# FEMALE REPRODUCTIVE POTENTIAL AND ITS APPARENT EVALUATION BY MALE MAMMALS

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ABSTRACT.—Among mammals it has been widely supposed that females are more discriminatory than males in mate selection. Little attention has focused on a related issue, whether males evaluate potential female mates. Data on bison (*Bison bison*) and possibly other mammals suggest that males discriminate among females based on female reproductive potential. Evidence is presented that older (≥6 year) males not only outnumber younger males early in the rut when females of higher fecundity are available for breeding, but that older males actively select and copulate with females that have greater probabilities of bearing offspring in the subsequent season. Although the proximate mechanism of mate selection has yet to be identified, the data may explain some previously misunderstood anomalies in male breeding behavior and they demonstrate previously undescribed, subtle discriminations made by male mammals.

Two mechanisms of sexual selection emphasize the interplay between sexual dimorphism and mating systems. Females, the prudent sex—often because they invest more in offspring than males—exercise choice of mates on the basis of some fitness-promoting quality, whereas the more ardent males seek to inseminate as many females as possible (Arak, 1983; Clutton-Brock et al., 1982; Darwin, 1871; Geist, 1971; Trivers, 1972). Although it has been argued that females should mate selectively when males vary in quality and such differences affect female reproductive success (Bateson, 1983; Ryan, 1985), a different yet potent phenomenon, mate discrimination by males, has been overlooked, particularly among nonhuman mammals. There is no reason to expect that male mammals will be nonselective for mates if female fecundity varies, as it does in some invertebrates (Hunte et al., 1985; Rutowski, 1982; Snead and Alcock, 1985; Thornhill and Alcock, 1983), fish (Sargent et al., 1986), anurans (Ryan, 1985), urodeles (Verrell, 1985), and birds (Burley, 1981; Robinson, 1986). In essence, each sex may benefit by identifying the reproductive potential of possible sexual partners. If so, male mammals also should judge female reproductive potential and maximize opportunities to mate with the most fertile females, and breed as often as possible.

Support for this putative process has been hampered by lack of an empirical base and by claims that experimental data may not represent events found in nature (Connor and Simberloff, 1986). Fortunately, reproductive events associated with the breeding biology of some large mammals in temperate regions now render it possible to evaluate whether males discriminate among females, and if males seek to mate only with relatively fertile females or with as many females as possible.

Although several investigators of mammals, particularly of primates (Anderson, 1986; Conaway and Koford, 1965; Galdikas, 1985), claim to demonstrate that males discriminate among females, data are either anecdotal or equivocal. To show that male mammals distinguish among potential partners has proved challenging because of difficulties in demonstrating four conditions in the same study area: (1) females vary in their probability of producing progeny annually, their reproductive potential. Females also might vary in the quality rather than number of offspring produced, features that also would form the basis for male discrimination; (2) females varying in reproductive potential are differentially available so that discrimination by males is possible; (3) males do not copulate with females randomly. Although male and female behavior might jointly influence nonrandom mating because females may make themselves differentially available to some males, it must be shown that nonrandom breeding is, at least in part, a consequence of male, and not exclusively female, behavior; (4) when given simultaneous presentations, males

selectively mate with females that promote higher fitness (e.g., females of a higher reproductive potential). Unfortunately, the current state of knowledge does not permit sufficient testing of this last point (e.g., adaptive models of fitness) except perhaps for a few invertebrates (Arnold and Wade, 1984; Boake, 1986). To some extent this limitation can be overcome by assuming that, when patterns of mating confer consistent interindividual reproductive advantages, they result in lifetime differentials. This concept has support from field data on several mammals (Berger, 1986; Clutton-Brock et al., 1982; Gibson and Guinness, 1980; Hoogland and Foltz, 1982). In this paper, I present empirical data bearing on these four conditions for wild bison (*Bison bison*), and demonstrate that bison males are capable of discrimination among females based on the reproductive potential of females.

## METHODS

From March 1985 through December 1986 the approximately 420 bison of Badlands National Park, South Dakota, were under observation for >3,700 h by my colleagues and me. The area contains the largest (e.g., 250 km²) native prairie ecosystem in North America hosting these sexually dimorphic ungulates. The animals occur naturally, coexisting with bighorn sheep (*Ovis canadensis*), pronghorn (*Antilocapra americana*), mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), and several small carnivores. None is artificially fed or moved. Ages, identities, body mass, and prior 1-year reproductive histories of >200 bison were determined by luring them into traps in late winter and early spring 1985, and early autumn 1986, and through chemical immobilization of individuals that could not be captured (Kock and Berger, 1987). Animals subsequently were marked, weighed on cattle scales (or mass estimated through regressions of body size on mass—Berger and Peacock, 1988) and ages determined either by known birth dates or ear tags from prior capture, or estimated from toothwear and horn rings.

Based on 81 observed copulations and on descriptions in Lott (1974, 1981) estrus was judged to have occurred only when females were guarded by males, repeatedly were blocked or chased (as has been inferred similarly in bighorn sheep—Hogg, 1984), had ruffled fur or chafing present, probably the result of male mounting, or had their tails in "up" or extended positions. This latter point is most important because, in 26 observed copulations in which a white exudate (presumably semen) dripped from female vaginal regions, all females subsequently extended their tails upwards (some in excess of 240 min); the additional 55 copulations also resulted in tails being extended upward although a white exudate was not seen. I assumed estrus occurred on such dates, and by noting periods when tails of females were upward for extended periods I retrospectively assigned estrous dates in conjunction with the first three criteria listed.

Most (85%) births occurred between 9 April and 15 May, the remainder from 19 May until December. Births occurring after 15 May were omitted from further analyses because late births in temperate ungulates are more likely to influence a mother's next estrus than early ones (Clutton-Brock et al., 1982; Dyrmundsson, 1978; Guinness et al., 1971; Gunn and Doney, 1975; Mitchell and Lincoln, 1973). This omission was a matter of convenience because my present focus is on consequences of differences in reproductive potential of females upon mate decisions of males, and not upon causes of differences in reproductive potential of females.

Data reported herein, based on 164 known dates of estrus and the 81 observed copulations, stem from about 2,000 h of sampling from March into September, 1985. Systematic observations during preassigned daily shifts were made on focal animals and tending pairs by a team of six researchers and myself. Data collection began as early as 0445 h and extended until the beginning of darkness; typical observation shifts were 5–8 h.

Data were collected on the following categories of females and males: barren—mature females that had not produced a calf in 1985; lactating—females that nursed calves; nulliparous—females that had not produced calves previously; young males—2–5-year olds usually characterized by small body sizes and upturned horns; and older males—males ≥ 6 years of age, characterized by larger body sizes, thick head hair, and shorter but thicker horns than younger males.

Analyses followed standard parametric and nonparametric techniques. In one case it was necessary to compare more than two proportions and I relied on the method outlined by Zar (1984). Briefly, the means of proportions were used in a multisampling testing procedure by arcsine transforming the data, then comparing standard errors in degrees for each contrast. In multiple comparisons such as these, use of the normal approximation to the binomial is acceptable although use of critical values of the $q$ distribution seems preferable (Zar, 1984).

Breeding by bison appears typical of that of many northern temperate ungulates; reproduction is seasonal with males mating polygynously (Bunnell, 1982; Geist, 1971; McCullough, 1979). During the rut, males

establish tending bonds with females just before and during estrus (Lott, 1974, 1981). Receptivity is short, lasting 1–2 days, and >95% of the cows copulate with only a single male (Lott, 1979). Throughout most of the year, males and females are segregated by sex, although males associate with females during a brief 4–8 week breeding period. This suggests that males visit females only for the purpose of breeding; the separation of the sexes is central to understanding the significance of arrival dates of males when females are becoming receptive. Typically, males approach herds of females and their young, which in the Badlands may be in groups of ≤350 animals, and females usually ignore male approaches (Rutberg, 1986).

## RESULTS AND DISCUSSION

### *Variability in Estrus and Female Reproductive Potential*

To determine whether females were differentially available to males, the distribution of 164 estrous females was recorded for the duration of the breeding season (Fig. 1). Median date of estrus was 27 July, although when females were segregated according to their reproductive performances the previous year, median dates of estrus progressed from early in the season to late as follows: barren females, mothers with daughters, mothers with sons, then nulliparous females (those ≥3 years that have never given birth—Fig. 1). Females attaining estrus earlier were heavier; late winter body mass and date of estrus were related inversely for females ≥3 years ($r = -0.81$; $n = 14$; $P < 0.01$; $y = 49.53 - 0.065x$). A similar relationship has been reported for other ruminants (Dyrmundsson, 1978; Guinness et al., 1971; Gunn and Doney, 1975; Mitchell and Lincoln, 1973). These data indicate that heavier or better-conditioned females entered estrus first; they indicate little about whether females of different masses varied in their reproductive potential.

Therefore, potential fecundity in the next breeding season was estimated by comparing the proportion of females with young in each class to those without young. Ninety percent of barren females in 1 year were likely to produce calves in the next year ($n = 30$); 38% of lactating females produced calves in the next year ($n = 81$; no sex differences occurred, $\chi^2 = 0.67$; $P > 0.75$), whereas 15% of nulliparous females produced calves in the next year ($n = 20$). These findings agree well with those on other female ungulates (Mitchell et al., 1976; Robinette and Olsen, 1944) that also show marked differences in fecundity stemming from breeding performances in the previous year (Clutton-Brock et al., 1982). Equally important from the perspective of males is that females bearing offspring early in the season are likely to have heavier calves with coincident greater survival probabilities than later-born calves (Albon et al., 1987); thus, with other factors equal, early breeding females should be a more valuable resource for males than late-breeding females.

### *Male Options and Discrimination*

Under ideal conditions males should be present during the entire rut if opportunities for mating are not to be forsaken. Given that not all males associate with females throughout the rut, costs of attendance must be presumed. Although at this point it is not possible to assess the magnitude of such costs, ways in which males choose females can be identified by determining whether male arrival times at the rut coincide with the estrous periods of females of high reproductive potential (a correlational approach), by demonstrating that males invest more in defense of females of relatively higher reproductive potential (a different correlational approach), or by showing that males select females of higher reproductive potential when simultaneous choices between females of differing reproductive classes are possible (a direct test). Evidence bearing directly on the first and third items are presented, whereas the second is addressed only indirectly.

It is possible to test whether breeding efforts by males are skewed toward more fecund females or as many females as possible. If males concentrated breeding efforts on the most fecund females, more males should have been present early in the rut. This is because 23 of 27 (85.2%) of estrous females during the first quartile of the breeding season were barren (Fig. 1) so had the highest probability of producing offspring that year. Alternatively, if males maximized reproductive success through maximizing the number of mates, rather than through selection of females of
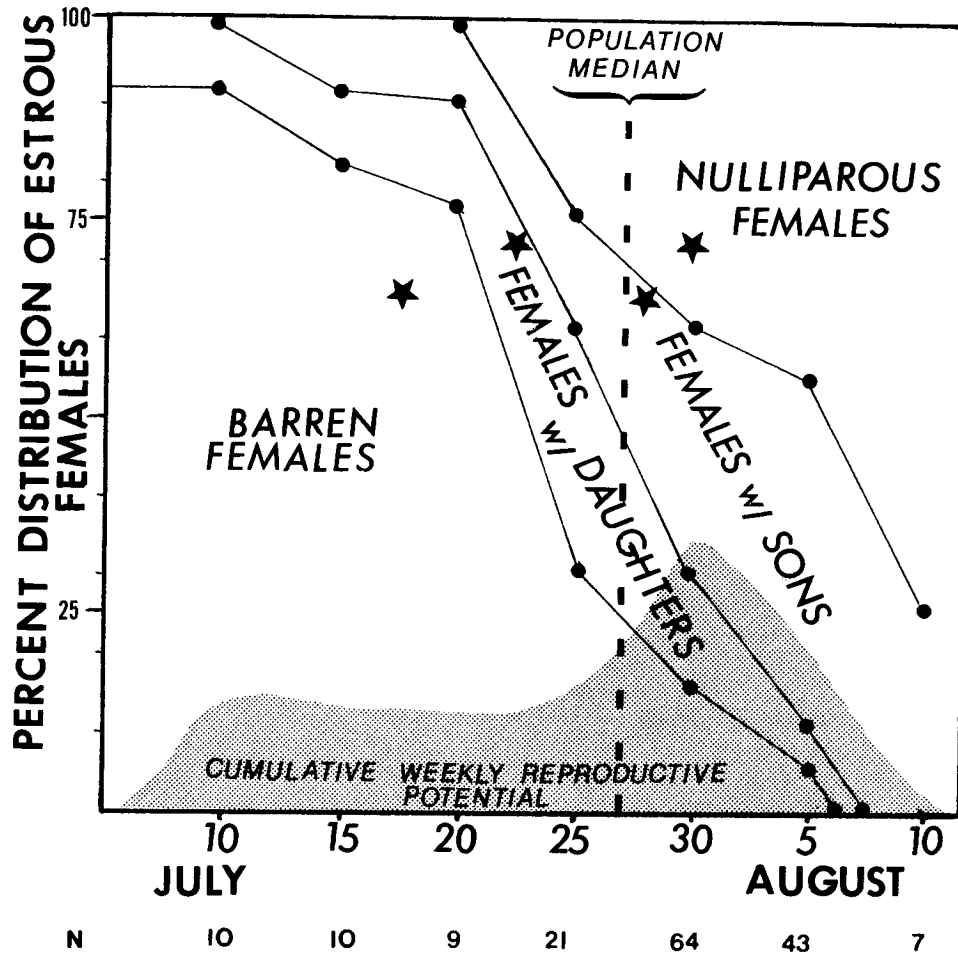
FIG. 1.—Distribution of dates of estrous females in relation to reproductive status during 1985. Asterisks refer to median date of estrus for each class of female. Cumulative weekly reproductive potential is the product of the frequency of estrous females and their reproductive potential. Percent distribution of estrous females is obtained by dividing the number of estrous females of different reproductive status by the total number of estrous females per 5-day period.

high reproductive potential (e.g., barren females), more males should have been present near the end of the rut. This period is when the greatest number of females entered estrus (Fig. 1). To examine the distribution of estrous females in relation to reproductive potential and absolute availability, I calculated female "cumulative weekly reproductive potential," the product of the sum of each female category multiplied by respective reproductive potential values. This measure was skewed toward the end of the rut (Fig. 1). In essence, given that males restrict participation in the rut to a few short periods, it is important to know whether they arrive early when females of relatively high reproductive potential are more available or later when the cumulative weekly reproductive potential is greatest.

To determine the period when males were most frequent, the distribution of 2,072 repeated sightings of bulls that visited groups of females was divided into those occurring before and after the median date of cumulative weekly reproductive potential (60% occurred before 26 July—

**OLDER MALES**

$\bar{X}$ = *9.4*

$\underline{SD}$ = *4.4*

$\underline{n}$ = *31*

**YOUNG MALES**

$\bar{X}$ = *16.9*

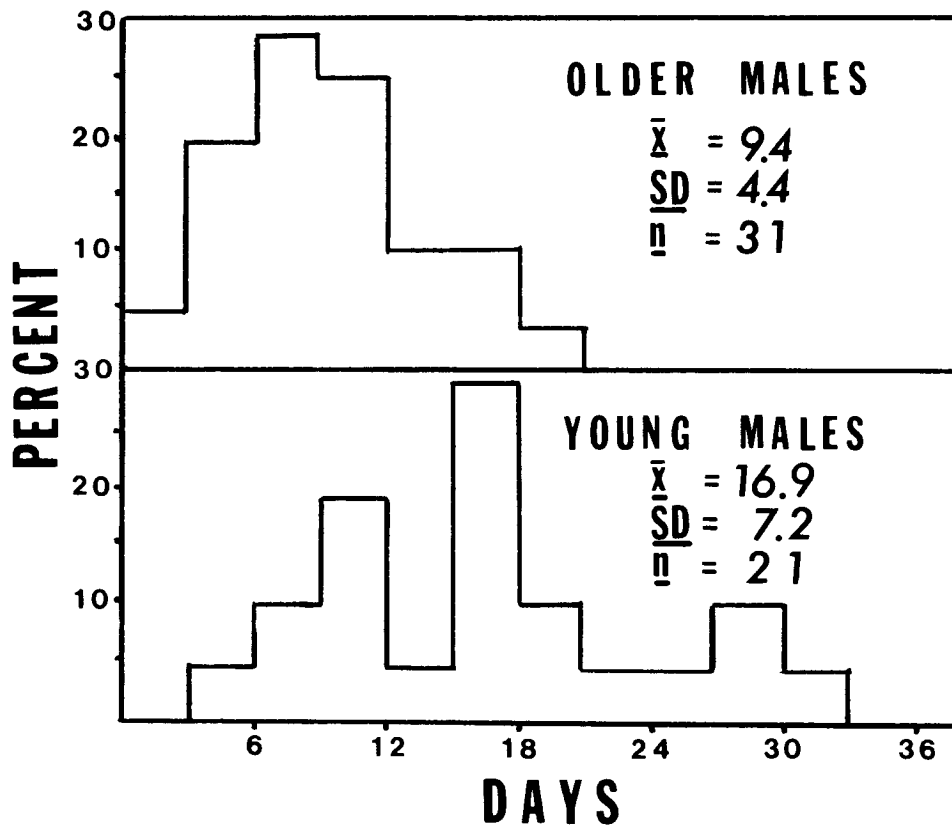$\underline{SD}$ = *7.2*

$\underline{n}$ = *21*

PERCENT

DAYS

Fig. 2.—Frequency distribution of the percentage of marked young and older males that spent different periods of time (in days) at the 1985 rut.

$\chi^2 = 89.23$; $P < 0.001$). Hence, there is an association between male arrival and estrous cycles of barren females.

Only 13% of 31 older males remained at the rut in association with females for $>15$ days, whereas more than half of the older males were present for $<10$ days (Fig. 2). Older males arriving early in the rut were observed on fewer days ($\bar{X} = 8.37$; $SD = 4.29$; $n = 19$) than those arriving after the 26 July median date ($\bar{X} = 11.16$; $SD = 4.00$; $n = 12$; $t = 1.98$; $0.05 < P < 0.10$). By dividing the rut into 9 weeks, a positive correlation between mean attendance time of older males (days/week) and week was found ($r_s = 0.94$; $P < 0.001$). These indirect data are tantalizing for they suggest that males may be less likely to remain early in the rut, perhaps because of increased competition.

Such data by themselves do not support the hypothesis that males select females of high reproductive potential for mating. If males discriminate among female reproductive categories, such behavior should be reflected by the frequency with which cows were investigated by males. To examine this possibility, the frequency that older males sniffed female anogenital regions was noted (Fig. 3) because a variety of vertebrates process information on female reproductive condition by employing such behavior (Wysocki, 1979). These data were gathered by recording the number of responses that different older males made to focal females during standard 3-h observation periods. The frequency with which females were sniffed in relation to their availability (Fig. 3) was influenced significantly by both their reproductive potential and the quartile of the breeding season (Fig. 3; two-way nonparametric analysis of variance: for female repro-
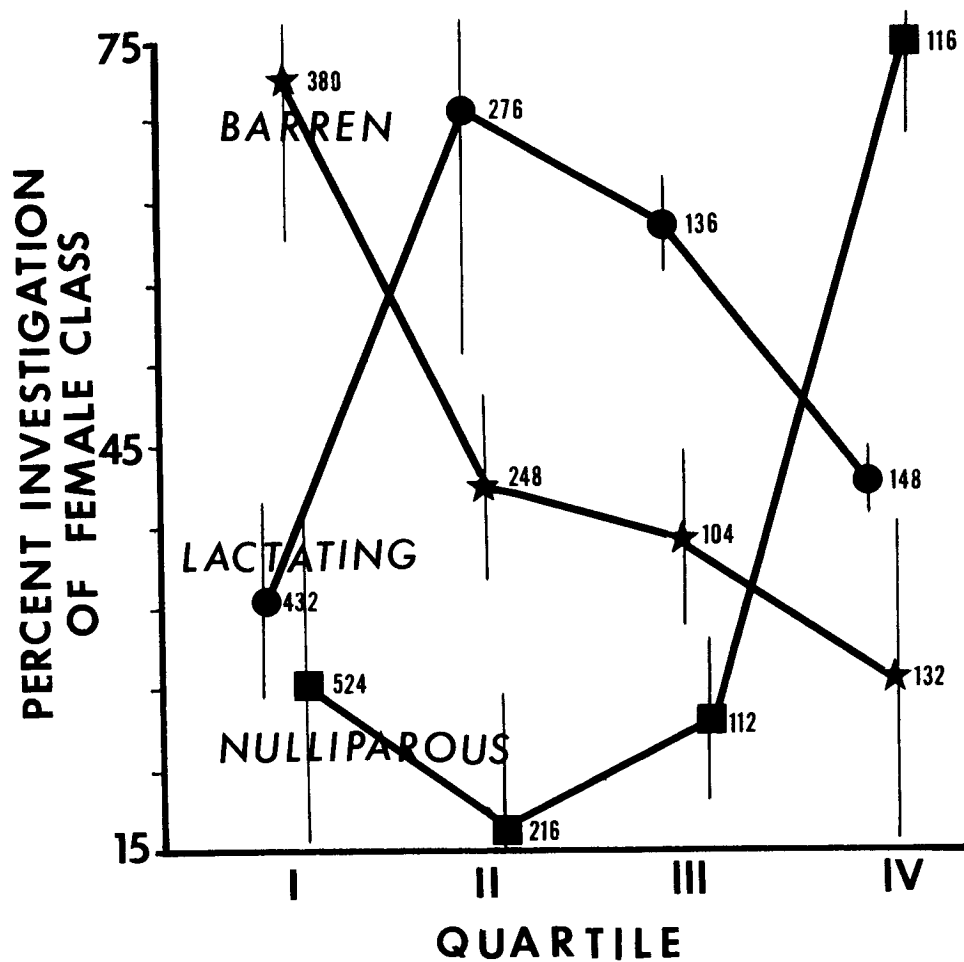
FIG. 3.—Relationships between breeding-season quartile and the mean percentage of male anogenital investigations of three classes of females. Data corrected for percent availability for each female class. Sample sizes refer to the number of marked females censused for at least 3 h/quartile. Multiple investigations of the same female by the same male within a 3-h period were excluded. Vertical bars = ±SD.

ductive potential—$\chi^2$ = 45.45; $P$ < 0.001; for quartile—$\chi^2$ = 42.42; $P$ < 0.001; $\chi^2$ [interaction] = 3.04, $P$ > 0.25). Barren anestrous females were selected most frequently during the first quartile and nulliparous anestrous females most often during the last; lactating anestrous females were investigated most during the middle quartiles (Fig. 3).

It was not possible to know whether changes in frequency of investigation by older males resulted in their ability to detect if some cows had become pregnant and others had not. Further, some cows experienced estrus more than once despite having copulated earlier in the season. However, older males directed approaches toward females in a nonrandom manner, selecting cows with the greatest reproductive potential in each quartile of the breeding season. Males that failed to capitalize on mating chances would be at a reproductive disadvantage if additional opportunities were forsaken. To examine the extent that males associated with groups of females during the entire rut, the total number of young and older males was compared with categories of female reproductive potential at weekly intervals (Fig. 4). Rank-related correlations indicate that, whereas more older males were present during earlier portions of the rut, males of all ages
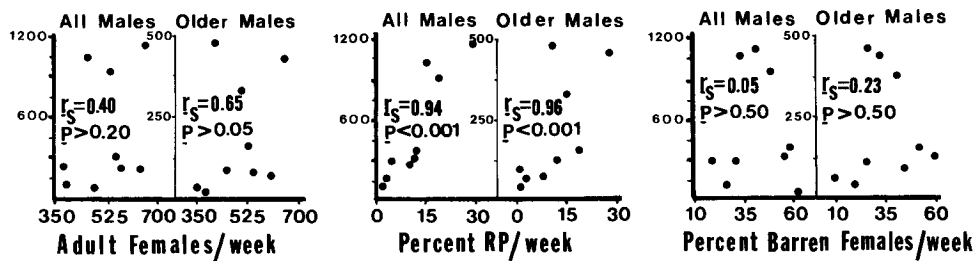
FIG. 4.—Relationships between total males (young and older males) and older males per week and the weekly number of females in groups visited by males (left); percent distribution of female reproductive potential (center); and percentage of barren females per group visited by males (right). Sample sizes for males shown on $Y$ axis, for females on $X$ axis: Spearman rank-correlation coefficients and levels of significance are indicated. Data from 1 July to 3 September 1985.

also associated with females during the entire 9-week period ($r_s = 0.94$ and $0.96$; $P < 0.001$). Thus, even though males may select females of higher reproductive potential, both young and older males sought other mating opportunities, at least as evidenced by continually associating with females (Fig. 4).

## A Direct Test of the Evaluation Hypothesis

Much of the evidence indirectly supports the hypothesis that males evaluate female breeding potential. Fortunately, a direct test is available because estrous females that differed in reproductive potential occurred within the same groups simultaneously. Thus, males had an option to choose among estrous females that differed in their probability of producing a calf in the next year. From 22 July to 3 August, males differentially approached 120 estrous females from different categories of reproductive potential; on any given day, females from at least two different categories of reproductive potential had to be present, experiencing estrus, and within 100 m of the other for data on male choice to be recorded. Choices by males were scored if they approached within 15 m of a cow. Both older and young males discriminated (Fig. 5). When females already were being tended, older males moved within 15 m of the tending pair significantly more often if females were of relatively high reproductive potential whereas young males moved toward nulliparous females. However, when females were not tended, males of both age categories moved toward females with greater reproductive potential. These data suggest that males evaluate female breeding potential. Males behaved in ways consistent with predictions that their mating patterns were adaptive because they were attracted differentially to females with the higher probability of producing an offspring in the next season.

*An alternative hypothesis.*—Rather than posing that males are most active in the mate selection process, females by themselves or some interaction between males and females may account for the patterns reported herein. For example, similar results might have been obtained had females approaching estrus or in estrus sought proximity to males. Because it is possible that females may employ subtle or difficult-to-detect physiological or behavioral cues resulting in observable male responses, it may be that females control male behavior, rather than playing no role in mate discrimination. To consider this possibility, the frequency of female approaches toward males was compared at estrus and for each of the 3 days before estrus (Table 1). Because all females should be equally motivated to mate, but because some differ in reproductive potential, it is possible to judge whether male discrimination was influenced by female behavior. The lack of relationship between female reproductive category and behavior toward males before estrus (analysis of variance among female reproductive status at days 1–3 before estrus, log-transformed data—$F = 1.15$; $P > 0.50$; Table 1) and at estrus (female reproductive status on day 0—$F = 1.16$; $P > 0.50$; Table 1) indicates that sexual consortships are not brought about by females. It

# OLDER MALES



# YOUNG MALES
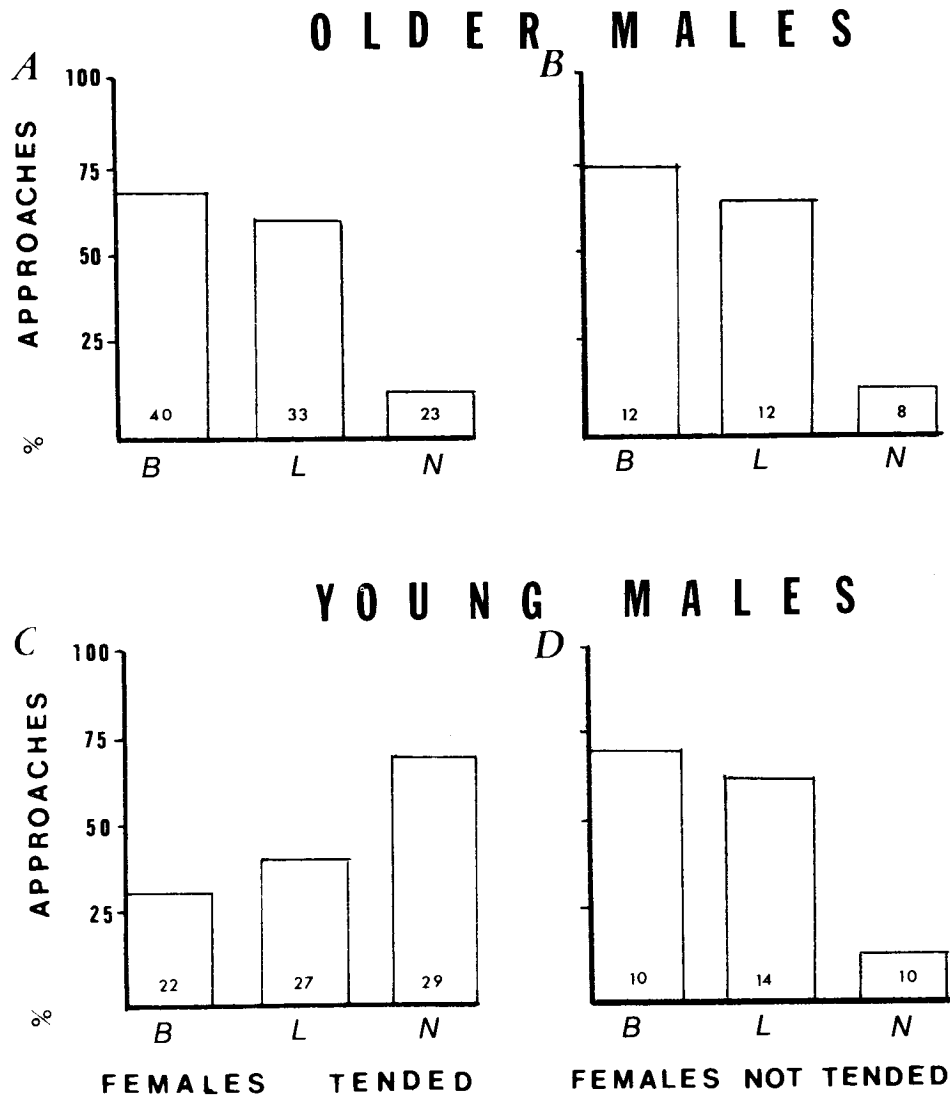


FEMALES TENDED        FEMALES NOT TENDED

FIG. 5.—Multiple comparison of percentage of approaches by young and older males to estrous females either tended by older males or not tended at all. Female categories are B — barren, L — lactating, and N — nulliparous. Sample sizes in bars. Q values and levels of significance for B *and* L, L *and* N, and B *and* L for each of the four histograms (A–D) are as follows: A, 2.45 (0.10 < $P$ < 0.20), 11.20 ($P$ < 0.001), 13.85 ($P$ < 0.001); B, 1.19 ($P$ > 0.50), 6.73 ($P$ < 0.001), 7.80 ($P$ < 0.001); C, 2.47 (0.10 < $P$ < 0.20), 5.27 ($P$ < 0.001), 7.50 ($P$ < 0.001); D, 0.69 ($P$ > 0.50), 7.69 ($P$ < 0.001), 7.79 ($P$ < 0.001).

still is possible that more subtle aspects of female behavior went undetected and that females of differing reproductive potential rendered themselves available to males, but the data suggest otherwise; males, not females are making the choices.

*Confounding variables.*—Possible confusion in interpreting these data could stem from the difficulty of sorting cause from effect. Perhaps older males that bred nulliparous females had less sperm resulting in lower female fertility, or young males were less fertile than older males. Perhaps females of all categories were equally likely to conceive, but nulliparous or lactating

TABLE 1.—*Mean (±SD) frequency/3-h observation period and* n *that different females approached to within 5 m of different males. Three cases in which females approached the same male multiple times were counted as only one approach per female.*

| Female reproductive status | Days before estrus | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | 3 | | 2 | | 1 | | 0 | |
| | $\bar{X} \pm SD$ | $n$ | $\bar{X} \pm SD$ | $n$ | $\bar{X} \pm SD$ | $n$ | $\bar{X} \pm SD$ | $n$ |
| Barren | 0.20 ± 0.44 | 5 | 0.40 ± 0.89 | 5 | 0.38 ± 0.70 | 16 | 0.50 ± 1.32 | 24 |
| Lactating | 0.40 ± 0.66 | 10 | 0 | 9 | 0.42 ± 0.86 | 12 | 0.14 ± 0.47 | 37 |
| Nulliparous | 0 | 5 | 0.25 ± 0.43 | 4 | 0.60 ± 0.80 | 5 | 0.21 ± 0.52 | 19 |

females were more likely than barren females to suffer prenatal deaths. If this latter point were true, arguments developed herein about male discrimination would still pertain because males were attracted differentially to potentially more fecund females. However, if either of the first two explanations (less sperm or less fertile young males) were true, then reproductive potential of females would be dictated by the interaction of physiological constraints and behavior of males, and not result from reproductive events during the reproductive history of females. Obviously, the past reproductive performance of a female will hinge upon the fertility of males with which she consorted.

It is clear that field studies cannot remove the possibility that sperm depletion or variation in male fertilization abilities can occur, and that these are the causes of differences in fecundity among females. Fortunately, other studies (Berger, 1986; Clutton-Brock et al., 1982; Mitchell and Lincoln, 1973; Mitchell et al., 1976) in addition to the present one offer an equally plausible explanation for variation in reproductive potential of females—the differential costs of rearing prior offspring. Hence, the basis for apparent male evaluation of females exists.

### Indirect Support from Studies of Other Mammals and Implications

Fisher (1958) indicated that either sex should be discriminating in choosing mates if its reproductive success will be affected. This appears true only where mating costs are involved (Dewsbury, 1982). For instance, if male bison incurred no mating costs, selection for females of different reproductive potential should not occur because indiscriminate mating would have no bearing on later reproductive success. Conversely, choice still might be favored if net benefits were derived from breeding with females of different classes and, because of time limitations, males could not breed with every female in the population. That older male bison depart from the rut after only short periods (Fig. 2), even though females capable of being fertilized are still available, suggests that mating costs are involved; included among these are substantial losses of body mass. At the National Bison Range in Montana, for example, four males >5 years old lost an average of 101 (SD = 12) kg/individual between 17 July and 8 October; even younger males (3 and 4 year old) lost mass—an average of 45 ± 30 (n = 3) each over the same period. Also, I have observed that young males feed more and are involved in less costly interactions during the rut than older males. Further, in other ungulates, energy expenditures by males increase with the number of female mates guarded (Berger, 1986), and wounds and death are common during rutting activities (Clutton-Brock et al., 1982; Geist, 1971; Wilkinson and Shank, 1977).

Nevertheless, because sexual relationships and consortships have been studied in many non-ungulate mammals, it is curious that demonstrations of male discrimination among potential mates are lacking. It seems unreasonable to believe that species other than bison are incapable of discriminating, and available, although disparate, evidence in other mammalian groups is suggestive that such choices may occur. This evidence includes the following: 1) Males identify and follow estrous females (Fig. 4). This is a generic pattern, expected for any group of mammals. Data from numerous orders (Eisenberg, 1981; Geist, 1971; Hrdy, 1977) indicate that males possess abilities to differentiate between receptive and nonreceptive females. 2) Females vary in reproductive potential. Field evidence from at least primates, ungulates, carnivores, rodents, and

pinnipeds (Altmann, 1980; Armitage, 1984; Clutton-Brock et al., 1982; Goodall, 1986; Reiter et al., 1981; Rood, 1980) demonstrates individual differences in reproductive potential among females. 3) Males distinguish among and choose the more fertile classes of females (Fig. 3; Table 1). Among nonhuman primates, males may select either dominant or more fecund females as partners (Anderson, 1986; Smuts, 1986; van Noordwijk, 1985). Unfortunately, these studies have not produced appropriate quantitative data, understandably because of observational difficulties or lack of simultaneous estrous cycles that would have made direct choices by males possible. Some intriguing additional evidence supporting a male-discrimination hypothesis is garnered from statistics on human rape; males select females from the most fertile age groups (Shields and Shields, 1983; Thornhill and Thornhill, 1983).

Although past research on mammalian mating behavior suggests that males refrain from breeding with certain females because of age-related incompatibilities (Geist, 1971), potential sperm depletion (Gibson and Jewell, 1982), or inbreeding (i.e., genetic) considerations (Pusey, 1987; Shields, 1982) it may be that males simply identify females as potentially infertile prospects. This could explain why, with other factors being equal, some males are reticent to mate with all available females; this occurs in zoos, in domestic species, and in the wild. The efforts may not be worth the reproductive benefits. Also, although evolutionary theory generally has been cited as a source for predicting that females ought to be the more selective sex when males mate polygynously, male mammals are likely to possess discriminatory abilities far more sophisticated than previously supposed.

## ACKNOWLEDGMENTS

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