13. Ecology and Sociality in Horses and Zebras

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FOR A FAMILY containing only seven species, the Equidae show a remarkable diversity of social systems. Horses (*Equus przewalskii* and *E. caballus*), plains zebra (*E. burchelli*), and mountain zebra (*E. zebra*) typically live in closed membership harem groups consisting of adult females, a single adult male, and their young (Klingel, 1974). In contrast, Grevy's zebra (*E. grevyi*) and the asses (*E. africanus* and *E. hemionus*) typically exhibit social systems in which female bonds are more ephemeral. Temporary aggregations of one or both sexes are common, but most adult males live alone in large territories (Klingel, 1974). Even though in both systems the young of both sexes reside with mothers until reaching sexual maturity and excess nonbreeding males live in all-male "bachelor" groups, in each details of these adult-juvenile and male-male relationships differ dramatically. The aim of this chapter is to show why these differences in social relationships have evolved in horses and zebras. Explanations relying on differences in niche or phylogenetic heritage are not likely to be important since horses and zebras are members of the same genus and make a living in more or less the same way, by grazing.

The social system of any species is shaped by the environment. As environmental forces change, group sizes, spatial dispersion, and mating systems also change. For example, Macdonald (1983) has shown that the size of fox groups increases as availability of prey increases; Gill and Wolf (1975) have shown that golden-winged sunbirds defend territories when flowers contain certain nectar levels but abandon the defense of resources after nectar levels reach a higher critical concentration; and Orians (1969) has shown that birds switch between monogamy and polygyny depending on the richness and patchiness of the resource. How this shaping process operates will depend on how environmental forces affect the behavioral "decisions" of individuals attempting to increase their reproductive success. Understanding how the process operates is likely to be complicated. There are many behavioral trade-offs, many environmental pressures pushing in different directions, and many differences among individuals constraining the behavioral options of some while altering the ecological perceptions of others. Moreover, every individual can potentially interact with every other member of the population and in ways that can range from ex-

tremely competitive to extremely cooperative. In order to understand how ecological circumstances shape social organization, a limited number of key paths through this maze must be found. By examining only a subset of social relationships—female–female, male–male, male–female, and breeder–nonbreeder—the major interactions can be described, and then examined to see how they are shaped by social and ecological pressures. In the next section a general model delineating how environmental forces structure these relationships is presented. It is then used to examine how particular environmental pressures shape horse and zebra sociality.

A GENERAL MODEL

Alexander (1974) proposed that living in groups was inherently disadvantageous. Costs associated with disease transmission and intensified competition automatically occurred and tended to increase as group size increased. To overcome these disadvantages at least one of three conditions had to be met. Group living either reduced an individual's chance of being preyed upon, enchanced feeding success, or was an unavoidable consequence of extremely localized resources. For ancestral horses and zebras the need to avoid being eaten was probably the major force leading to sociality. Even under contemporary conditions Schaller (1972) has shown that of all predatory attacks on zebra by lions, 35 percent were successful when zebras were solitary, whereas only 22 percent were successful when zebras lived in moderate-sized groups. But the need to reduce predation cannot be the sole ecological force shaping the social systems of horses and zebras today: no horses suffer predation yet all live in groups. Fulfilling other needs, such as acquiring food, water, and mates may also influence social relationships. But as Gakathu (1980) has shown, the interaction among ecological pressures may be strong. In Ambosoli Park, as the dry season commences, the plains zebra leave the bushy grasslands to graze on the more open plains. Given that vegetation quality on the plains is inferior to that of woodlands, and that quantity is lower than that of the swamp, their grazing movements seem surprising. But only if one ignores the fact that the number of predators is lowest on the plains and highest in the woodlands.

As Figure 13.1 shows, three ecological pressures, the need to avoid predators, and the needs to acquire food and water, can potentially affect female–female, male–female, and male–male social relationships. How they do so depends on: 1) major differences in the reproductive interests of males and females, and 2) a number of environmental and phenotypic constraints. The former influences the overall structure of the relationships, whereas the latter, by adjusting individual rankings of the ecological pressures, influences the magnitude and form of the relationships.

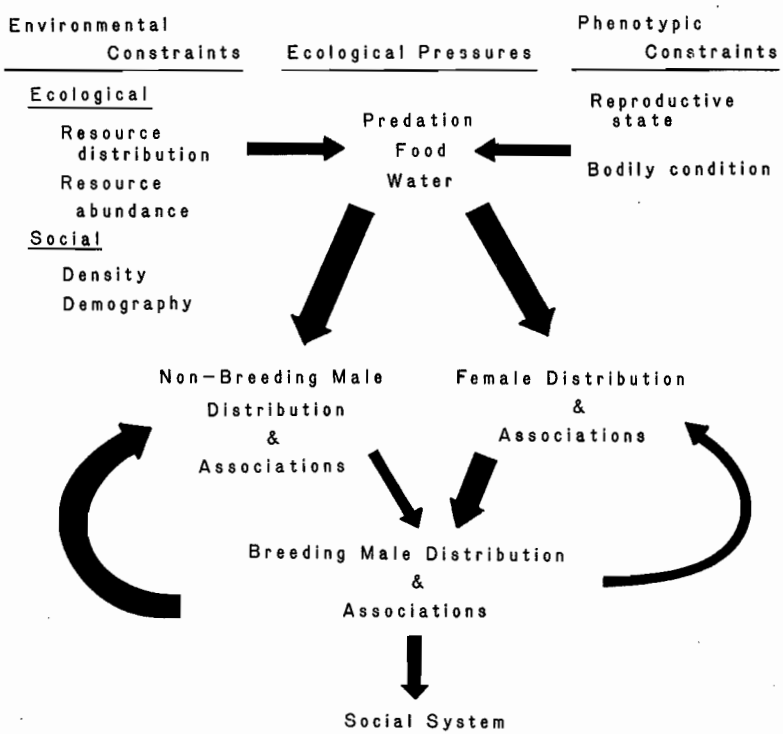

Fig. 13.1. Model of ecological pressures influencing intra- and intersexual relationship in mammals. Arrows depict social relationships and the width is proportional to relative importance.

Sex and Reproductive Strategies

According to Darwin (1871) investment in different reproductive activities will often have different consequences for each sex, especially in mammals. For males, reproductive success is usually limited by the number of progeny sired (Trivers, 1972). Reproductive effort put into acquiring mates will often have more effect on fitness than effort put into seeking food, water, or safety from predators. While it is true that males must eat and drink in order to maintain bodily condition, once a sufficient level has been reached, natural selection will favor subsequent investment into mating activities (Trivers, 1972). For females, the usual situation is different. Reproductive success is rarely limited by number of matings (Bateman, 1948; Trivers, 1972). Rather it is constrained mostly by the ability to acquire food, water, and find safe areas for offspring. Given these sexually differentiated reproductive interests, the ecological pressures exert a more direct effect on shaping female, rather than male, interactions. Consequently, as Figure

13.1 shows, female associations and distributions should be most strongly tied to resource distributions and abundances, whereas those of adult reproducing males are more tied to the distributions and abundances of females. This sexual dichotomy does not imply that females cannot augment fitness by investing in mating activities. Effort in discriminating among males can always enhance a female's reproductive success as long as males differ in attributes that enhance the condition or survival of the female or her offspring, or provide the offspring with superior genes (Bateson, 1983). Thus, as the loop in Figure 13.1 shows, male distributions and associations can potentially shape female-female interactions.

Environmental Constraints

The nature of the physical environment affects the operation of each ecological pressure listed in Figure 13.1. For example, when predators are concentrated, the need to reduce, or dilute, one's risk of being eaten favors joining groups (Pulliam, 1973; Triesman, 1975; Bertram, 1978; Rubenstein, 1978). Similarly, when food or water is concentrated in large patches, grouping is facilitated because competition is reduced (Jarman, 1974; Bertram, 1978; Rubenstein, 1978). But deciding how to behave when both pressures operate can be complicated, especially when the effects of food distribution oppose those of predation. Pulliam (1973) has shown that the conflict is reduced somewhat since scanning by others can lower vulnerability while allowing more time to be devoted to feeding. Nevertheless, the optimum level of each activity depends on the intensity of competition in relation to the probability of being eaten. Actual resource distribution affects these levels, but so does the social environment (Fig. 13.1). The size of a population, and its demography (e.g., operational sex ratio), determine the relative shortages of ecological resources and mates (Emlen and Oring, 1977). Since scarce resources are rarely apportioned equally among members of a population (Wilbur 1977; Rubenstein 1978, 1981a, b; Begon, 1984), phenotypic differences also alter the balance among an individual's behavioral options.

Phenotypic Constraints

More than anything else, phenotypic differences affect how individuals rank the environmental pressures. Among females, differences in reproductive condition alter dietary needs and susceptibility to predation. Maintaining bodily condition is important for survival, embryo development, and the raising of young to independence. Often, however, both quantitative and qualitative dietary requirements change throughout the reproductive cycle. While pregnant and nonpregnant, nonlactating females may place a premium on acquiring large quantities of high-quality vegetation, lactating females may place a premium on acquiring both food and access to predator-

free sources of water. If the distribution of high-quality food and safe water do not coincide, then different reproductive classes of females may be distributed in different areas. Depending on the fertility of females found in the different locations, the effects of female reproductive condition on male associations and distribution might be dramatic.

Social relationships are also affected by differences in body size and condition, especially among males. Both vulnerability to predation and dietery requirements scale with body size. All else being equal, smaller species and smaller individuals are exposed to a wider range, and higher intensity, of predation. They also require smaller quantities, but higher qualities of food than larger species (Jarman, 1974). Thus size differences should lead to differences in feeding and antipredator behavior.

Among males the social consequences of body size are even more profound. Given the high variance in male reproductive success, sexual selection favors superior competitors, which usually are the largest or strongest males (Geist, 1974; Clutton Brock and Albon, 1979). For smaller, or poorer conditioned males the chances of obtaining matings by employing aggressive tactics is so low that selection favors delaying reproduction and the channeling of energy into rapid growth, or adopting alternative mating strategies (Gadgil, 1972; Rubenstein, 1980; Dunbar, 1982b). For these males acquiring forage and water might take precedence over acquiring mates. Depending on population size and demography, a variable number of youngish males will be induced to oust reproducing males. Thus associations and distributions among the nonbreeders might affect relationships among reproducing males (Fig. 13.1). Too often this effect is ignored, and exclusive emphasis is placed on the effects that reproductive males have on the "surplus" or "bachelor" males (e.g., the male-male loop in Fig. 13.1).

In summary, the model in Figure 13.1 provides a framework that delineates how the major types of social relationships are connected both to each other and to environmental pressures. How these pressures determine the details of each social relationship depends on constraints imposed by the nature of the environment and the distribution of phenotypes. In the next few sections the social relationships of horses and zebras are examined in relation to particular interactions among these constraints.

STUDY SITES AND METHODS

Behavioral and ecological observation on free-ranging feral horses have been carried out on Shackleford Banks, a barrier island off the eastern coast of North America, since 1973. Those on both common and Grevy's zebras were made in 1980 in the Samburu-Buffalo Springs Game Reserves of northern Kenya.

Whenever horses or zebras were encountered they were identified individually by morphological features such as coat color, position of the mane, presence or absence of distinctive facial markings, or stripes. Each individual's activity patterns, associations, and location were noted. Bodily condition was estimated by examining the loin area for amount of fat (sensu Mulvany, 1977; Pollock 1980). In well-conditioned horses (score = 5) the line of muscle on either side of the lumbar vertebrate appears flat when viewed from behind. As condition deteriorates the muscle takes on a triangular shape and eventually becomes concave (condition = 1). Detailed observations of interactions were monitored by focal animal sampling (Altmann, 1974). Vegetation was characterized into zones and the biomass and protein content of individual species was measured periodically. Data were analyzed using standard statistical tests (Sokal and Rolf, 1969).

THE ROLE OF ENVIRONMENT: A STUDY ON HORSES

The way environmental forces affect equid social relationships is most easily demonstrated by a population of horses inhabiting Shackleford Banks, a barrier island off the eastern coast of the United States. Of the three potential ecological pressures, only one, the need to acquire vegetation, is of any importance since there are no predators on the island and during most seasons fresh water is abundantly and evenly distributed along the northern edge of the island.

The island is approximately fifteen kilometers long and ranges in width from one to one and a half kilometers. Two features make the island unique. One is that its horses exhibit a variety of different types of adult association patterns. Some females form long-lasting bonds with other females and live in closed membership groups, whereas others form more ephemeral bonds and live in temporary membership groups. As for males, some wander widely, never attending a particular female for more than a few weeks, whereas others tend females continuously, thus forming harems. Some of these harem-forming males also establish territories, which they demarcate with dung and defend vigorously (Rubenstein, 1981c). The second is that each of the adult association patterns is limited to a region of the island that is ecologically unique in terms of habitat structure as well as vegetation abundance and distribution.

Female–Female Relationships

On the eastern end of the island there are three major vegetation zones: low-lying dunes border the ocean, a narrow salt marsh borders the back sound, and a swale or grassland lies between the other two. Each is fairly continuous and runs the length of the island (Fig. 13.2). At this end of the

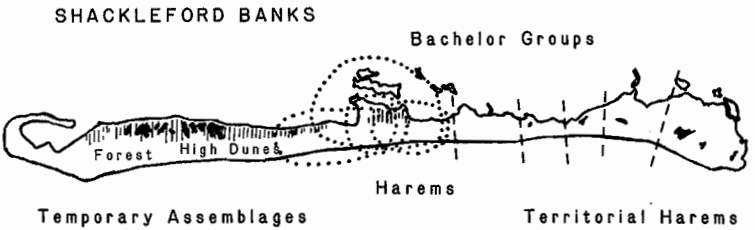

Fig. 13.2. Map of Shackleford Banks. Black areas represent fresh water and hatched areas represent forest. Dashed lines are territorial boundaries and dotted lines are home range boundaries. The western end of the island is on the left of the map; the east on the right.

island females live in permanent associations. Group movements are well coordinated and affiliative bonds among females, as measured by preferred grooming partners, are strong. Female dominance relationships exist, but are rarely expressed.

On the western end of the island the ecological situation is different. Tall dunes cover virtually the entire area except where they merge with a dense maritime forest. Swale occurs only in patches among the dunes, and some are no more than ten meters in diameter. Similarly, the marsh is restricted to small pockets that punctuate stands of forest. At this end of the island there are no permanent associations among females or males. Females leave or enter aggregations depending on patch size. When the patches are relatively large, groups grow as smaller groups fuse. But as soon as aggregations move to smaller patches, fissioning occurs. Such fission–fusion dynamics prevent permanent long-term associations from forming among females. As a result no strong grooming network or dominance hierarchy has appeared.

The existence of these two different patterns of female–female relationships is not easily explained. Grass is a resource that does not generally foster competition. Where it occurs it is relatively densely distributed, and one blade is not that much different from another, even if its neighbor is of a different species. Females should be able to associate for long periods, unless the overall structure of the habitat intensifies competition by reducing overall vegetation abundance or by partitioning the grassland into fragments too small to support average-size groups. On the western end of Shackleford patches of the swale and marsh grasses are few and variable in size and this explains why long-term associations are prevented. On the eastern end, however, the habitat is more continuous and could facilitate long-term associations. But showing that there is an environmental potential for closed membership groups is not the same as explaining why females live in them, especially since low levels of competition still occur, and there are also

costs of intensified endoparasitism (Hohman and Rubenstein, in prep.). Phylogenetic inertia could serve as one explanation. Although not adaptive under current conditions horses could still live in closed membership groups because in the past, when predators were abundant, the only way of ensuring that one's susceptibility was lowered was continuously to associate with others. By moving among open membership groups the possibility of being alone always remains. Given that some horses on Shackleford have already abandoned living in closed membership groups, the strength of this force seems limited. A more likely explanation is that females in closed membership groups derive some benefit that females in open membership groups do not. Such an advantage appears to exist, but is dependent on the nature of male–female relationships.

Male–Female Relationships

Given two distinct female distribution and association patterns, it is not surprising that there should be two different male–female relationships. What is interesting is that there are actually three: 1) single males tend single females, 2) single males tend groups of females, and 3) single males defend territories and tend groups of females. By comparing the benefits that females obtain from each of these sexual relationships it is possible to show that females living in closed membership groups derive an advantage that those living in open membership groups do not.

In theory males only have four behavioral options. They can either: 1) wander and tend individual females when they are in estrus; 2) tend groups of females, some of which are in estrus whereas others are not; 3) defend the resouces that females require; or 4) defend places along routes that females must travel in order to obtain critical resources. According to Emlen and Oring (1977), the behavior a male exhibits depends on the spatial and temporal distribution of females and resources. On the western end of Shackleford, where neither resources, females, nor the routes over which they travel are predictable, males have no alternative but to wander in search of estrus females and tend them when they can. As Figure 13.3 shows, the cost of this strategy, as measured in rates of aggression, is prohibitive. This option is almost always higher than the other strategies and shows no tendency to decline with age.

On the eastern end, tending groups of females is an alternative that all fully mature, reproducing males adopt. As Figure 13.3 demonstrates, the rate of aggression of this strategy is significantly lower than that of tending single females. But some males have modified this strategy. Not only do they defend females but they also defend an exclusive zone around their group of females. As Figure 13.2 shows, two-thirds (four of six) of the harem males defend the boundaries of the group's home range. Surprisingly, the costs of keeping other males far away from all his females are never as

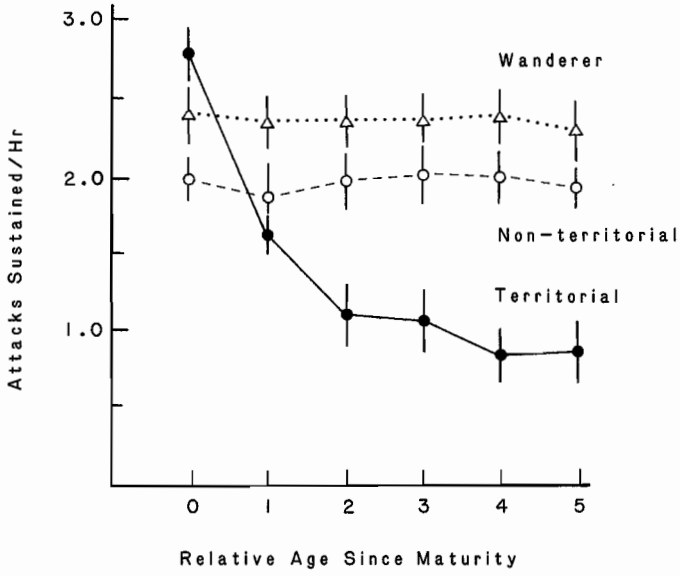

Fig. 13.3. Costs of aggression. Males tending individual females (Δ); males tending female groups (○); males tending female groups and defending territories (●). Two territorial, seven nonterritorial, and three wander males were observed each for at least one hundred hours over five years. Mean ± standard error.

high as those incurred by males tending individual females, and with age drop below those of males defending harems with overlapping home ranges. Only the most dominant stallions become territorial.

Ecological and demographic features of Shackleford account for these surprising cost relationships. First, the absolute number of potential intruding males is low because there are twice as many adult females on the island as there are adult males (Rubenstein, 1981c). High rates of juvenile male mortality and high rates of reproductive female mortality (Rubenstein, in prep.) account for this female-biased sex ratio. Second, approximately half of each territory is bounded by water. This severely limits access by intruding males (Rubenstein, 1981c). Third, the extreme openness of the habitat facilitates detecting intruders at a distance. And fourth, the ranges of bachelor males overlap only with those of nonterritorial males. All these factors contribute to lowering the long-term costs of establishing and maintaining a territory.

The advantages of territorial control do not stop at lowering a male's costs. In fact, as Figure 13.4a shows, the ultimate evolutionary measure of

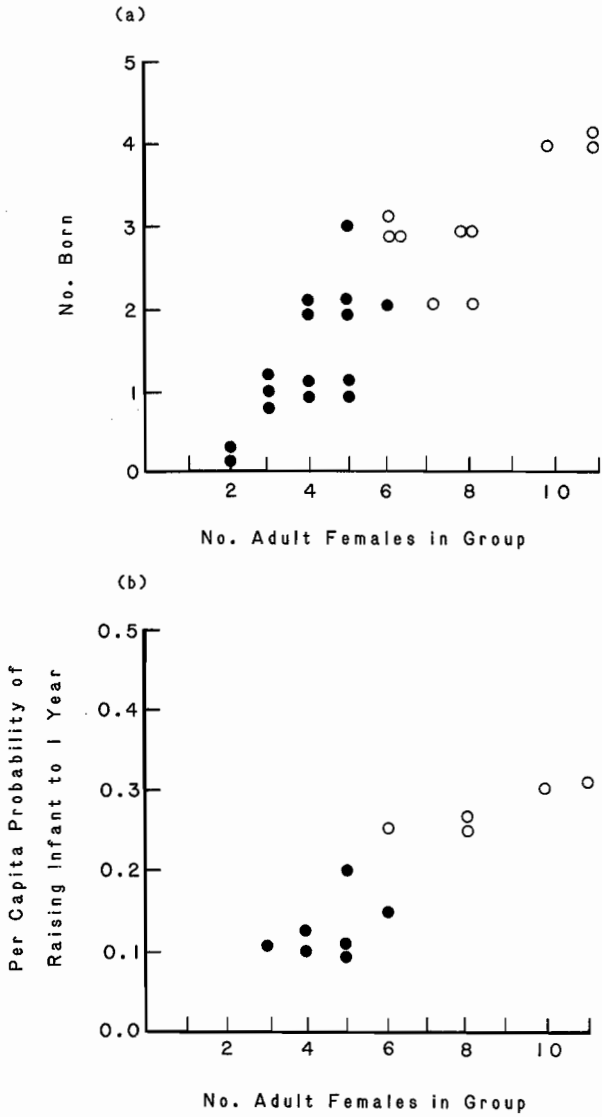

Fig. 13.4. Male and female reproductive success, (a) males, (b) females.
(a) male success—measured by number of young born per group where groups differ in number of adult females residing there. No. born = 0.40 (no. adult females per group) − 0.22; $F_{1,23} = 71.9; p < .001$.
(b) female success—measured by the probability of each female's likelihood of bearing a young and rearing it to independence (one year old). Per capita probability = 0.03 (no. adult females per group); $F_{1,10} = 43.0; p < .001$.
● nonterritorial harems vs. ○ territorial harems.

success, reproductive success, increases when males defend territories. On average, territorial males sire more offspring than nonterritorial males largely because they have more adult females in their groups. Since both sexes disperse from the natal group in the Equidae, these increases cannot be the result of success in previous breeding seasons. For equid groups to grow, females must move to the territorial areas and then restrict their movements in order to remain within the territories. As the loop in Figure 13.1 suggests, females are responding directly to male distributions and associations.

The benefits for females of monitoring differences among males and adjusting their behavior accordingly are many. First, territorial females derive a feeding benefit. Females consistently require large quantities of high-quality vegetation if they are to survive, reproduce, and raise a foal to the age of independence. On average, horses on Shackleford feed for 70 percent of every hour during the summer and up to 80 percent of every hour during the winter (Rubenstein, 1981c). Despite this extensive commitment to foraging, the most frequent cause of death can be ultimately linked to malnourishment. All individuals are scored for bodily condition by examining the loin area for amount of fat (sensu Mulvany, 1977; Pollock, 1980). Among all Shackleford adults the average condition score is 2.8, whereas the average of the last score recorded before death for dead animals is 1.4. Although the difference was significant ($t_{17} = 2.73; p < .01$), it is possible that death was caused by some other factor that also caused condition to deteriorate. To account for this possiblity, the condition scores from one year prior to death were examined, and, again, the average value of 1.7 is significantly lower ($t_{16} = 2.02; p < .05$) than the average of overall population's score. In addition, nursing mothers show significantly lower condition scores ($\bar{x} = 2.0$) than do other females ($\bar{x} = 3.1; t_{23} = 2.96; p < .005$), and for mothers losing foals the score is significantly lower still ($\bar{x} = 1.7; t_7 = 2.91; p < .05$). Thus food limitation is a significant problem that has consequences for female longevity and reproductive success.

To measure whether females residing in territories derive a feeding benefit because of exclusive control of a renewable resource (cf. Davies and Houston, 1981), vegetation regeneration rates were measured. Sample plots (1 m^2) in the open swale in both the ranges of territorial and nonterritorial horses were marked with hollow aluminum pegs. A square grid of wires spaced at five-centimeter intervals along both the x and y axes was placed on each plot. The height of each grass blade lying directly beneath the intersection of every pair of wires was recorded at two-week intervals. Figure 13.5 shows that during these intervals about 50 percent of the vegetation grew on average between one and three centimeters within territories, whereas within ranges that overlap with those of others, about 50 percent of the grass grew less than one centimeter during the same two-week period.

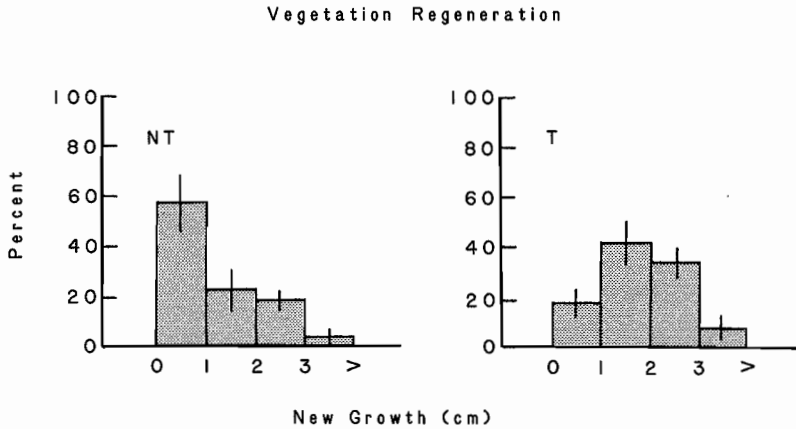

Fig. 13.5. Vegetation regeneration. Regrowth of *Spartina patens* at two-week intervals for ten weeks during spring and summer 1976. N = 1,000 for both territorial (T) and nonterritorial (NT) plots. Mean ± standard error.

At least with respect to swale vegetation, territorial females can expect to acquire more vegetation per mouthful than their counterparts that live in nonterritorial harems, or even open membership groups where home ranges also overlap.

A second advantage of living with territorial males is that harassment by *all* males is reduced. When males are grazing, or are on the lookout for intruding males, they monitor the estrus condition of their females. They also attempt to control the position and movements of their females, often with limited success, and they invade foreign groups in search of estrus females. These male activities interrupt the behavior of females, those both in and out of estrus. Since males are not discriminating in their sexual investigations, escape attempts by harassed females usually disrupt the behavior of nearby females. Table 13.1 shows the magnitude of the direct and indirect effect of male harassment; females residing with territorial males suffer significantly fewer disruptions than females residing with a nonterritorial male. An analysis of time budgets (Fig. 13.6) shows that the consequences of harassment are strikingly different for territorial and nonterritorial females. Territorial females graze about 9 percent more per hour than nonterritorial females, and this increase occurs despite the fact that territorial groups of females are larger and should suffer reductions in grazing time because of intensified female–female competition. Not only is the difference statistically significant ($p < .001$), it is biologically significant as well. A gain of about 5½ minutes per hour, when summed over the twenty to twenty-two hours a day

TABLE 13.1
Average hourly rate of interruptions sustained by an individual female during the breeding season, and caused directly by males, or indirectly by females harassed by males

	Causes of interruptions	
Harem type	Male	Harassed female
Territorial	0.6	1.1
Nonterritorial	1.6	3.7

NOTE: Data derived from over 250 hours of observation on five territorial and seven nonterritorial harems. Male interruptions $t_{42} = 2.55$; $p < 0.01$; harassed female interruptions $t_{67} = 2.41$; $p < 0.01$.

that horses graze, is amplified to a feeding gain of about two hours per day. Thus by associating with males that are able to defend territories, and hence reduce intrusions (see Fig. 13.3 for rate of aggression), females derive another significant feeding advantage.

If foraging success is coupled to reproductive success, then territorial females should have a higher fitness than nonterritorial females. As Figure 13.4b reveals, this appears to be the case. Females residing with territorial males have higher per capita probabilities of raising foals to one year of age, the age of independence.

Thus on Shackleford Banks the maintenance of a territorial system benefits both males and females because both benefit from mate guarding. From the general model diagrammed in Figure 13.1, when food is the only critical resource, its distribution in a fairly continuous fashion is a prerequisite that permits females to live in closed membership groups. Whether or not they do appears to depend on the harshness of the environment, and on the negative consequences of male sexual activity. On Shackleford Banks, acquiring sufficient resources for survival and reproduction is difficult enough without the added stress imposed by males. As a result, selection seems to favor females that channel some of their reproductive effort into competing for access to high-quality dominant males. Such males not only effectively defend their own reproductive interests, but in doing so also augment a female's foraging and reproductive success.

PHENOTYPIC CONSTRAINTS: COMPARISIONS AMONG HORSES AND PLAINS ZEBRA

Male–Male Relationships

The horses of Shackleford Banks show how female associations affect

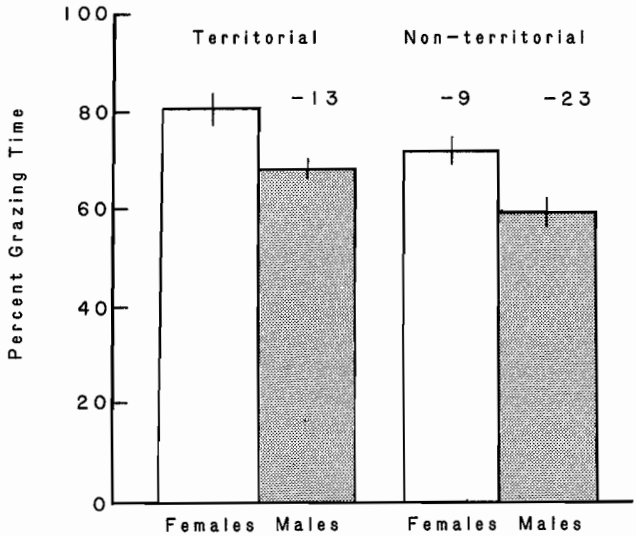

Fig. 13.6. Percent time spent grazing by males and female in territorial and nonterritorial harems. Over 1,000 hours observing five territorial and two nonterritorial harems. Mean ± standard error.

male associations and how male associations affect those of females. According to the model depicted in Figure 13.1, the associations and distributions of "surplus" or "nonreproductive" bachelor males should also affect the pattern of sociality by affecting the behavior of the reproductive males. In equids do such effects exist? They do, and in a significant way. But the impact can only be seen in comparision with situations where the demography or social behavior among bachelor males are markedly different. Two such comparative situations exist. One involves major demographic changes that occurred on Shackleford Banks in 1980. In general, male infants on the island die at a higher rate than female infants (Rubenstein, in prep.). As a result Shackleford Banks rarely supports a large bachelor male population. From 1973 to 1978 the bachelor male population varied from two to ten individuals. After a series of mild winters in 1976 and 1977, this number swelled to seventeen in 1980.

With the aging of the harem males, a demographic shift occurred in the population. By 1980 harems were headed by weaker individuals and, with the unprecedented number of young, agile males, the pressure imposed on the harem stallions by intruders increased dramatically. Virtually all the harem males were overthrown and the females were divided into fifteen new

TABLE 13.2
Patterns of association among six common zebra harems during spring 1980

	Torch	Y^2	Zeus	Achilles	Saddle	Hermes
Torch		.63	.11	.00	.11	.00
Y^2			.06	.06	.17	.00
Zeus				.55	.06	.00
Achilles					.00	.08
Saddle						.46
Hermes						

NOTE: Index of association computed by the formula $IA = 2C/(A + B)$ where C is the number of times both harems are seen together, and A and B are the total number of times each harem is seen.

harems. Group sizes dropped from a mode of seven to a mode of two, and all the territories disappeared. Perhaps what is most striking is that the population birth rate was reduced from a mode of fourteen to a mode of eleven. Thus the dramatic increase in bachelor males and their intrusion rates led to a social revolution.

The second comparison that shows how bachelor male-breeding male relationships influence social systems involves a comparison among horses and plains zebras. Ordinarily, horses and plains zebras are classified as having identical social systems (Klingel, 1974). One striking difference exists, however, and that concerns the nature of the relationships that form among bachelor males. In horses the relationships are weak and ephemeral as males live in temporary associations of two to three individuals. At least in northern Kenya in the Sambura-Buffalo Springs reserve, plains zebra bachelor males have strong relationships, are organized by linear hierarchy, and live in closed membership groups averaging nine individuals (Rubenstein, in prep.). According to the general model this difference should result in differences in the distribution and relationships of the harem males. And indeed it does. By using an index of association $IA = 2C/(A + B)$ where A is the number of occurrences of group A alone, B is the number of occurrences of group B alone, and C is the number of occurrences where groups A and B were seen within twenty-five meters of each other, it is possible to measure how likely different harems are to associate together. As Table 13.2 demonstrates, there are strong associations among particular pairs of plains zebra harems.

To understand the possible significance of this result we have to appreciate that both horse and zebra harem males almost always charge away from their females when they detect an intruder male. The agonistic interaction that ensues is usually of low intensity with dominance determined quickly. Nevertheless, the two males often graze together until one, usually

TABLE 13.3
Numbers of successful and unsuccessful attempts by single and paired common zebra harem males to prevent bachelor males from entering a harem

	Defensive outcome	
Type of defense	Successful	Unsuccessful
Single male	0	8
Paired males	11	1

NOTE: Fisher exact proobability, $p = 0.00014$.

the subordinate, leaves, walking back slowly to his females. On Shackleford Banks if a single harem male meets a bachelor group he has little trouble dominating the two to three horses comprising it. He then remains and grazes with them, thus keeping them away from his females. In the plains zebra, a single harem male was never able to dominate all nine males and was never able to keep them from mixing with his females (Table 13.3). However, if a pair of harem males were already together because their two groups of females had come together, then they could almost always dominate the nine bachelor males and keep them away from their females (Table 13.3). So it appears that the nature of relationships among the younger subordinate males has a major affect on the nature of equid social organization. When the threat to male and female reproductive success is high a new level of sociality emerges. It involves strong intergroup male relationships and effectively neutralizes the reproductive challenge (Table 13.3). Why horse bachelor males live in open membership groups whereas plains zebra bachelors live in closed membership groups remains an exciting question. Perhaps, as argued earlier, the higher risk of predation faced by zebras necessitates that males also live in closed membership groups, so that the antipredator benefits due to dilution are assured.

REPRODUCTIVE CONDITION: A COMPARISON OF HORSES AND GREVY'S ZEBRA

The general model suggests that phenotypic attributes such as differences in reproductive condition should affect female social relationships. They do weakly in horses, but strongly in Grevy's zebras.

Female–Female Relationships

In horses, group movement is usually determined by females, and in particular by dominant females. From data gathered over a decade (1973–1984), 68 percent (± 12 percent) of movements from one vegetation zone

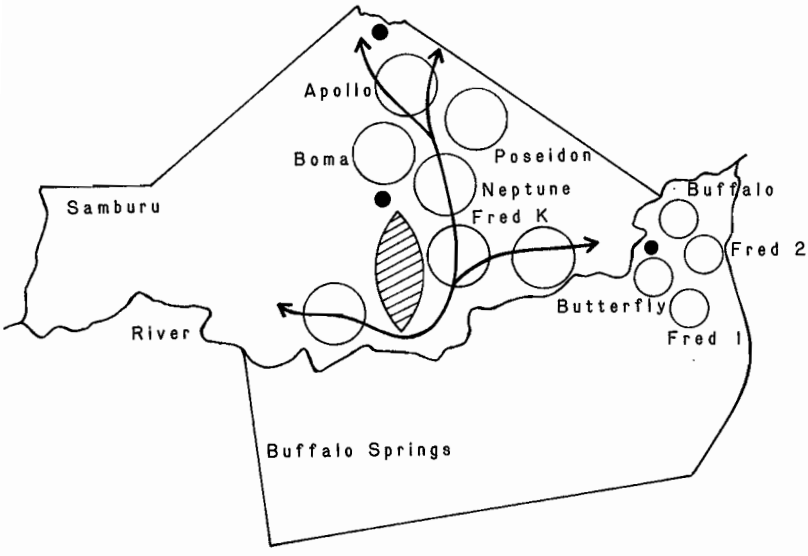

Fig. 13.7. Location of male Grevy zebra territories in relation to female ranging routes and predator-free standing water (●).

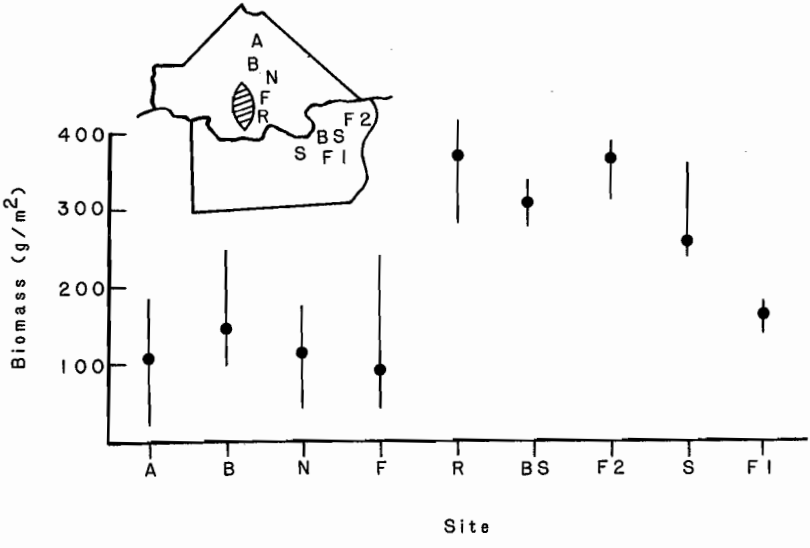

Fig. 13.8. Biomass within Grevy zebra territories. N = ten samples for each location. Mean ± range.

to another were initiated by dominant females (top half of hierarchy) in the season before the birthing begins. After the birth season commences, however, in those situations where the dominant female is without a new foal, her initiation of vegetation zone changes drops to 36 percent (± 14 percent). During this period, which lasts about six months, lactating females assume a more prominant role in controlling the foraging movements of the group. Thus reproductively induced changes in dietary requirements appear to have a profound effect on female distributions and associations among horses.

Female–Male Relationships

In Grevy's zebra, the effects of reproductive conditions are more pronounced since the bonds among adult females are less strong and individualistic tendencies are more readily expressed. Normally Grevy's females range between ten to fifteen kilometers per day (Rubenstein, unpubl.). In the Samburu Game Reserve there are two major movement routes (Fig. 13.7), and males establish territories along them. Some territories are nearer to peripheral water holes that afford protection from predators while drinking (Fig. 13.7), whereas others are nearer areas of highest biomass (Fig. 13.8). Although all types of territories are visited by the females that wander daily, only those having just borne a foal stop ranging long distances and take up long-term (two to three months) residence with males near safe standing water (Fig. 13.9). Again, reproductive condition appears to affect female associations and distribution. In the Grevy zebra old bonds are broken and new ones form, especially those with males.

Normally territorial Grevy's zebra males have a low confidence of paternity when copulating with wandering females; rarely does a wandering estrus female remain within male's territory for the duration of her heat. But since all female equids come into estrus shortly after giving birth, males associating, and copulating, with a newly arrived sedentary mother will increase their paternity confidence and gain a reproductive advantage (Rubenstein and Ginsberg, in prep.). Although the gain associated with exclusive mating access to these females is reduced somewhat because he protects another male's offspring, infanticide is not favored. Without the foal, and the mother's need for forage and access to safe watering sites, the female abandons the territory within one day (Rubenstein, pers. obs.). Thus the male is in a cruel bind: he has to assist another male's offspring to augment his own reproduction. The actual magnitude of this advantage will depend on whether or not territories near watering sites have enough good vegetation to attract as many estrus females that remain wanderers as do territories in other sites. From the biomass data shown in Figure 13.9, it appears that both types of territories on average offer females about the same amounts of vegetation. The territories in the proximity of water, however, are somewhat less variable, and appear to lack those few superrich patches.

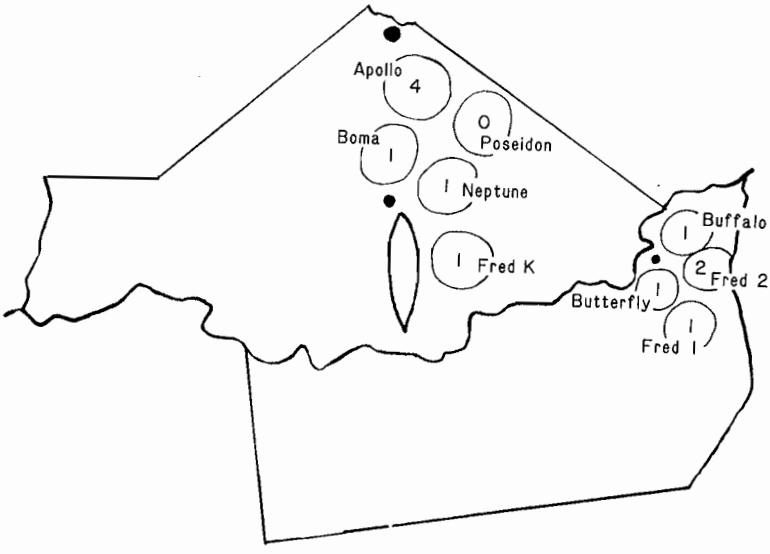

Fig. 13.9. Location of male Grevy zebra territories in relation to predator-free standing water (●) and the number (within circle) of resident females with newborn foals.

Whether or not these differences in variance are important (sensu Rubenstein, 1982), is yet to be determined. In any event, it appears that in the Grevy's zebra, female reproductive condition affects female relationships and may have a significant effect on distributing males of different phenotypes in different areas, and influencing their reproductive success as well.

CONCLUSIONS: COMPARISONS WITH OTHER STUDIES

Horses and zebras exhibit few niche, or phenotypic differences, yet they display a wide range of social systems. The social diversity seen on Shackleford Banks is mirrored in other feral equid populations. Female horses associating with territorial males are found in Exmoor (S. Gates, 1979), on Cumberland Island (Lenarz, 1982), and in the New Forest (Pollack, 1980), and female asses living in closed membership harem groups occur on Ossabaw Island off the southeastern United States. Although few detailed measurements of the pertinent phenotypic and environmental constraints outlined in the general model (Fig. 13.1) were made in these studies, the basic ecological descriptions suggest that for each population exhibiting a deviation from the "typical" pattern, one of the external constraining variables is somewhat atypical. On Ossabaw Island lush vegetaion is fairly

evenly distributed (NRC, 1982; McCort, 1979), a situation not commonly encountered by asses. Amicable behaviors outnumber aggressive ones and permanent harems occur. In the New Forest, the sex ratio is extremely biased by the commoners, who prefer to rear females. With a shortage of males, many females wander unassociated with, and unhindered by, males, who limit their range to territories encompassing the best grazing areas (Pollack, 1980). And at Exmoor, a river bisects the range making it easier for groups to remain apart (S. Gates, 1979). On Cumberland Island, both the extent to which a male can exclusively control an area and the quality of the vegetation he controls depend on his dominance status (Lenarz, 1982). Only the most dominant males can control the areas of highest quality vegetation on a year-round basis, and Lenarz suggests that in doing so they assist the reproductive success of their females. Unfortunately, he provides no data on group size or fertility of dominant versus subordinate males. The same correlation of male dominance status and territorial quality occurs on Shackleford (Rubenstein and Balbo, in prep.), and on Shackleford females associating with dominant males derive a significant fitness advantage (Fig. 13.4).

This social diversity results from a variety of factors. As these examples demonstrate, the distribution of resources affects the potential for females to form groups. Except in extreme environments, like on the western end of Shackleford, or in the steppe deserts of northern Kenya, closed membership groups of females are permitted because feeding competition is low. Whether or not they form is dependent on other factors and only indirectly on food. Predation is one factor that appears to provide a sufficient advantage. By forming permanent membership groups mutual reduction in one's personal vulnerability is assured. Another advantage derives from the sexual activities of males. At least on Shackleford Banks, females, by forming closed membership groups, assist males in becoming effective protectors of their own reproductive interests as well as those of females.

This is a novel advantage that seems to have evolved in a number of phylogenetically distinct harem-living groups of primates—the gorillas (Harcourt, 1979b), the hamadryas baboons (Kummer, 1968), and the gelada baboons (Dunbar, 1980a). The details of the social organization of these species are similar but not identical. One difference concerns the role of breeding-nonbreeding male relationships. In all, the nonbreeders are repulsed by the harem males, but the success is varied. In both gelada baboons and gorillas, harems often contain secondary males who attempt to steal copulations, or females. This rarely occurs in horses (cf. Miller and Denniston, 1979) or hamadryas baboons. Another difference involves the nature of the female-female bonds. In the gorillas and hamadryas baboons few relationships exist among females so that when the resident male disappears the female group fragments. In horses and gelada baboons the disappear-

ance of a male leaves the female relationship unchanged; new males take over the entire group (Klingel, 1974; Dunbar, 1984a). Thus despite a common need for a male shield or hired gun, other relationships in these social systems are different. Whether they are the result of phylogenetic differences or are the result of subtle differences in ecology is as yet poorly understood. Perhaps small differences in the levels of feeding competition among females are involved. Gelada baboon females can apparently stress other females and suppress reproduction (Dunbar, 1980a). And on Shackleford Banks female horses already in a group attempt to deny strange females entry. Hints of density-dependent reproductive suppression can be gleaned from Figure 13.4b, and suggest that competition among females may be as reproductively important in equids as is male-male intergroup cooperation.

In horses and zebras relationships among males are affected by features of both the social and physical environment. Predictability of female associations and movements are most important in structuring male associations. When females form cohesive groups, males defend them against incursions by other males. When females live in temporary assemblages, male strategy is varied. If daily female movements are predictable, then males compete for territories along these highways. This is typically the case in Grevy's zebra (Klingel, 1974) and in asses (Moehlman, 1979a). But even in the New Forest where interference by commoners limits permanency of female bonds (Pollock, 1980), some males limit their activities to the areas where unattached females prefer to graze. When even these daily movements of females are unpredictable, males have no alternative but to search for, and attend, individual females in estrus. Apart from the Shackleford population this rarely occurs in equids, because at least movements to and from water are somewhat predictable.

Ecological pressures have some effect on male behavior, but mostly by fine tuning the major male alternatives. Extreme topographical features, such as those found on parts of Shackleford Banks, Exmoor, the New Forest, and Cumberland Island, can make the simultaneous defense of females and territories economical. Similarly the presence or absence of predators seems to induce nonbreeding males to form either cohesive or transitory assemblages. For horses and zebras the number of combinations of particular ecological and social features is large, and as the general model shows, can account for the social diversity displayed by the family.