

The Ecology of Female Social Behaviour in Horses, Zebras and Asses

by

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Societies are the outcome of the reproductive strivings of their members, their interactions and their relationships. The precise nature of social relationships is shaped by features of the physical and social environment. Knowledge of the resources available to, and resource needs of, society members should contribute to an understanding of the form of sociality exhibited.

This chapter examines the female social behaviour of four equid species (horse, Plains Zebra, Grevy's Zebra, and Onager) which, despite biological similarities, differ in their types of sociality. Female horses and Plains Zebras form long-term bonds within stable groups accompanied by a single male; female Grevy's Zebras and Onagers change associates frequently and form unstable groups with brief association with each of several territorial males. The differences relate to the former two species occurring in more mesic habitats, the latter in arid climates.

Females of all the species compete little while foraging. Rates of agonistic interactions, bite rate, and time spent feeding are generally unaffected by group size. By living in groups females reduce the amount of male harassment that they experience, without sacrificing their feeding time or freedom of movement. Horse females with dominant males gain up to 6 minutes per hour advantage in feeding time, which consequently enhances their reproductive success. Mares may change group from one with a high-to one with a lower-ranking male, but only when the latter has recently improved his rank, demonstrating his long-term potential for rank-holding.

Not all equid females live in persistent groups, because intensity of female competition increases as resources become patchy, or because the physiological needs of females sometimes diverge. Females in early lactation need to drink more than others, and stay nearer to water to do so. Thus groups of dissimilar females cannot persist.

Social flexibility is common in equids. Being species limited by time available for foraging, their females associate to gain foraging time; even their choice of male may be made for that reason. Fission-fusion society is a mere variant upon the theme of a society based on female association.

Introduction

Animal societies take many forms. The underlying mating systems for either sex can be either monogamous or polygamous, and, while variations on the monogamous theme depend upon whether or not males assist with the rearing of the young, polygamous variants entail females (polyandry), males (polygyny) or both (polygynandry) having more than one mate. Many varieties of polygyny exist because males can defend groups of females directly, defend the resources females require, wander in search of those in oestrus, or aggregate on resource-deficient advertisement sites called leks and wait for receptive females to arrive (Emlen & Oring 1977). Moreover, when aggregations form, they can be either long- or short-term, and at least with respect to associations consisting of members of the same sex, they can comprise kin or genetically unrelated

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animals, or both. Yet, despite this seemingly bewildering array of possibilities, a framework built upon evolutionary first principles and based on a few general rules has emerged, allowing us to understand why species exhibit the societal patterns that they do (Emlen & Oring 1977, Bradbury & Vehrencamp 1977, Rubenstein & Wrangham 1986, Dunbar 1988, Clutton-Brock 1989). The framework is based on three general rules, or central themes.

First, relationships among individuals represent the threads that hold societies together (Bradbury & Vehrencamp 1977, Rubenstein & Wrangham 1986). Societies are not themselves evolved characteristics of species, but rather the outcome of the reproductive strivings of individuals and the interactions they generate. For permanent societies to form, for example, relationships must be both stable and long-term.

Second, the relationships themselves can be either cooperative or competitive, and both will result from conflicts of interest that arise because individuals differ in their abilities and needs (Trivers 1974, Armitage & Downhower 1974, Hrdy 1977, Davies 1985). Although conflicts can be among members of the same sex, between parents and their offspring, or between individuals of opposite sexes, most develop from the need of individuals to maximise reproductive success. For most mammalian species, female reproductive success is limited by access to critical environmental resources, whereas male reproduction is typically limited by access to females (Emlen & Oring 1977, Bradbury & Vehrencamp 1977, Rubenstein & Wrangham 1986, Clutton-Brock 1989). Thus relationships among females not only directly determine their own association and distribution patterns, but they also influence those of males. Thus relationships within and between the sexes are both involved in shaping animal societies. Even for species that breed cooperatively, the behaviour of one individual is usually constrained by the activities of others. Thus the behaviour that comes to characterise each animal society develops, in part, to mitigate the effects of these constraints.

Third, the precise nature of these social relationships is shaped by features of both the physical and social environment (Wrangham & Rubenstein 1986, Clutton-Brock 1989). Particular distributions and abundances of food, water and sites safe from predators in conjunction with the physiological demands of females differing in size and reproductive state, will shape their time budgets and activity patterns (Rubenstein 1986). These in turn will determine female distributions and associations and ultimately those of the males as well. In general, environments in which resources are abundant, particularly when evenly distributed, facilitate long-term stable relationships and thus foster more permanent societies than those in which resources are rare and patchily distributed (Rubenstein 1989).

Yet despite the elaboration of these general rules and a framework for finding the roots of animal societies, few studies have identified how the three general principles interact to produce a particular type of society. The highly visible and frequent nature of male activities has made it relatively easy to assess the adaptive significance of the strategic alternatives facing males. Unfortunately, such analyses help solve only half the problem, as the relatively subtle and rare social interactions of females make it difficult to understand the adaptive value of female behaviour, and these gaps complicate identifying the ultimate roots of any society.

The purpose of this chapter is to begin rectifying this situation by providing detailed data on female social behaviour and its ecological determinants for four closely related species of equids: the horse (*Equus caballus*), the Plains Zebra (*E. burchelli*), the Grevy's Zebra (*E. grevyi*) and the Asiatic Ass, or Onager (*E. hemionus*). The comparative approach is facilitated because these species make their living in more or less the same way by grazing, and occasionally browsing, and all are members of the same genus so that phylogenetically their common heritage guarantees that basic physiological and morphological constraints will be similar.

The Problem

Despite their overall biological similarity, these four equid species exhibit different types of sociality. Whereas horses and Plains Zebras form societies in which unrelated females forge long-term associations and live in permanent groups that include their offspring and usually a single male (Klingel 1969, Rubenstein 1981, 1986, 1989), females of Grevy's Zebra (Rubenstein 1986, Ginsberg 1989) and Onager (Rubenstein 1989) typically change their associations on a more frequent basis. As a result, relationships among females are temporary, the groups they inhabit are highly unstable in size, and associations with males are intermittent and brief. Males of these latter two species are generally solitary, wander widely and often defend extremely large territories (Klingel 1969, Rubenstein 1986, 1989, Ginsberg 1989, Ginsberg & Rubenstein 1990).

The problem is to understand why such similar species form such different societies. Two clues suggest that ecological differences are ultimately responsible for the social variants. One is the fact that the species living in persistent groups inhabit mesic habitats while those with more transitory female relationships live in arid climates. The other is the observation that when Burros, feral descendants of the arid-adapted African Ass (*E. asinus*), inhabit mesic habitats, female social relationships stabilise and unimale-multifemale groups (harems) form (Moehlman 1979, McCort 1979).

Given that behavioural flexibility appears to be at least in part driven by changing ecological circumstances, it is possible to use both intra- and interspecific comparisons to measure the relative costs and benefits of behavioural alternatives. Behavioural observations were made on known individuals of each species. The horses have been studied since 1973 and inhabit Shackleford Banks, N. C., a barrier island off the east coast of the U. S.; both Plains and Grevy's Zebras were studied in the Samburu-Buffalo Springs Game Reserves, Kenya in 1979 and Plains Zebra in Ngorongoro Crater, Tanzania from 1986-1988; and the Onagers have been studied in Mahktesh Ramon, an erosional cirque in the Negev desert, Israel, from 1987. Instantaneous scan samples were used to construct time and activity budgets, whereas focal animal samples were used to record more fine-grained details of social behaviour (Altman 1974). Rare events such as agonistic encounters were scored on an *ad libitum* basis. All interactions, ranging from peaceful approach and retreats to escalated bites and chases, were used to construct dominance hierarchies. Simple matrices of pairwise combinations of wins and losses reveal that dominance hierarchies are stronger for males than for females, although for both sexes they are linear (Rubenstein in prep.). Between scan samples, rates of feeding and walking were recorded. The composition of a group and its grid location were noted whenever a group was discovered. Hourly censuses and maps depicting relative locations were used to determine nearest neighbours and association patterns.

Metric data are analysed using standard parametric tests (Sokal & Rolf 1969); counts are analysed by contingency table analyses. All statistical tests are two-tailed, except where specific hypotheses are being tested.

The Solution

Costs of Competition

The most salient feature of female equid social behaviour is tolerance. For all four studied species females rarely compete while they forage. Among horses, for example, little overt aggression is exhibited during feeding (Fig. 1). On average, females suffer about 0.1 agonistic encounters per hour, and the rate does not appear to be affected by the number of potential competitors present. Females in larger groups are not supplanted, nor even attacked, more frequently than females in smaller groups ($F_{1,10} = 2.41$; $p < 0.20$). If there is any trend at all, it appears that the rate of

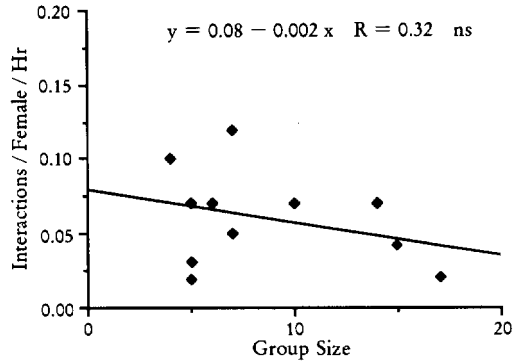


Figure 1. Relationship between group size and per capita rate of aggression among female horses. Although agonistic interactions among females decreases slightly as the number of conspecifics in a group increases, the relationship is not statistically significant ($r^2=0.10$). N in this and subsequent figures, represents the sample of independent observations on focal animals included in the analysis.

aggression decreases slightly as group size increases.

One outcome of such peaceful co-existence should be unhindered foraging. And this appears to be the case as illustrated by Plains Zebras. Increases in group size, which would ordinarily intensify competition, have no significant effects on the proportion of time spent foraging (Fig. 2). On average, Plains Zebras devote about 0.65 of each hour to grazing, which is about the same proportion exhibited by horses (Rubenstein 1981). Among the zebras some variation exists, with animals in the smallest groups increasing their grazing time by about 0.05 hours, and those in the largest groups finding theirs reduced below the average by the same small amount. Yet even these differences are small and statistically insignificant. Moreover, actual feeding rates as measured by zebra bite rate is largely unaffected by increases in group size (Fig. 3). Although zebras in the largest groups crop vegetation at a slightly higher rate than the average of 0.3 bites per second, while those in the smallest groups bite at rates slightly lower than the average, these differences are small and statistically insignificant.

Thus when it comes to foraging, competition in these mesic-adapted species is largely unaffected by changes in group size. Females appear to organise their grazing in ways so that they do not interfere overtly with each other and reduce foraging success. As Figure 4 illustrates, competition among the arid-adapted Onagers while foraging is also rare. Each female can expect to be supplanted about once every two hours. But competition does clearly occur, primarily over access to

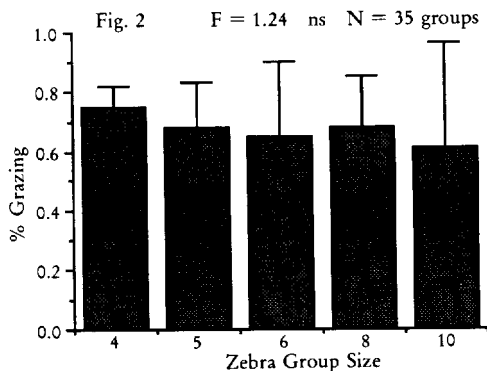


Figure 2. Relationship between zebra group size and the proportion of time individuals spend grazing. Although the average decreases slightly with increasing group size, the small increases in the variance that accompany these changes and the trend are not statistically significant.

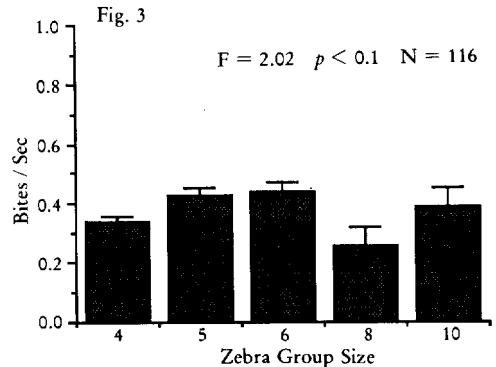


Figure 3. Relationship between zebra group size and feeding rate. Although moderate sized groups show a small increase in feeding rate, none of the differences are significant.

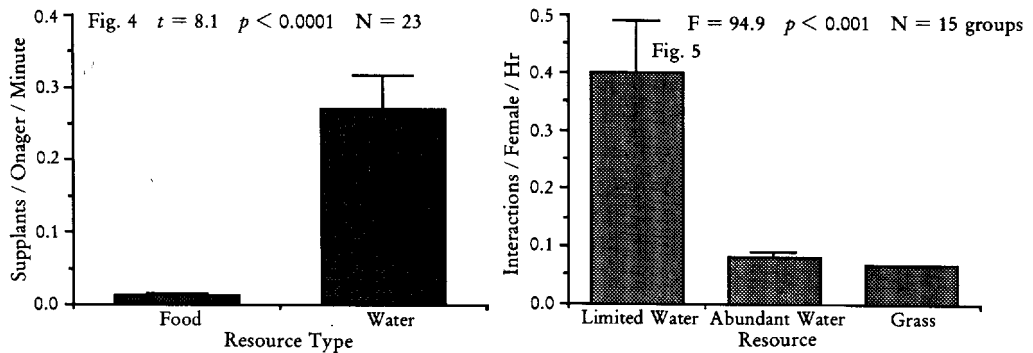


Figure 4. Relationship between per capita rates of aggression among female Onagers for food and water. Whereas competition for food is low as in the other equids, it is much higher for water.

Figure 5. Relationship between per capita rates of aggression among female horses for vegetation and water of different types. Rates of aggression between vegetation and water that can be obtained simultaneously from many access points do not differ, but are significantly different from that associated with acquiring water where access is limited.

water. Is such frequent strife over water, however, unique to the arid-adapted species? The answer is no. At least for the horses inhabiting Shackleford Banks water comes from two sources, large pools and small pits or holes. Pools are the more common source, occur throughout the year, and vary in size from a few to tens of metres across. Pits and holes are used regularly for watering, but primarily during periods of drought when the shallowest of the ponds dry and water can be obtained only by digging to the fresh water lens that comprises the island's water table. As Figure 5 shows, even for mesic species, when access to water becomes limited, as it does when horses crowd around these holes that are only tens of centimetres wide, rates of aggression increase markedly. Thus the major difference between Onagers and horses is the fact that Onagers usually find water sources with limited access, whereas horses do not. And as the behaviour of these horses illustrate, when water sources allow many females access at the same time, rates of aggression are no different from those experienced during feeding (Fig. 5).

Although competition for water can at times heighten aggression, most equids go to water only once each day, and then only for as brief a period as possible. Grazing is the activity that consumes most of an equid's time. Horses, for example, graze for approximately 16 hours per day (Rubenstein 1981, 1986) and the other species do not deviate much from this pattern (Rubenstein & Ginsberg in prep.). Thus for about two-thirds of every day equids find themselves active and in peaceable social situations. To an equid, vegetation is a resource whose distribution and abundance is critically important in determining whether or not individual females can co-exist in coherent groups.

Benefits of Group Living

Although the distribution and abundance of vegetation may permit the existence of groups by minimising the costs individuals encounter by living together, these features themselves do not account for why the two different types of equid groups form. To account for this dichotomy we need to determine what benefits accrue to group-living individuals that offset even the most minimal costs of competition. Alexander (1974) recognised that, while there are no automatic benefits of group living, there are automatic determinants. These are associated with enhanced disease and parasite transmission, as well as competition. At least for horses, the likelihood of being parasitised and having bodily condition reduced because of this parasitism, increases as sociality increases (Rubenstein & Hohmann 1989). And even though competition for food is minimal, low levels of aggression still occur even in the smallest groups. It is true that group living may reduce the chances of an individual being eaten; of all predatory attacks by lions on zebras, those that are

most successful occur when zebras live alone rather than in moderate sized groups (Schaller 1972). Nevertheless, the need to reduce predation can not be the only ecological benefit that is derived from living in groups since few contemporary equid populations live in habitats where predators are a problem. Yet all equids continue to live in some sort of group. What then provides the benefits that make group living economical?

If anti-predator benefits do not provide an advantage large enough to make group living economical, then enhancements to foraging success usually do. But as Figures 2 and 3 show, increased sociality does not *on average* increase feeding opportunities. Thus at first sight it would appear that even foraging benefits fail to occur when living in groups. But averages can be misleading. Equids, like all ungulates, ferment vegetation so that they can extract nutrients and energy locked within plant cells protected by tough cellulose walls. Unlike their ruminating counterparts, however, fermentation takes place after food has been digested in the stomach. Thus there is no constraint on the rate at which food is processed. In fact, food is continuously pushed through an equid's gut which means that contact with the absorptive surfaces of the intestine are limited. To survive equids must therefore consume large quantities of vegetation, which, because of their large body size, can fortunately be of low quality (Janis 1976). As a result, the foraging success of equids will be limited mostly by the time they have available for grazing, or browsing, not by the quality of food available.

Given this time constraint, any change in behaviour that could increase time available for feeding would be selected for since it could enable individuals to augment reproduction as well. And for equids the link between female foraging and reproduction is particularly strong. All equids show some reproductive seasonality, although for the zebras the peak is the smallest and the spread is the greatest (Rubenstein & Ginsberg in prep.). Regardless of species or habitat, the peak is typically timed to coincide with conditions that are best for vegetation growth. But with gestation ranging from 11.5 months in horses to just over twelve months in Grevy's Zebras, mating and birthing periods overlap in all species. Thus when females are stressed physiologically by lactation, and when they should be acquiring maximum amounts of food to increase bodily condition and thus enhance their chances, and those of their offspring, of surviving during the ensuing cold winters or dry periods, females find themselves contending with the added stresses of persistent reproductively active males. For female horses, rates of harassment by males can be quite high, ranging from 0.6 to 1.6 per hour (Rubenstein 1986). From a female's perspective, males may be necessary for conception, but their presence and activities can limit overall reproductive success (Rubenstein 1986, Berger 1986). Clearly, males are a problem.

Interestingly, this is a problem that group living helps overcome. Because males vary widely in their instantaneous dominance rank, as measured by their ability to win encounters with other harem-tending males (Table 1), some of the males tending females are better than others at limiting

Table 1. Win-Loss records among males inhabiting the western end of Shackelford Banks during one year. Linearity of the dominance hierarchy is revealed by the fact that few entries lie in the half of the table below the main diagonal and of those that do, their values are always equal to, or less than, the appropriate value of the appropriate dyad above the diagonal.

	Wins				Losses			
Males	1.	2.	3.	4.	5.	6.	7.	8.
1. Thor	—	7	14	4	9	7	1	4
2. Saturn		—	5	5	10	9	7	6
3. Pluto		2	—	8	15	6	4	5
4. Jupiter		5	4	—	7	7	5	1
5. Wodin					—	5	9	1
6. Apollo		1			3	—	3	
7. Wellington					2	1	—	
8. Caesar					1			—

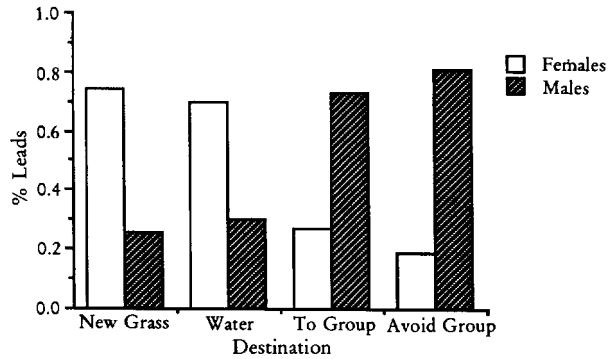


Figure 6. Sex differences between propensity to initiate movements to and from other groups or to and from critical ecological resources. Whereas males control social movements, females control ecological ones.

harassing approaches by wandering males. Females associating with high-ranking males are disturbed much less frequently than those associating with low-ranking males (Rubenstein 1986). Moreover, males of high rank allow their females more freedom of movement than do low-ranking males. Typically, females initiate movements from one feeding area to another, or to water, and males follow behind or to the side (Fig. 6). Although males sometimes attempt to direct these movements by either altering slightly the angle of the route or by turning the group around and reversing its direction entirely, male status affects how often these types of interference occur. As Figure 7 illustrates, low-ranking males direct their females' movements about twice as often as do high-ranking males. Such rank differences in control become even more exaggerated when female movements bring groups close together. High-ranking males are much more likely than low-ranking individuals to attack a nearby rival and let their females continue on the route upon which they are travelling. Conversely, low-ranking males are more likely to turn their females back (Fig. 8).

For females the proximate consequence of freedom from harassment and the ability to initiate and control movement is time; time that can be spent grazing. Females associating with dominant males gain up to six minutes more time per hour grazing which on a daily basis can accumulate and provide such females with up to two more hours for grazing (Rubenstein 1986). Ultimately this increased freedom from harassment translates into enhanced reproductive success. As Figure 9a shows, females associating with males in the top half of the hierarchy rear more foals to one year of age, the age of independence, than females associating with males in the bottom half of the hierarchy. This is a particularly striking result considering that a female's own rank, as measured

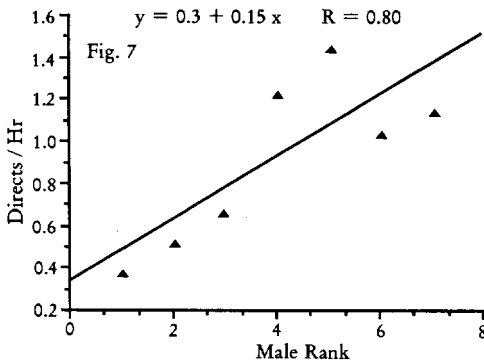


Figure 7. Relationship between male rank and tendency to direct female movements. Control increases as male rank in the dominance hierarchy decreases. High dominance rank is designated by low scores.

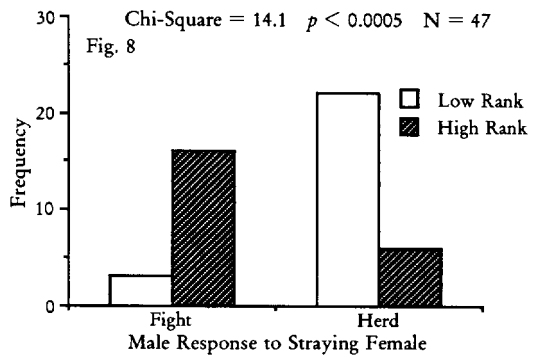


Figure 8. Relationship between male rank and male response to females that move close to other breeding groups. High ranking males attack the nearby male, while low-ranking males round-up or herd their females away from the potentially threatening male.

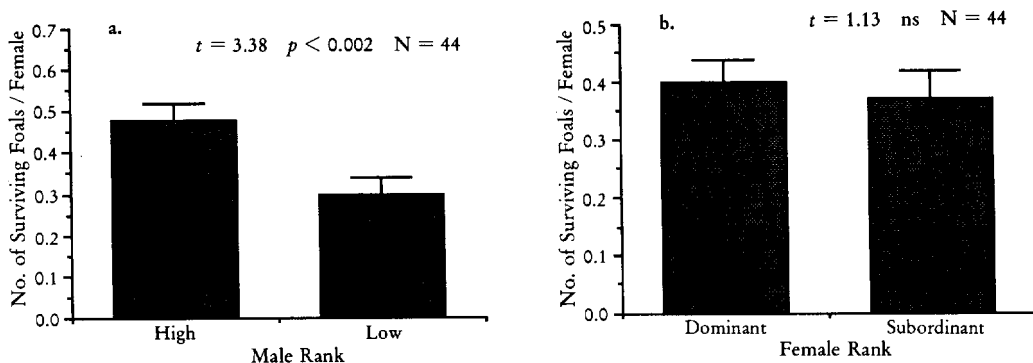


Figure 9. Relationship between per capita female reproductive success and (a) male dominance rank within the population at large and (b) female rank within her group. Female fitness increases with male rank but not significantly so with female rank.

by her ability to supplant other members of her group, has a much smaller and statistically insignificant effect on reproductive success (Fig. 9b).

Female Choosiness

Since females living in groups with dominant males derive feeding benefits that ultimately enhance reproduction, females should choose carefully with whom they associate. And they do, but making the choice is complicated by the fact that male rank changes over time (Fig. 10). About ten percent of all Shackleford adult females change groups twice in their lifetime, once when they leave their natal group and again after they begin reproducing (Rubenstein 1981). So we can examine from and to which mature males, reproductively active females go. As Figure 11a illustrates, 0.70 of adult females that change groups appear to voluntarily leave males of high rank and join groups associating with males of lower rank. At first sight this pattern seems strange given that male rank has such important fitness consequences. But as Figure 10 indicates, most males maintain a constant rank and then experience a monotonic, or steady change, until a new level is reached. Thus an initial change, no matter how small, appears to be a good predictor of bigger changes to come and should favour any female that can detect rank changes early and act upon her assessment as quickly as possible. Monitoring rank change, rather than absolute rank, is critical if females are attempting to increase their chances of joining a group that is associated with a soon-to-be effective male. From Figure 11b it appears that females are doing just this. Females are joining groups whose male's rank has recently increased, regardless of his absolute place in the hierarchy, and leaving those in which a male's rank has declined or remained unchanged. Joining early is important because once a group gets large it gets more difficult for females to enter (Rubenstein 1986,

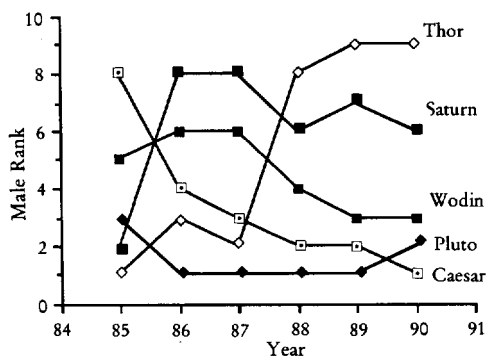


Figure 10. Relationship between male dominance rank and time. For most males, rank changes monotonically over short periods of their lives. Only horses followed for the entire period are included.

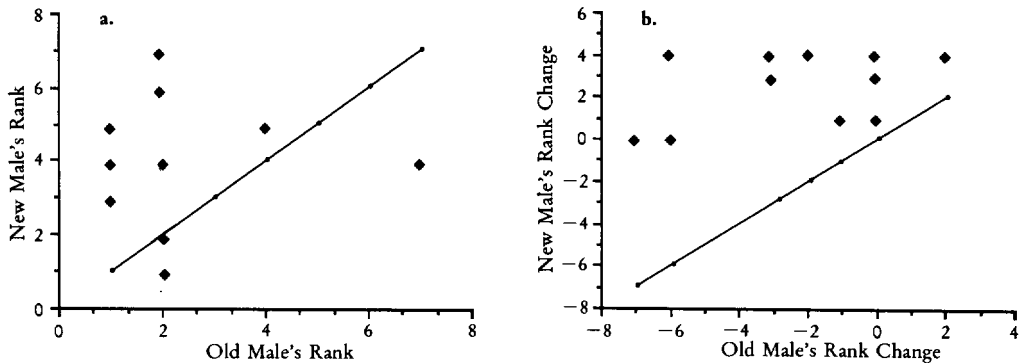


Figure 11. Relationship between attributes of the male a female leaves and those of the male she joins. (a) Absolute rank. Females leave males of high rank to associate with males of low rank. (b) Rank change. Females join males whose rank has increased since the last breeding season and leave those whose rank has either decreased or remained unchanged.

Rubenstein & Ginsberg in prep.).

Ecological and Physiological Constraints

Clearly groups form because males can provide material benefits that enhance female reproductive success. While it is possible that females could obtain these benefits by banding together without a male, by doing so the net gain each would obtain would be lower. No matter how the roles of individual group members are apportioned among activities such as defence, grazing, grooming, herding and others, some time and effort would have to be invested in activities that are currently performed solely by the male. Yet if group living in association with dominant males is good, why then do not all the equid species do so all of the time?

Social breakdowns occur simply because the intensity of competition does increase under certain conditions for some females and when this happens no level of benefits can make permanent associations economical. These conditions occur when the distribution of resources becomes more patchy, or physiological needs among individuals diverge, so that time and activity patterns become sufficiently different causing different individuals to organise their movements in mutually incompatible ways (Rubenstein 1986, 1989). That changes in the patterning of resources can act as a constraint on the formation of permanent-membership groups is illustrated by the societal changes exhibited by the horses of Shackleford Banks. Prior to 1976 a portion of the western tip of the island (the area in which horses today prefer to graze) was mostly subtidal, only remaining above sea level at spring low-tides. As a result, during the spring and summer when searching for preferred vegetation, horses rarely had access to these high quality continuous grazing swards. Instead they were restricted to patches that varied tremendously in size (Rubenstein 1981). Large aggregations could only be accommodated with a minimum of strife in the largest patches and since these patches could only support large aggregations for short periods, horses would have to move to new and often smaller patches. Here competition was more intense and peripheral or inferior competitors were forced to leave, fragmenting the group. Eventually, when vegetation in the larger patches regenerated, large aggregations could once again be supported and small groups and solitary individuals would come together and fuse. Thus the patchy nature of the landscape prevented the formation of permanent groups and imposed a fission-fusion society on the horses. Otherwise, females on the western end of the island would have profited by adopting the more closed society of their counterparts inhabiting the island's eastern region (Rubenstein 1981). Not only are rates of male-male competition and of female harassment significantly higher in open, as opposed to closed, societies (Rubenstein 1986), but when the landscape was dramatically altered by dredging of the seabed behind the island so that the regions that had been mostly subtidal be-

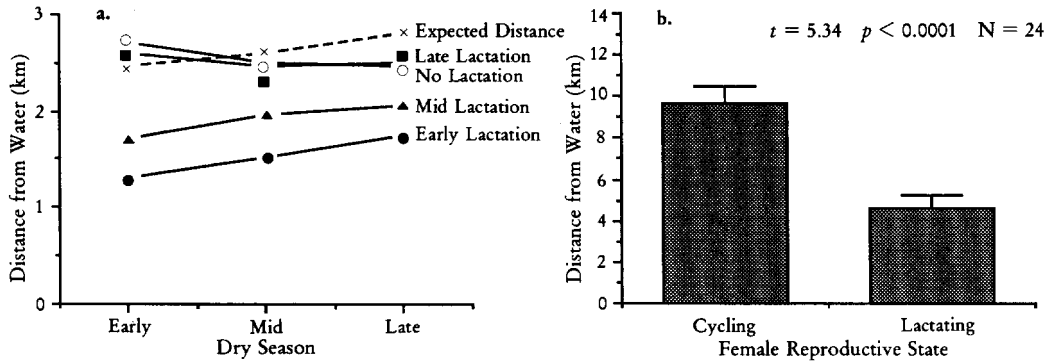


Figure 12. Relationship between a female's water needs and her tendency to stay near water. (a) Grevy's Zebras. As the dry season progresses water sources become more widely distributed (expected distance) and all females find themselves farther away from water. Females in the earlier stages of lactation keep this distance smaller than do non-lactating females or those approaching weaning. (b) Onagers. Lactating females remain significantly closer to water than non-lactating females.

came mostly supratidal, females quickly formed permanent bonds with males and other females, and the fission-fusion society gave way to the more typical uni-male or harem, variety.

Although the formation of a closed society can be prevented by the patterning of the landscape, this type of social control is likely to be a special case. An alternative force that can help maintain a fission-fusion society, and one that will be more general, derives from the fact that the physiological differences that ordinarily exist among females can under certain circumstances become accentuated. When this happens females with exaggerated needs are forced to behave in different ways if they are to meet these needs. As a result, changes in time and activity patterns will sometimes require that bonds be broken with individuals having only 'ordinary' needs as individuals with increased needs change their movements. New associations, some of which may only be transitory, may be all that is possible. As a result, the social fabric tears.

That such tears occur repeatedly is best seen in the arid-adapted species, the Grevy's Zebra and the Onager. In these species, females in the early stages of lactation become more dependent on water than any other individuals in the population (NRC 1978, Pollock 1980, Oftedahl 1984,

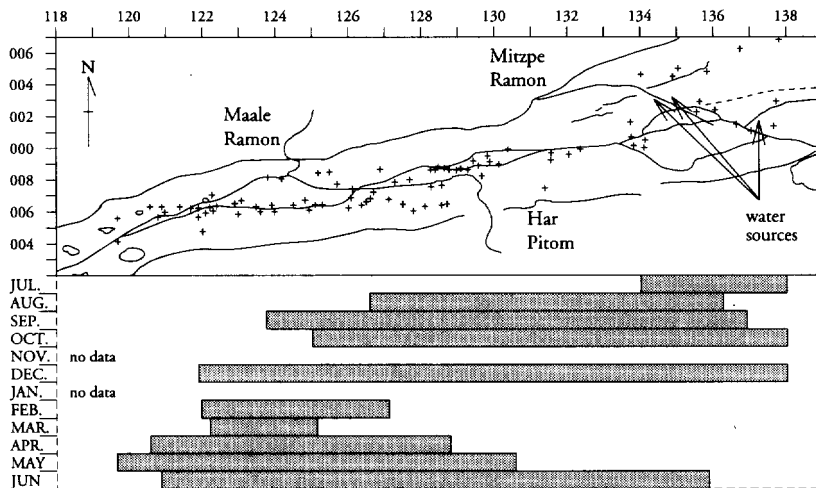


Figure 13. Map of all the sightings of one lactating Onager. + denote sightings regardless of season whereas bars show extreme sightings by month. As the dry season progresses and the foal is young the home range expands but includes the water sources. As the foal becomes more independent and as the rains begin the female continues to increase her ranging away from the water sources, although the home range is reduced. (map courtesy of D. Saltz).

Rubenstein 1986). Such females are essentially drinking for two since young foals do not drink free-standing water, only mother's milk. Point-samples collected for both species from daily surveys of female locations in relation to their grazing areas and watering spots reveal that lactating females remain nearer to water than non-lactating females (Fig. 12a, b). For Grevy's Zebra females as the dry season progresses water sources become scarce and the likelihood of females of any reproductive state being near water declines (Ginsberg 1989). Yet the average distance from water remains smaller for early and middle lactating females than for the others.

Among Onagers the same pattern exists and the temporal pattern is easily seen by the detailed seasonal movements of one lactating female (Fig. 13). While her foal is young (July) the mother's home range includes the water sources and continues to do so even though the home range increases as the foal matures. Vegetation, especially near the water sources, declines as the dry season progresses and not until the spring rains increase the supply of standing water do females reduce their range, curtail their daily movements and abandon the area containing the permanent water sources. As Figure 12b shows, during the dry season when foals are less than three months of age, the average distances from water for lactating Onager females and non-lactating females are significantly different because they shuttle different distances between grazing areas and drinking sites.

The most significant consequence of these different ranging patterns that develop for different classes of Onager females is that permanent groups consisting of dissimilar females can not be maintained. On days when we saw more than half the individuals comprising the Onager population we recorded the sizes and locations of all the groups we spotted. From a plot of the maximum size of group seen on such days, we see that maximum group size increases quickly after the rains cease and water becomes abundant and evenly distributed within the extensive wadi system (Fig. 14b). As the dry season progresses, however, and both the abundance of vegetation (Fig. 14a) and

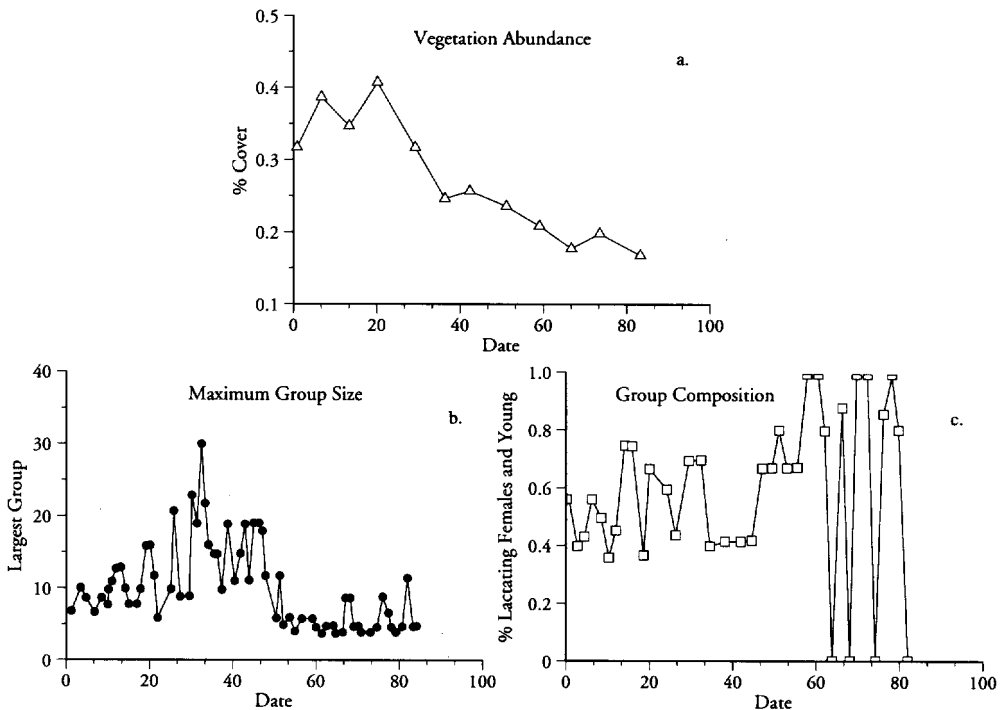


Figure 14. Temporal relationship between vegetation abundance (a), and the maximum size of groups (b), and group composition as measured by the proportion of lactating females comprising the groups (c). As the dry season progresses vegetation becomes scarce, group sizes at first increase, but then decrease, and groups become more homogeneous, being composed either of all lactating females and their young or all non-lactating females.

the availability of water declines, maximum group size decreases. But more importantly, the composition of groups during this period changes (Fig. 14c). For some time after the rains cease, groups develop from temporary associations but they are heterogeneous consisting of lactating and non-lactating females in approximately equal numbers. And this mixture persists regardless of changes in maximum size of groups recorded. As water stress becomes more limiting and the stress on certain types of females becomes more severe, groups become more homogeneous in their composition. Either they consist of all lactating females and their young, or all non-lactating females. Thus among Onagers, when the differences among females become exacerbated, the forces that bind weaken and the social fabric tears.

An Exception Proving the Rule

If the emergence of differing needs is the force that drives females to adopt different ranging patterns, then why should females of different reproductive states in horses and zebras continue to move together and function as an integrated unit? Although even in these species differences among females do indeed exist, the mesic environments they inhabit are much more mild and rarely seem to push lactating females to the point where they have to reorganise their time budgets and activity patterns. As a result, rarely are these lactating females stressed to the point where they are forced to forego the benefits derived by forming tight associations in order to get enough of an essential, and, what has not become for them, a limiting resource.

The test of this hypothesis comes from the rare occasions when lactating females with very young foals experience an exceptionally prolonged drought. During the summer of 1990 one such drought occurred when no rain fell on Shackleford Banks from the middle of May until the beginning of July. Four foals were born during this period and we were able to follow the movement patterns and activities of their four mothers and compare them to those we recorded for the non-lactating members of their groups. Just like lactating females with young foals in Grevy's Zebra and Onagers, these females stayed closer to water and they changed groups significantly more often than the others whose water needs were much less (Fig. 15).

Thus on Shackleford Banks an exception proves the rule. Lactating females who need more water than non-lactating females ordinarily can acquire sufficient quantities without having to stray from the group and the protection of their male. When demands are high and water becomes limiting so that access is restricted and not every trip to water guarantees that a sufficient quantity will be consumed, lactating females begin to adjust their activities so that they linger near the few water sources. Since the cost to non-lactating females of not getting their fill appears to be less than that of remaining near the few remaining water sources where harassment by strange males is great, non-lactating females quickly leave when they have finished drinking. As a result the male is faced

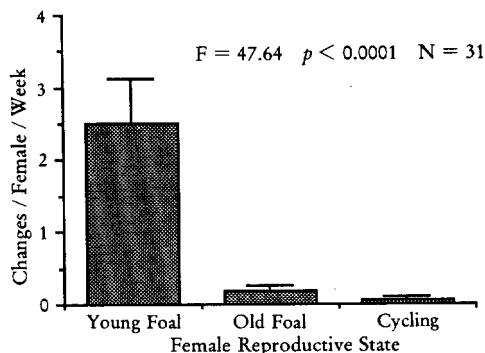


Figure 15. Relationship showing the tendency of horse females with foals of different ages or without foals to change groups. During an extreme drought the four females with young foals changed groups significantly more often than the other types of females.

with a dilemma. He can either associate with the one lactating female and her young foal, a female who will ovulate shortly, or he can leave with his many females, some of which may still ovulate since not all will have conceived. All four males in our sample abandoned the lactating female with the youngest foal and followed their group of females to the grazing grounds. The lactating female, as an unprotected female occupying a highly travelled area, is quickly seized by the next male that arrives at the water hole with his females. Yet because the new male will be no more successful than the original one at integrating her permanently into his harem until the foal is much older, or until the rains bring respite, rates of movement from one group to another for females with young foals must necessarily be high (Fig. 15). Although a true fission-fusion society has not developed among the Shackelford horses, the behaviour of particular females under exceptional conditions demonstrates that even the ordinarily strong bonds of the harem society can weaken and that the tight fabric of that society can fray at the edges and begin to unravel.

Discussion

At least for equids, females can benefit from living in groups because they can associate with males and derive substantial material benefits for themselves and their offspring. Males clearly profit by this arrangement as well since their reproductive success increases as more females join their groups (Rubenstein 1986). When these aggregations are stable they are characterised as uni-male, multi-female, or harem groups, but in reality they are systems in which females mate monandrously and because several females prefer the same male he mates polygynously. In the equids this type of mating system develops when relationships are stronger between males and females than they are among females themselves (Rubenstein in prep.). This asymmetry in the strength of the relationships arises because the benefits to females of choosing the right male are high while associating with particular females yields few benefits or induces few costs. At least when groups do not exceed ten members, females are engaged in activities that rarely induce them to interfere with each other, suggesting that female-female relationships are usually peaceful.

This does not mean, however, that female-female relationships do not exist. Two lines of evidence suggest that relationships among females can be quite strong and do have important consequences, although they are rarely exhibited during the routines of daily life. The first line of evidence comes from the changed nature of social interactions that develop once groups get large (> 10). Equids are atypical mammals in which individuals of both sexes disperse from their natal groups. Whereas males routinely end up wandering with bachelor males before becoming resident in a breeding group, females join breeding groups almost immediately, especially if the group is small. When the group is large, however, resident females act in concert to exclude new females as they try to join the group (pers. obs.). They may do so because at these densities strife during grazing begins to increase and females often find themselves grazing on substandard patches of vegetation or having to drink last when the water is often fouled (Rubenstein & Ginsberg in prep.). The end result is reduced reproductive success (Rubenstein 1986). Unless their harem male is at the top of the male dominance hierarchy, by banding together females will be able to override his attempts to integrate new females into the group (Rubenstein & Ginsberg in prep.).

The second line of evidence emerges from situations in which groups of females find themselves without males. Twice we have witnessed the unanticipated death of males in their prime. On both occasions the groups of females and their young have stayed together without males for more than two weeks. Similar sightings have been reported in zebras (Penzhorn 1984). At least for both instances among the horses, other males, particularly males from neighbouring all-male, or bachelor, groups approached the unattended females frequently and tried to direct peripheral members away from their group. When provoked in this way females typically move close together and charge such males. As these sexual forays by males increase, the long term response of these females with-

out males is to alter their ranging patterns by moving to areas where they can avoid harassment altogether. But avoiding contact with conspecifics creates its own problems. The only areas where interactions can be avoided are those which no other females frequent because such places lack adequate food and water. Moreover, unattached males eventually find even these areas, and harassment increases.

Yet in neither case did a young, inexperienced bachelor male ever succeed in acquiring a mate by either taking over a group in its entirety, or by breaking the existing female bonds and establishing new ones between himself and one or more of the females. Even though neither of these groups remained without males, only one maintained its integrity. In this group the females were repeatedly able to drive away up to three harassing bachelor males at a time. But eventually they allowed a solitary, but previously dominant breeding male to associate with them. Once this new male joined the group, the females reoccupied their previous range and, although their new stallion was not as able as their previous one, harassment levels dropped and the females stayed with him for the remainder of the breeding season. The fate of the other group was somewhat different. Although it also remained intact for a few weeks, once the females began to frequent the common grazing and drinking areas, harassment levels by both bachelor and harem males increased. The group split up as each female moved independently to another breeding group. Thus bonds among females can be strong, but the need to associate with a dominant male ultimately means that female-female bonds can be weakened. Although bonds are present, they are exhibited less often than those between males and females.

It is important to realise that even though males provide material benefits in the currency of time, whenever females form associations with males they immediately incur some extra costs in the form of feeding competition. As we have seen, however, even among females, levels of competition are typically extremely low. Since males graze on average twenty percent less per hour than do females (Rubenstein 1986), the effects of males on female foraging success are further reduced.

It is also important to note that the type of polygyny exhibited by horses and Plains Zebras is often classed as the 'Female Defence' variety. While it is true that males defend groups of females, the strong element of female choice that accompanies the formation and maintenance of these equid groups questions the idea that for all harems the existence of groups of females is a necessary prerequisite. The fact that these harem groups develop from female choosiness predicated on material gains suggests that the 'Resource Defence' variety of polygyny, which is typically thought to be very different from that of 'Female Defence', need not be all that different after all. In equids, both varieties consist of males providing females with substantial material rewards. In the case of the harem-dwelling species, increases in grazing time produce the benefits, while in the fission-fusion societies, where breeding males establish territories, the benefits arise from access to critical resources, mostly water, with a minimum amount of sexual harassment (Moehlman 1979). Yet despite these underlying similarities, the fact that female-female relationships in each are so different guarantees that male behavioural, morphological and physiological characteristics will be affected. At least in the equids, males that interact with females living in fission-fusion societies have significantly larger testes and copulate as well as ejaculate more frequently than do males that associate with females living in cohesive groups (Ginsberg & Rubenstein 1990).

Harassment as seen among Shackleford horses entails males repeatedly attempting to secure matings with oestrous females from other groups, or males forcefully attempting to prevent females with whom they associate from enticing other males to engage in sexual behaviour. But other more escalated forms of harassment can occur. Berger (1986), for example, has shown that harassment can lead to foeticide. Copulations by males can be so forceful that pregnant females abort. Or harassment can result in infanticide, as Duncan (1982) has observed. Stallions enter groups and kill newborn foals, increasing the chances that females will not only commence cycling,

but that her chances of conceiving and being able to sustain the foal increase. These additional examples represent more extreme situations than have been seen in any of the four populations we have studied. Nevertheless, they all are related since from a female's perspective the best defence against any level of hostile male behaviour is to associate with an able male. While he bears all the costs of vigilance and defence, he provides stability for females by minimising the risks of immediate reproductive failure and he increases their chances of reproductive success in the future.

As we have seen, not all equids live in permanent-membership groups, because external, or internal, constraints can prevent them from doing so. Unless vegetation is more or less continuously distributed, competition among grazers can become quite high. And when it does so aggregations will either be permanent but small, or more often, variable in size because the size of the patches will also vary. But even when vegetation is more evenly distributed, differences among females may arise because particular reproductive states may generate different needs. It is not surprising to find that lactating females seem to place importance on acquiring water, whereas non-lactating females emphasise forage acquisition. But all equid species will have groups composed of females of both reproductive states. What is interesting is the fact that both the mesic- and arid-adapted species frequent water on a daily basis (Moehlman 1979, Ginsberg 1989). Apparently the adaptation of the arid-dwelling species has been to keep the watering rate down to this same level. In doing so, however, lactating females seem to be pushed to their physiological limit, one that the lactating members of the mesic species rarely experience. Thus only under extreme conditions would we expect the mesic species to exhibit the breakdown of both the male-female and female-female bonds that hold the harems together. And this is precisely what we have found. Conversely, we would expect that under more mesic conditions the arid-adapted species should switch from the fission-fusion social arrangement to a more permanent harem-type system. This, too, is precisely what occurs. Ossabaw island, like Shackleford Banks, is a barrier island off the east coast of the U.S. It is semi-tropical and as a result is covered with lush vegetation that is evenly distributed and has an abundance of water sources. Feral Burros (*E. asinus*) reside on this island and females regularly form closed-membership groups in which one male secures all the matings (Moehlman 1979).

Social flexibility is common among equids, suggesting that a common thread unites the living species despite the fact that their evolutionary histories diverged more than three million years ago (Clabby 1976). Depending upon ecological circumstances and how they interact with physiological needs individual female equids adopt activity and movement patterns to meet these needs. Associating with a male that can keep other males away while at the same time not imposing his time budget and activity pattern on others provides the best option for any reproductive female. By belonging to a species in which time limits foraging, and hence reproductive success, any extra time saved through not being harassed, or not having to guard against that possibility, will mean the difference between having and not having a fitness that is the same as, or better than, other females. At times, however, associating permanently with a male and a consistent group of females will be impossible. When this occurs a fission-fusion society will emerge, but it is a variation on a common theme, not a qualitatively different type of organisation.

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