wilson, 1981)], and (3) females often exercise prerogative in copulation [baboons (Hausfater, 1975; Seyfarth, 1978); macaques (Tokuda, 1961-1962; Lindburg, 1971; Sugiyama, 1971; Stephenson, 1975; Kurland, 1977; Taub, 1980)]. The more-independent cycling of females in multimale groups than of females in one-male groups (e.g., Kummer, 1968; Rudran, 1973; Hrdy, 1977) may have evolved because it increases females' access to preferred mates. As a force promoting male competition for dominance, however, intersexual selection may not be truly alternative to intrasexual selection. The latter may itself select females to prefer males that are superior competitors, since such males will sire sons with above-average fitness (Fisher, 1930).

Bernstein (1976) proposed a form of intersexual selection without intrasexual selection in multimale groups. He suggested that males compete for rank in order to gain not mates or other resources but rather the opportunity for parental investment through leadership of the group. Assuming roughly equal mating opportunities for males, the proportion of a group's offspring sired by each male will be a function of his seniority in the group. Therefore a male that remains in a group for an extended period will benefit most from defending the troop and controlling it internally. Bernstein hypothesized that noninvesting males that move between troops may father as many offspring in a lifetime, but the most capable investing males will outcompete the most successful noninvestors, which must distribute their offspring among groups led by males of varying abilities. Females should then be selected to favor high-ranking (leader) investing males. It is clear, though, that the male-investing strategy cannot evolve within groups as Bernstein envisioned; nor can a female preference for investing males evolve within groups in the absence of an initial fitness difference between investing and noninvesting males. Even though the most successful investing males will have higher fitnesses than the "best" noninvesting males, it is the degrees of fitness not of particular individuals, but of competing strategies that are at issue. The investing strategy could initially propagate by trait-group selection (Wilson, 1980), but it is unlikely that baboon or macaque dispersal is spatially random enough to maintain intrademic trait-group variation sufficient to fix alleles contributing to this strategy. As trait-group variation reaches low levels, selection against the investing strategy within groups (social groups would equal trait-groups for the proposed strategy) should overwhelm the remaining weak between-group selection favoring the strategy (see Wilson, 1980). This is due to the fact that, within groups, noninvesting males would receive the same benefits on average as would investing males from the latter's investment without incurring any of the associated costs. Similar obstacles confront the evolution of a female preference for investing males in the absence of an initial fitness difference for the alternative male strategies, but it might be possible for such a female preference to evolve during the initial stage of trait-group selection for the male strategy and subsequently maintain within-group selection for that strategy when trait-group selection has been exhausted (see Fisher, 1930, and Dawkins, 1980, for analogous examples). Although it is generally thought that neither interdemic nor intrademic mechanisms for the evolution of relatively indiscriminate altruism are likely to operate in most natural populations (e.g., Alexander and Borgia, 1978), future theoretical developments could enhance the plausibility of Bernstein's model.

3. Female Age. Age is another aspect of female reproductive capacity that is potentially important for male mate choice. Both young and sexually mature females and very old females have a reduced capacity to bear offspring and raise them to maturity [baboons (Altmann, 1980); macaques (Drickamer, 1974b; Hird *et al.*, 1975; Sade *et al.*, 1976; Silk *et al.*, 1981)]. Lindburg (1971) noted that adult males occasionally mated with older low-ranking females in preference to young high-ranking females, and Conaway and Koford (1965) reported that dominant males preempted the more "attractive" older females for most of the mating season. Loy (1971) found a similar relation between male rank and age of consorts. Such a male preference should tend to depress the correlation between the ranks of mates, since female rank is determined mainly by maternal rank rather than age (e.g., Koyama, 1967; Missakian, 1972; Lee and Oliver, 1979; Silk *et al.*, 1981). It is possible that stochastic variation in the relation between ranks and ages (and other attributes noted below) of available estrous females could account for some of the variation in correlations between ranks of mates.

4. *Age of Most Recent Offspring.* Probably on account of nutritional and energetic constraints, female macaques have extended interbirth intervals following surviving births (Koford, 1965; Tanaka *et al.*, 1970; Fedigan and Gouzoules, 1978; Hadidian and Bernstein, 1979; Takahata, 1980; Silk *et al.*, 1981). These females show reduced sexual activity and conception rates even though they come into estrus and consort with males during the mating season (Rowell, 1963; Hanby *et al.*, 1971; Enomoto, 1974; Takahata, 1980; Silk *et al.*, 1981). Takahata (1980) demonstrated that their reduced conception rate need not be associated with diminished mating activity.

Because dominant females have more infants surviving into mating seasons than do subordinate females, their attractiveness as mates will be lowered by this factor for a greater proportion of their menstrual cycles than will that of subordinate females. Hence, if dominant males tend to select the highest-quality mates available, they will choose the highest-ranking of the available estrous females less often than expected purely on the basis of dominant females' better-than-average reproductive success. This should tend to depress correlations between ranks of mates. There is some evidence suggesting that estrous females with infants are less attractive than other estrous females as mates (Hanby *et al.*, 1971; Silk *et al.*, 1981), but there is no evidence concerning the effect of this factor on the correlation between ranks of mates.

5. *Females' Relatedness to Males.* Because of the deleterious effects of inbreeding, males should take genetic relatedness into consideration when choosing among prospective mates. Preference for nonkin does appear to account for some of the variation in consort selection [macaques (Bernstein, 1963; Sade, 1968; Enomoto, 1974; Stephenson, 1975; Fedigan and Gouzoules, 1978; Baxter and Fedigan, 1979); baboons (Packer, 1979a)], but females are probably more responsible than males for inbreeding avoidance (Packer, 1979a). For this reason, the effect of male-female relatedness on mate choice is discussed in the next section.

Negative Effects of Female Choice on Dominant Males' Reproductive Success

Although females may prefer dominant males as mates to some extent, there are male attributes other than rank that females might assess in choosing mates. These include (1) genetic relatedness, (2) genotype novelty, (3) aiding and parental behavior, and (4) age. In this section we discuss these attributes and their relationship to male rank in the context of female choice.

1. Genetic Relatedness. Male baboons and macaques typically emigrate from their natal groups as subadults or young adults (Harcourt, 1978). Packer (1979a) showed that natal male olive baboons may attain high dominance ranks but rarely mate and that their lack of success as breeders is probably due largely to inbreeding avoidance by females. Selection on females for inbreeding avoidance may partly explain reports of females' heightened sexual interest in extratroop males and recent immigrants [baboons (Hausfater, 1975; Cheney and Seyfarth, 1977; Packer, 1979a; Ransom, 1981); macaques (Lindburg, 1979; Dittus, 1977; Kurland, 1977; see also Gartlan and Brain, 1968, for *Cercopithecus aethiops*)]. Packer (1979a) argued persuasively that the general male strategy of increasing mating opportunities leads to an intolerable loss of fitness for males that remain in their natal troops with rejecting females, whereas the relative unimportance of the quantity of matings for females enables them to reject natal males without a reduction in mating success. Since in most primates there appears to be no countervailing sex-differential selection making it more critical for males than for females to remain in natal groups or ranges (see Greenwood, 1980), this asymmetry may explain the observed sex bias in natal dispersal.

Unless adult natal males are typically low-ranking, their reduced mating success should tend to mask a positive relation between male rank and mating success. Packer's (1979a, b) exclusion of adult natal males from his analysis substantially enhanced the correlation between rank and mating success. In Enomoto's (1974) study the three highest-ranking males were natal males whose inclusion in the study masked a strong relation between rank and mating success for nonnatal males. Natal males have also attained high ranks in other groups (Koford, 1963; Norikoshi and Koyama, 1975). Unfortunately, natal and nonnatal males are rarely distinguished from one another in the literature.

Low mating success of adult natal males should have its strongest negative impact on the correlation between male rank and reproductive success in relatively isolated groups in which reduced opportunities for transfer cause males to remain longer in their natal groups. On the other hand, high transfer rates due to both natal and breeding dispersal will place within groups high numbers of recent immigrants whose dominance relationships with residents and each other may be unstable for some time (e.g., Drickamer and Vessey, 1973; Ransom, 1981; see Duvall *et al.*, 1976, for a possibly analogous captive situation). A female preference for these immigrants could afford them greater mating success than expected from their ranks and, consequently, mask a positive effect of rank on mating success. One might predict, then, that recent immigrants that quickly achieve high rank would have the greatest mating success of all males. This is the case in chacma baboons (Busse and Hamilton, 1981; S. Smith, personal communication), but Ransom (1981) reported that an immigrant olive baboon male devoted so much time to establishing dominance over other males quickly that he had far fewer matings than another immigrant that rose in rank more slowly. Of course, any subsequent mating advantage associated with the first male's tactics could not have been detected by Ransom's study (see also Tutin, 1979, for chimpanzees). Clearly, the potential for complex intercorrelations and interactions among factors affecting male reproductive success is great, underscoring the necessity for detailed long-term studies of whole populations.

2. *Novel Genotypes.* We suggested above that females may solicit sexual activity with strange males to ensure that they and their younger female relatives will avoid intolerable levels of inbreeding. It is also possible that this behavior has been selected due to its beneficial effect on the genetic variability of females' offspring, although the importance of such variability may be minimal for long-lived ecological generalists (Kurland, 1977).

3. *Male Aiding and Parental Behavior.* Some authors have suggested that females may prefer to mate with males that have cultivated special relationships with them and their immature offspring via grooming, protection, and agonistic aiding (Ransom and Ransom, 1971; Lindburg, 1971; Saayman, 1971; Seyfarth, 1978b; Packer, 1979b). There is some evidence for selective association with or protection of their own offspring by males [baboons (Altmann, 1980; Packer, 1980; Busse and Hamilton, 1981); macaques (Berenstain *et al.*, 1981)], but far less evidence exists for a mating advantage for investing males. Ransom and Ransom (1971) reported that a low-ranking male olive baboon performed extensive care of an infant of the alpha male's favorite consort, and Seyfarth (1978a, b) showed that nearly all chacma females that associated with the protective and care-giving subordinate male during lactation mated instead with the dominant male. Busse and Hamilton's (1981) analysis of paternal defense against potentially infanticidal immigrants suggests that the care-giving males observed by Saayman (1971) and Seyfarth (1978b) may have performed paternal care as a defense against infanticide rather than as a means of soliciting future consorts. In the chacma groups studied by Seyfarth and by Busse and Hamilton, dominant males performed little or no infant care but did nearly all the mating. The old subordinate male Saayman observed, however, obtained more matings than higher-ranking males even though his consorts were occasionally taken over by them.

Packer (1979b) found a tendency for consorts to have cooperative extraconsort relationships as well. As nonnatal males aged they increased their grooming with females, perhaps because their fighting ability declined.

Packer suggested that subordinate males may be able to consort with females they have groomed and aided often, while dominant males monopolize females without needing to cultivate special extraconsortship relationships with them. This pattern has been observed in chimpanzees (Tutin, 1979).

4. Age. Rowell (1972) suggested that the greater mating success of dominant males is attributable to female choice for longevity, which is correlated with rank. However, among adult male olive baboons, rank is an inverted-*U* function of age, and consorting activity of nonnatal males is related much more strongly to rank than to age (Packer, 1979a). Nevertheless, Packer found that of seven older-than-average nonnatal males, six had consorting ranks higher than their dominance ranks. He suggested that this was due to the older males' greater experience in coalitions rather than to female choice. S. Smith (personal communication) notes that older chacma males are poor breeders. Kaufman (1965) reported that an old dominant male rhesus macaque tended to mate with older females that were already pregnant, and two very old Japanese macaque males that maintained their high ranks by alliance mated relatively infrequently with fertile females (Stephenson, 1975). If females in these groups had selected primarily for longevity, these males would have achieved much greater mating success. In two captive groups of rhesus macaques male reproductive success was closely related to rank but not age (Smith, 1980), and in another group the oldest male produced no offspring in three breeding seasons (Duvall *et al.*, 1976). In a chacma group, females' preference for the oldest male caused a negative rather than a positive relation between rank and mating success (Saayman, 1971).

In general, the above data do not support female choice for longevity and indicate that if females do favor long-lived males, the preference is more likely to have a negative than a positive effect on the correlation between male rank and reproductive success. This conclusion is further supported by data from chimpanzees (Tutin, 1979).

SUMMARY AND CONCLUSIONS

If baboon and macaque mating systems constitute a form of female defense polygyny, male mating strategies should provide evidence for intrasexual selection. Substantial evidence for such selection is found in several aspects of male behavior: (1) males increase the frequency or intensity of aggression toward one another in mating contexts, often in defense of consorts or in attempting to take over rivals' consorts; (2) males compete by initiating sexual relations with estrous females; (3) males aggressively sequester estrous females; and (4) males attempt to maximize access to mates by transferring even from nonnatal groups in which females have accepted them as mates. We found in a very limited qualitative analysis that variation in female defensibility appears to explain some of the variation in these behaviors as expected from sexual selection theory: (1) male fighting increases when male coalitions tend to disrupt existing dyadic competitive asymmetries in groups with many males; and (2) the ratio of intermale to male-female aggression in mating contexts and, hence, the risk of injury in competition for mates is greater in baboons than macaques, for which female defensibility is reduced by a greater female influence on consort relations.

We argued that not only the tendency of males to compete directly for access to estrous females, but also their tendency to try to dominate potential competitors, is at least in part intrasexually selected. Since relatively enduring dominance relationships reflect only the most stable features of dyadic competitive asymmetries, and because access to estrous females is affected by many factors other than such features, it is not surprising that male dominance rank does not always strongly predict reproductive success. In this light, the substantial evidence that does exist for a positive relation between male rank and reproductive success tends to support the hypothesized effects of intrasexual selection on male mating strategies. Dominant males tend to (1) gain access to more mating opportunities than do subordinate males and (2) mate most often with females at peak estrus and with dominant high-quality females. The expected correlation between the ranks of mates may be offset to some extent by male choice for female attributes other than rank, such as (1) intermediate age and (2) lack of a dependent infant. Though tentative, there is some indication that the degree of correlation between male rank and reproductive success is related to female defensibility, as predicted. Factors that may influence this correlation by affecting female defensibility include (1) the numbers of breeding males and females per group, (2) the breeding seasonality, (3) the precision of ovulation cues, and (4) the female capacity to exercise mate choice. Available data are far too limited to be more than suggestive about these influences, but our review indicates the utility of further investigation along these lines. Though we did not find support for our prediction that low female defensibility causes high mating selectivity by males, the data here are especially limited and their degree of comparability across taxa and populations is especially uncertain. Future testing of this prediction, using a much larger and more detailed data base, seems warranted.

Though some authors have suggested that female choice alone can explain the tendency of dominant males to outreproduce subordinate males, we found such suggestions both lacking in empirical support and theoretically problematical. Female choice for group-investing males that compete for leadership opportunities could evolve via trait-group selection, but it seems unlikely that sufficient trait-group variation for either the male or the female strategies would exist in baboon and macaque populations. There is also little indication in the literature that females choose among adult males on the basis of longevity, and it is unlikely that even if such a preference were common, it would produce positive correlations between male rank and reproductive success. We found that female choice for (1) unrelated males, (2) genetically novel males, and (3) parental males might also depress correlations between male rank and reproductive success. Of these, we concluded that the evidence for an effect of factor 1 was somewhat stronger than that for the other factors.

Taken together, the evidence of overt intermale competition for mates and of a positive effect of rank on male reproductive success strongly supports the hypothesis that the mating strategies of male baboons and macaques have been subjected to substantial intrasexual selection. As yet it is unclear for most of these species whether female choice has a net reinforcing or counterselective effect on intrasexual competition. Both this effect and the other influences on the form and intensity of male intrasexual competition can be expected to vary with phylogenetic (e.g., preexisting degree of size dimorphism), demographic, and habitat variables. Even with detailed fossil evidence, a strong tendency toward identity of potential causes and effects in sexual selection will make the influences of the first set of variables difficult to untangle. Our attempt here to evaluate the effects of other variables has been merely preliminary and suggestive but has indicated that future study of them will be useful. It may be possible in the future to quantify female defensibility rigorously on the basis of careful measurement of the potentially influential factors discussed in this paper. In addition, future work on baboon and macaque mating strategies should focus on the degrees and forms of mating selectivity in males as well as females. To determine the values of these variables, researchers must monitor the ongoing availabilities of mates by rank, age, parity, condition, group tenure, matriline, and other attributes. When the data base on mate choice has grown substantially, it may be productive to subject it to multivariate analyses in which the intercorrelations among the above factors can be controlled statistically.

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