

Sperm competition and variation in zebra mating behavior

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Summary. Data are presented on the breeding behavior of two zebra species to test whether intra- and inter-specific variation in male reproductive behavior and physiology are correlated with differences in female promiscuity. In one species, plains zebra (*Equus burchelli*) females live in closed membership single male groups and mate monandrously. In the other species, the Grevy's zebra (*E. grevyi*) females live in groups whose membership is much more temporary. Typically, associations with individual males are brief and mating is polyandrous. However, some females – those having just given birth – reside with one male for long periods, mating monandrously. These differences in female mating behavior generate variability in the potential for sperm competition. We show that behavioral differences in male investment in reproductive activities correlate with the potential for sperm competition. When mating with promiscuous mares, Grevy's zebra stallions made a greater investment in reproductive behavior (calling, mounting, ejaculations) than did stallions of either species when mating with monandrous females. The evolution of large testes size in the Grevy's zebra, when compared to the congeneric plains zebra, horse, and mountain zebra, allows for this increased investment.

Introduction

In many animals, males compete for access to sexually receptive females. This competition typically involves aggressively defending females or the resources they require. The intensity of male-male competition depends largely on the distribution of resources and on the resultant patterns of distribution, association, and reproductive synchrony of females (Emlen and Oring 1977; Rubenstein and Wrangham 1986). Male-male competition

is not limited to activities preceding mating (Parker 1970): sperm competition is widespread among mammals (Smith 1984; Ginsberg and Huck 1989).

Adult female plains zebra (*E. burchelli*) live in fixed membership groups and associate with only one male. As a result, plains zebra mares mate with one male and are monandrous (Klingel 1969). In contrast, in the Grevy's zebra (*E. grevyi*), adult females form temporary associations (Rubenstein 1986; Ginsberg 1989) and during a day typically wander through the territories of up to four males (Klingel 1974; Rubenstein 1986). By mating with many of the males with which they associate, these females are polyandrous. However, other females – those with newborn foals – remain near permanent sources of water in one male's territory and mate exclusively with that male in a monandrous pattern similar to that of the plains zebra (Rubenstein 1986; Ginsberg 1989). Females initiate the switch from polyandry to monandry and by doing so receive significant material benefits (Rubenstein 1986).

When females are promiscuous, male-male competition concerning sperm precedence may select for a suite of behavioral and physiological adaptations that will increase a male's probability of fathering an offspring. By increasing the number of spermatozoa a male delivers to a female, a male may increase his chances of fertilizing available ova. To effect such an increase, selection must necessarily operate on behavioral, morphological, and physiological components of the phenotype. Mammalian species in which females are usually polyandrous appear to evolve disproportionately large testes (Harcourt et al. 1981; Clutton-Brock et al. 1982; Kenagy and Trombulak 1986). Since species with large testes have high daily sperm production rates, large numbers of sperm per ejaculate, and large sperm reserves (Møller 1989), increased testes size should provide a high density of viable sperm in each of these ejaculates. In addition, males consorting with promiscuous females tend to mate more frequently (Short 1979; Wirtz 1983). In this paper, we present data on the breeding behavior of the Grevy's zebra and plains zebra – in an area where the two species

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occupy the same habitat – in order to test whether intra- and inter-specific variation in male reproductive behavior, physiology, and anatomy are correlated with observed differences in female mating behavior.

Methods

Reproductive behavior of both the Grevy's zebra (*Equus grevyi*) and the plains zebra (*E. burchelli*) was observed in the Buffalo Springs/Samburu Game Reserve in northern Kenya during an 8-week period in the summer of 1980 and for 22 months from March 1983 to August 1985. Over 1100 Grevy's zebra and nearly 200 plains zebra were individually identified by their stripe patterns. Individuals could be repeatedly identified with greater than 99% accuracy (Ginsberg 1987). Point-sample data, collected for 9795 sightings (5061 males; 4734 females), provided records of associations of individual grevy's zebra. Only uninterrupted observations were used in analyses. However, if two individuals were seen in association on the evening of day one and relocated on the morning of day two, then association was considered to be "uninterrupted."

The two species of zebra exhibit similar overall patterns of pre- and post-copulatory behavior. Between matings, males of both species herd and mount females, but only in the Grevy's zebra do males emit loud calls. Interruption of copulatory behavior by bachelor males was extremely rare, but data on mating rates and the length of inter-mating intervals were only derived from undisturbed mating bouts. Copulation is defined as a mount followed by intromission and ejaculation. In both species, ejaculation was followed by changes in the male's posture, after thrusting ceases, his body relaxes and his head falls against the female's neck (Waring 1983). In the Grevy's zebra copulation was also followed by a discharge of seminal fluids from the female's vagina. Females were considered in estrus when sexually receptive. The length of estrus was estimated only for females that were observed on both the days preceding and following the first and last day of receptivity.

Reproductive behavior was observed for 33 Grevy's zebra mares and 6 plains zebra mares. Twenty-four (73%) of Grevy's zebra females observed in estrus were polyandrous, 9 (27%) were monandrous. Twelve territorial male Grevy's zebra were observed mating with polyandrous females; 5 of these males were also observed mating with monandrous females. Six plains zebra harem males were observed mating with females in their harems. As our interest is in the variation of male behavior in relation to that of females, most analyses are made using individual males as the independent variable. Where a single male was observed mating with more than 1 female, mean values were calculated from the raw data for each variable examined.

To examine the inter-specific relationship between mating system and testes size in ungulates, data were collected from the literature on body weight, combined weight of testes, and mating systems. Where only the mean weight of a single testis was available, the combined weight was calculated as twice that of a single testis.

Statistical tests used when comparing patterns of reproductive behavior include the *t*-test (where data were not significantly different from a normal distribution) and the Mann-Whitney *U* test (where data were found to violate parametric assumptions). Comparative analyses of the relationship among body mass, combined testes weight, and mating system were made using an Evolutionary Covariance Regression (ECR; M. Pagel and P. Harvey, personal communication). Many earlier tests of the relationship between body mass, testis size, and mating system in mammals have relied on statistical methods that give disproportionate weight to species-rich genera and families (e.g., Kenagy and Trombulak 1986). In such analyses, each species in a genus such as *Mus* is assumed to have an independent evolutionary history, an obviously untenable assumption. This makes statistical tests invalid and leads to inflated *P*-values. The ECR was derived by Pagel and Harvey from

a model developed by Felsenstein (1985) in which comparisons are made between pairs of taxa at each bifurcation of a phylogeny. Felsenstein's model weights each comparison by the branch length in the cladogram, assuming equal rates of evolution in all branches and characters. Felsenstein's model requires precise knowledge of a true phylogeny. The ECR developed by Pagel and Harvey assigns equal weight to each branch length in a cladogram, does not require a bifurcations phylogeny, and thus can be used without knowledge of the true phylogeny. The method derives a set of mutually independent comparisons, each of which bears on the comparative hypothesis. The model has good type I and type II error rates (Pagel, personal communication).

Results

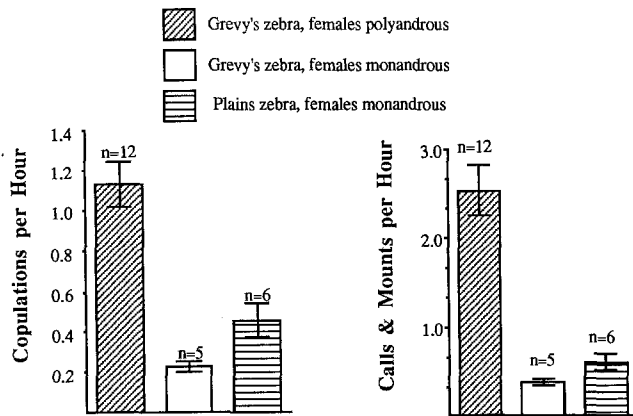
Association with estrus females

Male associations with females varied in length from hours to months. Plains zebra males were seen in association with particular females for a minimum of 9 months and a maximum of 26 months preceding the onset of estrus. Grevy's zebra males were seen in association with monandrous mares for a minimum of 3 days and a maximum of 59 days preceding estrus (18.1 ± 6.6 days). In contrast, Grevy's zebra stallions were observed in association with polyandrous females for a total duration of 1 to 48 h (12.1 ± 2.64 h).

Male mating behavior

Two variables were examined to measure the relationship between potential female promiscuity and male mating behavior: the frequency of copulation and the frequency of intercopulatory stimulation as measured by mounting and calling between successive copulations (Figs. 1, 2). Grevy's zebra stallions mating with polyandrous females mated more frequently and showed greater inter-copulatory stimulation than did Grevy's zebra stallions mating with monandrous females (copulations/hour: polyandrous 1.13 ± 0.11 , monandrous 0.23 ± 0.03 ; $t = 5.75$, $df = 15$, $P < 0.001$; calls and mounts/hour: polyandrous 2.54 ± 0.28 , monandrous 0.38 ± 0.03 $t = 5.29$, $df = 15$, $P < 0.001$). Grevy's zebra stallions mating with polyandrous females mated more frequently and showed greater inter-copulatory stimulation than did plains zebra stallions mating with monandrous females (copulations/hour: plains monandrous 0.46 ± 0.08 ; $t = 4.05$, $df = 16$, $P < 0.001$; calls and mounts/hour: plains monandrous 0.61 ± 0.08 ; $t = 4.69$, $df = 16$, $P < 0.001$). In the comparison between Grevy's monandrous and plains monandrous, Grevy's zebra stallions mated less frequently ($t = 2.96$, $df = 10$, $P < 0.05$) and showed lower investment in inter-copulatory behavior ($t = 2.74$, $df = 10$, $P < 0.05$).

If the five Grevy's zebra males observed copulating with both monandrous and polyandrous females are examined, the patterns observed are consistent with those observed in the sample as a whole; males copulated more frequently with polyandrous females ($t_{\text{paired}} = 4.6$, $P < 0.01$) and displayed higher levels of inter-copulatory behavior ($t_{\text{paired}} = 2.66$, $P < 0.05$).



Figs. 1, 2. Summary of parameters describing mating activity in the two zebra species. In the Grevy's zebra, 12 males were observed mating with polyandrous females; 5 of these males were also observed mating with monandrous females. Mating behavior was observed for 6 plains zebra males. Means were calculated for each male in each category and are considered independent points. Numbers presented are means \pm one standard error. Differences between Grevy's zebra polyandrous and monandrous are significant in both comparisons (copulations/hour: $t=5.75$, $df=15$, $P<0.001$; calls and mounts/hour: $t=5.29$, $df=15$, $P<0.001$). Differences between Grevy's polyandrous and plains monandrous are significant in both comparisons (copulations/hour: $t=4.05$, $df=16$, $P<0.001$; calls and mounts/hour: $t=4.69$, $df=16$, $P<0.001$). In the comparison between Grevy's monandrous and plains monandrous, there was a significant difference in both the rate of copulations ($t=2.96$, $df=10$, $P<0.05$) and in the number of calls per hour ($t=2.74$, $df=10$, $P<0.05$).

For matings with both polyandrous and monandrous females, we calculated the interval between the first and second copulations observed and the interval between the last and the penultimate copulation observed when at least four successive copulations were observed. In both cases, polyandrous females were remated much sooner than monandrous females (Fig. 3; minutes between first pair of copulations: polyandrous, 68.4 ± 26.2 ; monandrous, 208.0 ± 51.8 ; $t=6.1$, $P<0.01$; minutes between last pair of copulations: polyandrous, 109.2 ± 22.1 ; monandrous, 255.2 ± 42.6 ; $t=4.4$, $P<0.01$). When mating with polyandrous females, stallions showed an increased latency in the interval between the ultimate and penultimate matings when compared to the interval between the first and second matings ($t=2.6$, $P<0.05$). No significant difference was observed in a similar comparison of monandrous females. Despite an increased latency between successive mating with polyandrous females, the mean interval between the ultimate and penultimate copulation with polyandrous females was shorter than the mean interval between first and second matings with monandrous females ($t=3.4$, $P<0.01$).

Following mating, a large volume of seminal and/or vaginal fluids were observed to emanate from the vagina of female Grevy's zebra. Using the formula, volume = $\pi r^2 d$, where r is the radius of a cylinder and d is the depth, the volume of a single puddle resulting from this emission of fluids was estimated at 300 ml. No such emissions were observed in plains zebra.

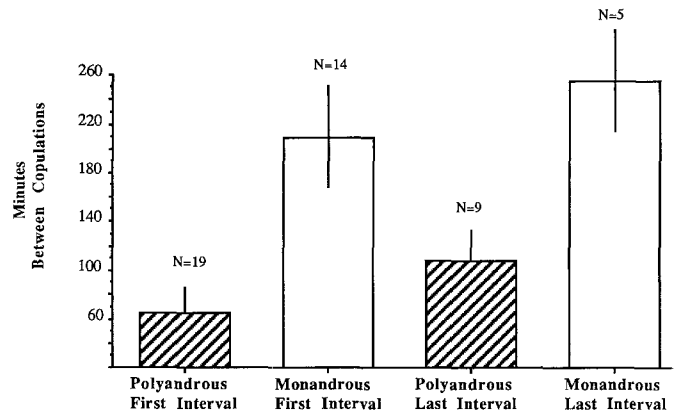


Fig. 3. A comparison of the interval between copulations. N = number of male/female pairs. First interval is defined as the interval between the first and second copulations observed. Last interval is the interval between the last and the penultimate copulation observed when at least four successive copulations were observed. In both cases, polyandrous females were remated much sooner than monandrous females (polyandrous first vs monandrous first: $t=6.1$, $P<0.01$; polyandrous last vs monandrous last: $t=4.4$, $P<0.01$). When mating polyandrous females, males remated the female more quickly after the first mating than after the penultimate mating (polyandrous first vs polyandrous last: $t=2.6$, $P<0.05$). Polyandrous females observed in the later stages of mating were remated more quickly than monandrous females on their first matings observed (monandrous first vs polyandrous last: $t=3.4$, $P<0.01$).

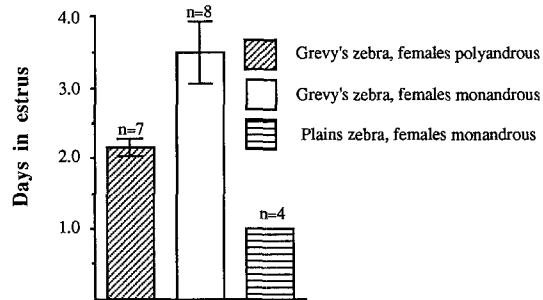


Fig. 4. Duration of estrus in polyandrous and monandrous zebra mares. Females were considered in estrus when sexually receptive: length of estrus included only for females observed on both the first and last day of receptivity. Differences between Grevy's zebra polyandrous and monandrous are significant (days in estrus: $U=45.5$, $n=7/8$, $P<0.05$). Differences between Grevy's polyandrous and plains monandrous are significant (days in estrus: $U=28$, $n=7/4$, $P<0.05$). Grevy's monandrous were in estrus significantly longer than plains monandrous ($U=27$, $n=4/8$, $P<0.05$).

Mating by males other than the territory owner

Matings by bachelor males have previously never been observed in either the plains or Grevy's zebra (Klingel 1974, 1969). In this study, 9% (9 of 101) of all Grevy's zebra copulations observed were "sneaked" by bachelor males or territorial males off their territories. These matings occurred with two polyandrous females. In all nine instances, sneak copulations were neither preceded nor

Table 1

Species	(a) Body Wt.	(b) Testes Wt.	(c) Mating	Source(a)	Source(b)	Source(c)
<i>Aepyceros melampus</i>	62.5	120	P	Haltenorth and Diller 1980	Skinner 1971	Jarman 1975
<i>Alcelaphus buselaphus</i>	132	107	P	Skinner et al. 1973	Skinner et al. 1973	Gosling 1986
<i>Alces alces</i>	789	106	M	Scadweiler and Stevens 1973	Peek 1962	Clutton-Brock et al. 1982
<i>Antidorcas marsupialis</i>	35	71	P	Haltenorth and Diller 1980	Skinner 1971	Smithers 1983
<i>Antilocapra americana</i>	61.7	76	P	Mitchell 1980	Mitchell 1980	Mitchell 1980
<i>Bison bonasus</i>	675	509	P	Hogg 1984	Hogg 1984	Nowak and Paradiso 1983
<i>Capreolus capreolus</i>	20.4	43	M	Short and Mann 1966	Short and Mann 1966	Clutton-Brock et al. 1982
<i>Capricornus crispus</i>	120	64	P	Tiba et al. 1981	Tiba et al. 1981	Nowak and Paradiso 1983
<i>Cervus canadensis</i>	280	220	P	Clutton-Brock et al. 1982	Clutton-Brock et al. 1982	Clutton-Brock et al. 1982
<i>Cervus elephas</i>	122	218	P	Mitchell et al. 1976	Mitchell et al. 1976	Clutton-Brock et al. 1982
<i>Connochaetes gnou</i>	136	137	P	Skinner et al. 1973	Skinner et al. 1973	Smithers 1983
<i>Connochaetes taurinus</i>	227	306	P	Ledger 1963	Watson 1969	Estes 1969
<i>Dama dama</i>	63.7	133	P	Chapman and Chapman 1970	Chaplin and White 1972	Clutton-Brock et al. 1982
<i>Damaliscus dorcas</i>	72.5	160	P	Haltenorth and Diller 1980	Skinner 1971	Lynch 1974
<i>Elephas maximus</i>	4545	4000	P	Shulte 1937	Shulte 1937	Eisenberg et al. 1971
<i>Equus burchelli</i> ^a	238	302	M	Foster and Coe 1968	Smuts 1976	Klingel 1969
<i>Equus caballus</i>	450	416	M	Cox 1982	Cox 1982	Berger 1986
<i>Equus grevyi</i>	386	1150	P	Ledger 1964	King 1965	Klingel 1974
<i>Equus zebra</i>	298	140	M	Joubert 1971	Penzhorn and van der Merwe 1988	Joubert 1971
<i>Giraffa camelopardalis</i>	1201	1074	P	Hall-Martin et al. 1978	Hall-Martin et al. 1978	Kingdon 1972
<i>Hippopotamus amphibius</i>	1600	650	M	Laws and Clough 1966	Laws and Clough 1966	Kingdon 1972
<i>Hylochoerus meinertzhageni</i>	202	500	P	Parkes 1966	Parkes 1966	Kingdon 1972
<i>Kobus defassa</i>	243.2	148	M	Ledger 1964	Spinage 1969	Wirtz 1983
<i>Kobus kob</i>	90	130	P	Buechner et al. 1966	Buechner et al. 1966	Buechner 1974
<i>Loxodonta africana</i>	4365	4530	P	Johnson and Buss 1967	Johnson and Buss 1967	Moss 1983
<i>Madoqua kirki</i>	5	8.4	P	Kellas 1954	Kellas 1954	Kingdon 1972
<i>Odocoileus hemionus</i>	112	87	M	Anderson et al. 1971	Anderson et al. 1971	Clutton-Brock et al. 1982
<i>Odocoileus virginianus</i>	71	76	M	Scanlon and Lenker 1983	Scanlon and Lenker 1983	Clutton-Brock et al. 1982
<i>Ovis canadensis</i>	122	338	P	Hogg 1984	Hogg 1984	Hogg 1984
<i>Phacocoerus aethiopicus</i>	88	93	M	Ledger 1964	Mason 1986	Kingdon 1972
<i>Rangifer tarandus</i>	145	132	P	Leader-Williams 1979	Leader-Williams 1979	Clutton-Brock et al. 1982
<i>Sus scrofa</i>	172	36	M	Hunter 1975	Hunter 1975	Frädriich 1974
<i>Tayassu tayacu</i>	12.3	11	P	Knepp 1939	Knepp 1939	Sowls 1966
<i>Tragelaphus strepiceros</i>	248	92	M	Haltenorth and Diller 1980	Skinner 1971	Owen-Smith 1984

^a Includes weight of epididymides

followed by mounting, chasing, or calling. Having achieved intromission and ejaculation, sneaky males abandoned females and did not attempt to remate. Given these differences in behavior, "sneak" copulations were excluded from the above comparisons.

Duration of estrus

Polyandrous Grevy's zebra mares remained in estrus for significantly fewer days than did monandrous Grevy's zebra mares (Fig. 4: polyandrous, 2.15 ± 0.12 days;

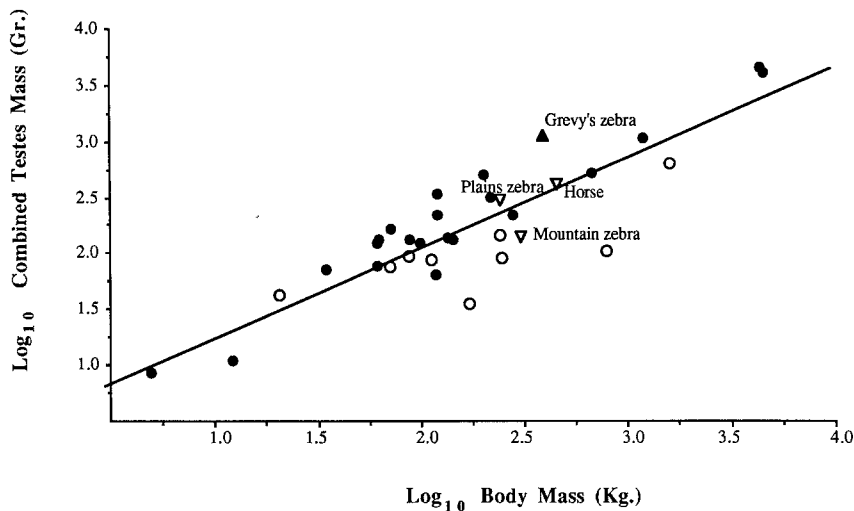


Fig. 5. Plot of paired testes weight as a function of bodyweight for 35 species of ungulates. Species in which females are usually polyandrous (●) have significantly heavier testes than those in which are females are usually monandrous (○) (Evolutionary Covariance Regression $df=1.14$, $F=13.866$, $P<0.01$). The Grevy's zebra (*E. grevyi*) shows unusually large testes for their body size when compared to all three species of congeneric monandrous equids: the horse (*E. caballus*), the plains zebra (*E. burchellii*), and the mountain zebra (*E. zebra*). Regression equation: $y=0.81x+0.42$; $r^2=0.77$

monandrous, 3.5 ± 0.42 days; $U=45.5$, $n=7.8$, $P<0.05$). Plains zebra mares were observed in estrus for significantly fewer days than either type of Grevy's zebra mare (plains monandrous, 1.0 day: vs polyandrous Grevy's zebra $U=28$, $n=7/4$, $P<0.05$; vs monandrous Grevy's zebra $U=27$, $n=4/8$, $P<0.05$).

Combined testes weight, body size, and mating system

Data were collected from the literature for 35 species of ungulates in 24 sub-Families on combined testes weight in grams, body mass in kilograms, and the potential for female promiscuity (polyandrous or monandrous, Table 1). When the allometric effects of body size are controlled, testes weight is significantly greater in species in which females are usually polyandrous (Fig. 5: Evolutionary Covariance Regression $df=1.13$; $F=13.55$, $P<0.01$). This result is not confounded by differences among taxa because the ECR tests comparative hypotheses within each taxon. The Grevy's zebra has unusually large testes for its body size when compared to all three species of congeneric monandrous equids: the plains zebra, the horse (*E. caballus*), and the mountain zebra (*E. zebra*). No data were available on the other polyandrous species, *E. asinus* and *E. hemionus*, the asses.

Discussion

In zebra, intra- and interspecific differences in female behavior during estrus gives rise to variability in the opportunity for sperm competition: some females are monandrous while others are polyandrous. We show that variability in male copulatory behavior is correlated with the nature and duration of male-female consortships. Data presented in Fig. 1 show that when a Grevy's zebra male associated with a polyandrous estrus female, he copulated twice as frequently as when consorting with relatively sedentary monandrous females. Grevy's zebra territorial males consorting with polyandrous females

also copulated at a higher frequency than the congeneric plains zebra males, which normally consort with monandrous females. When in consort with monandrous females, Grevy's zebra stallions mated even less frequently, however, than did plains zebra stallions. Similar differences are also observed in comparing pre- and post-copulatory behavior. Perhaps most striking, Grevy's zebra stallions called and mounted polyandrous females at a frequency approximately seven times greater than that exhibited when consorting with monandrous females.

Intraspecific differences in Grevy's zebra male copulatory behavior are not the result of individual differences among males (e.g., age, experience). By comparing a sub-set of the data from only males that mated with both polyandrous and monandrous females, the patterns observed are similar to those observed in the population as a whole. Males copulated more frequently with polyandrous females and showed higher levels of inter-copulatory behavior.

Grevy's zebra stallions mating with polyandrous females did show an increase in the interval between matings with repeated copulations (Fig. 3). Because the length of time spent in association with monandrous females greatly exceeds that spent in association with polyandrous females, changes in male mating behavior could be the result of increased latency to ejaculate with successive matings. Our data suggest that this is unlikely. Even after relatively frequently repeated ejaculations, stallions remated polyandrous mares much more quickly than they did after the first observed mating with monandrous females.

The reproductive behavior of other members of the genus *Equus* is consistent with the differences seen when comparing the Grevy's and plains zebra. Female asses (*E. asinus*), like the Grevy's zebra, are polyandrous (Moehlman 1974). Breeding males are usually, but not always, territorial. The competition for mates and the potential for sperm competition is extreme. The time between successive copulations by a single male when mating a multiply mated female was even shorter than that of the Grevy's zebra (3 to 23 min Moehlman 1974,

p. 223–227). Between copulations, males sniff female genitalia, bray and “drive,” or herd the female (Moehlman 1974, p. 223–227) in a pattern similar to that exhibited by the Grevy’s zebra when mating with polyandrous females.

Horses (Berger 1986; Tyler 1972) and mountain zebra (Penzhorn 1985; Joubert 1971), like the plains zebra, breed in fixed membership, uni-male groups. Females are monandrous and sperm competition is unlikely. Joubert (1971) notes that males exhibit little or no pre- or post-copulatory behavior. Although no quantitative measures of mating frequency are given, mating occurs at intervals greater than 1 h (Joubert 1971). In the horse, little pre- or post-copulatory behavior was observed (Tyler 1972).

While the function of multiple ejaculation may be obvious, the function of mounting with or without intromission, neither of which results in ejaculation, is less so. Four hypotheses have been suggested for the adaptive value of such behavior (Dewsbury 1981): (1) excess stimulation is required for ejaculation; (2) a series of short copulatory bouts, leading to ejaculation, minimize predation risks; (3) intromission and thrusting remove copulatory plugs and sperm; (4) stimulation is required for, or accelerates, pregnancy initiation. The pattern of inter-copulatory mounts in zebra allows us to examine the validity of several of these hypotheses. First, Grevy’s zebra males, especially bachelors, when “sneaking” copulations can, and do, ejaculate without pre- or inter-copulatory mounting. This suggests that males do not *always* require extra stimulation. Nevertheless, extra stimulation might be helpful after a series of copulatory bouts. Second, since multiple mounts and intromissions are not necessary for ejaculation, any extra mounts necessarily increase, rather than decrease, predation risks. Third, copulatory plugs have not been reported in equids. While the large ejaculate volume in the Grevy’s zebra may be a mechanism for displacing the sperm of other males, thrusting alone did not displace previously deposited sperm.

Of the four hypotheses, only the one suggesting that multiple matings function to enhance fertility can in part be supported by the data. Physical stimulation has been shown to advance estrus in a large number of mammals (Jöchle 1975). And at least in the Golden hamster, extra vagino-cervical stimulation is required for females mated during or after ovulation to prevent declines in fecundity (Huck et al. 1986). Grevy’s zebra males do provide significantly more stimulation to, and estrus is significantly shorter in, polyandrous as opposed to monandrous females (Fig. 4). Thus this behavior may help increase a male’s probability of paternity by reducing a subsequent male’s fertility. Increased calling by males is also associated with increased mounting frequency, however, (Fig. 2). And if, as observed in red deer (*Cervus elephas*; McComb 1987), frequent vocal stimulation advances estrus, then increased vocalizing may also be involved.

Apart from these hypotheses concerning the function of multiple matings, it may be that the most important factor in determining a male’s chances of “winning” a sperm competition when mating with polyandrous fe-

males is simply the number of sperm he provides (Ginsberg and Huck 1989). If the probability of paternity is a function of the number of sperm provided, then evolution should favor males with the capacity to produce large volumes of sperm. Sperm production is proportional to testis size (Willet and Ohms 1957) and in various ways to the presence of elevated levels of testosterone (van Tienhoven 1983), and the amount actually delivered is proportional to the number of ejaculations. In both species of zebra, breeding stallions have been shown to maintain higher levels of testosterone when compared with non-breeding males (Chaudhuri and Ginsberg 1989). Relatively larger testes have been found in promiscuous species of primates (Harcourt et al. 1981), cervids (Clutton-Brock et al. 1983), and mammals from elephants to mice (Kenagy and Trombulak 1986). In polyandrous primate species, males have disproportionately large testes and produce larger ejaculates with higher densities of motile sperm (Møller 1989). Penzhorn and van der Merwe (1988) note that equids show large variation in testis size, and that this variation appears correlated with female promiscuity. Our data confirm this observation and suggest that among ungulates, Grevy’s zebra have evolved particularly large testes (Fig. 5).

Large testes provide the ability to produce larger numbers of sperm. Although, there is some evidence that male mammals can control the number of sperm in each ejaculate when intercopulatory intervals are not too short (Baker and Bellis 1989), delivery of large numbers of sperm will most often be mediated by the frequency of copulation. Interspecific studies of the great apes (Short 1979; Harcourt et al. 1981) have shown that males mate more often and more vigorously when females are polyandrous. The same pattern appears even within a given population of ungulates. In bighorn sheep (*Ovis canadensis*), copulatory bouts involving promiscuous females tend to be scheduled immediately after those of subordinate males (Hogg 1984, 1988). And in water buck (*Kobus ellipsiprymnus*) even though only a small proportion of females were polyandrous (9%), in situations in which polyandry was likely, males were more likely to mate repeatedly with an estrus female (Wirtz 1983).

The large testes of the Grevy’s zebra, a species in which females typically mate polyandrously, appear to be an evolutionary response to the high potential for sperm competition. This morphological change appears to have occurred quickly. The evolutionary divergence of the plains zebra and the Grevy’s zebra has occurred relatively recently; in five of six different phylogenies of modern equids, the usually polyandrous Grevy’s zebra is shown to be more closely related to the monandrous plains zebra than to any other extant equid species (George and Ryder 1986). The potential for such rapid evolutionary change in testicular size can be inferred from breeding experiments involving domestic ungulates (Toelle et al. 1984; Neeley et al. 1982). These experiments show that variation in testicular size is highly heritable and can be rapidly manipulated through artificial selection. Thus like many secondary sexual characters,

primary sexual characters such as testis size appear to be extremely labile and offer the potential for rapid evolutionary change.

Given that males have evolved the physiological capacity to produce a large ejaculate volume with great frequency, why do Grevy's males mate less frequently with monandrous females? There are two possible, but not mutually exclusive explanations. On the one hand, mating behavior imposes costs, both temporal and energetic. Time spent in copulatory and pre-copulatory behavior may reduce the time available for performing other critical activities such as feeding and vigilance; hence, a decrease in copulatory behavior that does not reduce a male's probability of paternity will increase time available for other activities. On the other hand, sperm may not be cheap to produce (Dewsbury 1982). If sperm can be limiting, conserving sperm when mating with monandrous females assures the availability of sufficient sperm to mate with polyandrous females. Although a male can not facultatively reduce ejaculate volume, he can reduce the total volume of sperm provided to a particular female by reducing the number of ejaculates. Facultative reduction in sexual behavior when breeding with monandrous females suggests that Grevy's zebra males reduce the cost of breeding when paternity certainty is high. They may do so to hedge their bets against the need to sequentially breed with other females.

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