

Sociality and reproductive skew in horses and zebras

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Summary

The outcome of competition for resources or mates often leads to individual differences in reproductive success. In populations of equids, such as those of horses and zebras, skewed distributions of reproduction emerge because a limited number of individuals achieve disproportionate gains. For both sexes, skew results from differences in rank, age, and degree of social stability, although skew is generally greater for males than for females. Adult male horses and zebras typically establish "harem" groups by bonding with a number of mature females. Although the number of females that dominants bond with can be quite variable, potentially high levels of skew are rarely reached because subordinate males adopt alternative mating tactics that exact concessions from partners, whether they are dominant stallions or other subordinates. Successful breeding females also rely on support from subordinates to minimize feeding competition by keeping group size small, and this, too, reduces skew among females. The conflict of interest between the sexes arising over differences in optimal group size, along with the tendency for females to leave groups when sexually harassed, induces, but limits, the aggression that males direct towards females. Thus female concessions can shape both female and male levels of skew, but they also can be modulated by male behavior. Thus it appears that for equids the level of skew that emerges depends on key phenotypic traits and how their distribution among individuals constrains reproduction, as well as on how social relationships within and between the sexes affect the ability of a small number of individuals to monopolize resources involved in reproduction.

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Inequality is a pervasive feature of virtually all societies, as is the attempt by the disadvantaged to attenuate it. Humans (*Homo sapiens*) have gone so far as to construct political systems to reduce, if not eliminate, differences in payoffs or outcomes. The Marxist ideal "From each according to his abilities, to each according to his needs" (Marx 1875) represents an egalitarian extreme. While animals may not codify behavior into philosophical norms, actions within many animal societies often redistribute payoffs away from the successful few, thus moderating heavily skewed resource allocations and reproductive opportunities. In mammals alone, skewed patterns of reproductive success are seen in male macaques (*Macaca mulatta*: Widdig *et al.* 2004), rhinoceroses (*Diceros bicornis*: Garnier *et al.* 2001), and even sex-role-reversed species such as hyenas (*Crocuta crocuta*: Engh *et al.* 2002). And in gorillas (*Gorilla beringei*: Robbins *et al.* 2006), meerkats (*Suricata suricatta*: Clutton-Brock *et al.* 2001), marmots (*Marmota* spp.: Allainé 2000), and mountain zebras (*Equus zebra*: Lloyd & Rasa 1989), skewed patterns of reproduction occur among females as well. Reductions in inequality often emerge when the less favored change the rules of the game by adopting strategies that deviate from the typical strategy (Rubenstein 1980). Alternatively, when the haves and the have-nots need each other to prosper, the status quo is maintained by the actions of those receiving the least. Either those having gained the most provide incentives to the less well-off, or the well-off are unable to completely impose their will when confronted by the actions of others (Rubenstein 1978, Vehrencamp 1983, Reeve *et al.* 1998, Johnstone 2000, Reeve & Shen 2006). In order to understand why particular strategies and relationships evolve and produce skewed payoffs and outcomes, knowing the underlying causes of inequality is critical.

In many animal societies inequality results from differences in rank or fighting ability. Dominant females often monopolize resources needed to produce and raise offspring, while dominant males often monopolize reproductive access to females (Rubenstein 1994). For males, status and the bodily condition necessary for achieving and maintaining dominance is driven by sexual selection. But less well understood are the factors affecting status in non-sex-role-reversed females, especially in species such as equids, where competition for essential ecological resources is minimal (Rubenstein 1994). Dominance itself is influenced by many other factors such as age, bodily condition, reproductive state, and environmental harshness, thus pushing an understanding of the causes of reproductive skew one step back. Factors other than dominance and its determinants are also likely to play a role in shaping patterns of reproductive skew. These might include kinship as well as the nature and strength of relationships with individuals of different ages and sex. In this chapter we will explore these issues in order to understand the causes

and consequences of unequal and skewed reproduction in populations of feral horses (*Equus caballus*) and plains zebras (*E. burchelli*). We will illustrate the degree to which reproduction is skewed in each sex and we will identify causes. We will then examine strategies that develop to attenuate these differences among both females and males. Lastly, we will explore management and conservation consequences of these attenuation strategies.

Patterns of sociality and methods

Equid societies come in two forms (Klingel 1977, Moehlman 1979, Rubenstein 1986). In one, typified by feral and wild horses (*Equus caballus*) as well as plains (*E. burchelli*) and mountain zebras (*E. zebra*), females and their immature offspring associate for long periods with one male. This is the so-called "harem," and as offspring of both sexes mature they disperse. Thus the breeding members of these family groups are typically non-relatives, and kinship is unlikely to play a strong role in shaping social or reproductive decisions. In the other, typified by Grevy's zebras (*E. greryi*), Asiatic (*E. hemionus*) and African wild asses (*E. africanus*), and the kiang (*E. kiang*), females form loose and transitory associations with many other females and males. This is a fission-fusion society and, typically, females of different reproductive states segregate and use different habitats. Since both classes of females contain reproductively active individuals, males forgo bonding with any class, instead establishing territories around water. In this way these territories contain the home ranges of lactating females with young foals as well as the routes that non-lactating females use to come to water (Rubenstein 1986, 1994, Sundaresan *et al.* 2007).

Variants on these themes do emerge, and they provide insights into the ecological forces that shape social relationships as well as reproductive strategies and payoffs. For example, some horse populations have harems that defend territories (Rubenstein 1980, 1981) and some have "harems" with two stallions rather than one (Rubenstein 1982, 1986, Feh 1999, Linklater & Cameron 2000a, 2000b). Moreover, in plains zebra societies harems often coalesce into herds. Thus "harem species" can form multi-male as well as uni-male groups, providing polygynous opportunities for males and polyandrous opportunities for females. Harem males can also defend territorial space and, at least in plains zebras, males can bring their harems together to form herds. A second tier of sociality, with fission-fusion elements, emerges as herds form and dissolve.

The social and reproductive patterns described in this chapter come from long-term studies (1983 to the present) of free-ranging horses on Shackleford



Figure 8.1 A highly successful Shackleford female and her young on the Shackleford Banks, North Carolina, USA. Photo courtesy of Cheryl Burke, *Carteret County News Times*.

Banks, North Carolina, USA (Figure 8.1), and plains zebras on the Ol Pejeta Conservancy and unfenced commercial ranches around the Mpala Research Center, Kenya, from 2000 to 2004 (Figure 8.2). Standard behavioral observations on time budgets (Rubenstein 1986, Rubenstein & Hack 2004), associations (Rubenstein *et al.* 2007, Sundaresan *et al.* 2007), and movements (Rubenstein 1986, 1994) were made on individuals identifiable by unique color patterns and freeze brands (horses) or stripes (plains zebras). Patterns of reproductive success (means, variances, and skew) are represented by standard statistical moments. Paternity analyses were performed by the US National Park Service using allozymes and DNA (E. G. Cothran, personal communication).

Background features and framework

Equids illustrate some special social, ecological, and demographic features. First, equids, as large-bodied, hindgut fermenters with wide tooth rows, can subsist on low-quality forage. As a result, competition for such abundant food should be low, especially in mesic habitats. Instead of contesting for individual food items, females move to nearby items of equivalent

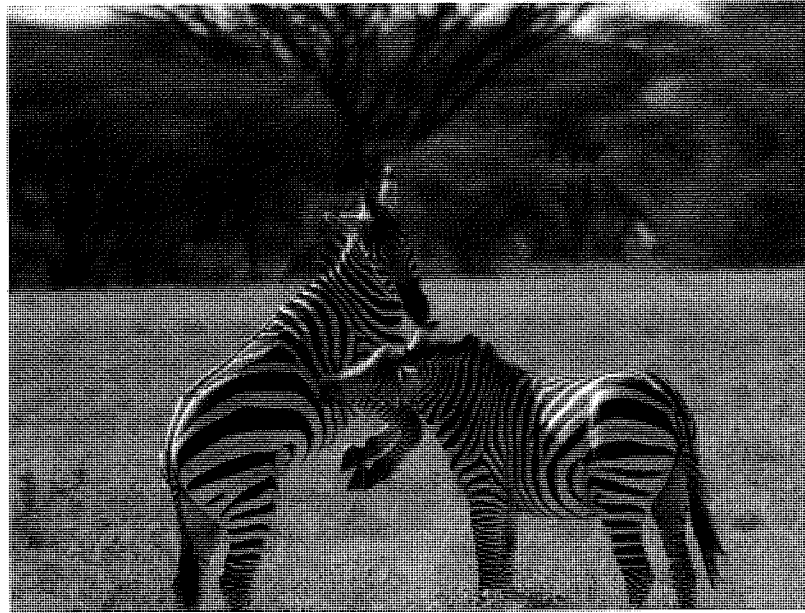


Figure 8.2 Two male plains zebras fighting. This species is characterized by harem structures where one, but occasionally a second, male defends a group of females. Fights occur both between intruder and resident males and between two resident males. Photo by Dan Rubenstein.

value. Rubenstein (1994) shows that contests among female horses are infrequent, occurring at a rate of about one every 10 hours. Similarly, foraging success of plains zebras is not impeded as harem size increases (Rubenstein 1994). This suggests that vegetation eaten by horses and plains zebras facilitates, rather than hinders, group living. As a result, contests over foraging location or individual food items should not be a major factor exacerbating reproductive differences among females.

Second, as Figure 8.3 illustrates, sex-specific survivorship schedules for Shackleford horses are somewhat atypical for polygynous, sexually selected mammals. In this population male survivorship is not always lower than that of females. Instead the curves cross shortly after maturity. As Berger (1986) notes, competition is intense among juvenile equid males as they attempt to establish dominance relationships early in life. Not surprisingly, female survival is much higher during this period, when females are building up bodily condition. Once a male's place in society is established, however, the emergence of stable linear dominance hierarchies among harem males (Rubenstein 1994) lowers the costs of maintaining dominance, thus increasing male

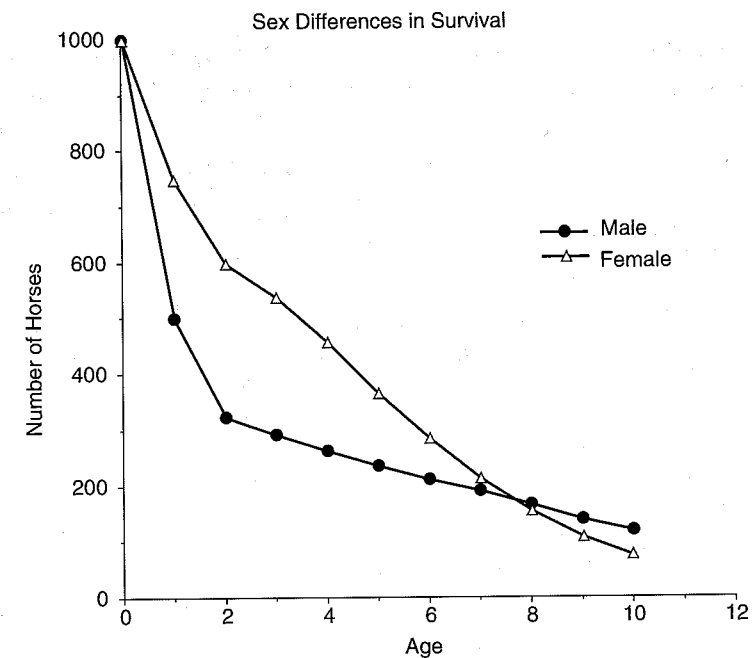


Figure 8.3 Age-specific survivorship of male and female horses on Shackleford Banks.

survival. For females the opposite is true: once foaling commences, female mortality increases and remains high and constant from year to year.

When taken together, both features suggest that augmenting feeding success to maintain good body condition will matter to females, but strategies for increasing intake should not involve contest competition. As hindgut fermenters and throughput feeders, foraging success is likely to be mediated more by time available for feeding, than by excluding neighbors from particular resource patches. Group-living females could increase foraging time by coordinating foraging and vigilance activities among themselves, or they could rely on males to assume most of the vigilance costs while they devote more time to foraging. Equid females choose the latter by selecting males that limit driving and herding behavior and whose heightened vigilance reduces sexual approaches and harassment by other males (Rubenstein 1986).

Since male reproductive success is determined by the number of females in the group, reproductive patterns of both males and females will be affected more by social than by ecological factors. Features such as age, rank, and social stability are likely to have important consequences on differences in reproduction and what individuals can do to ameliorate them. Since reproductive

success depends both on how many young are born over a lifetime and how many survive to the age of independence – the age when direct parental investment ceases – we will use *total number born* over an extended period of time and *total number that survive until 1 year of age* as measures of success. Our analyses will necessarily examine windows of time during which individuals of different ages will span different portions of these times. Consequently, reproductive rate as measured by *number of foals born per unit time* and *inter-birth interval* will also be measured. Since these measures of reproductive success are likely to be influenced by age, residuals about best-fit regression lines of each of the key reproductive variables on age will be used to control for age effects.

Patterns of reproductive inequality and skew

Reproduction among females and males in both horses and zebras is highly variable, but not always skewed (Table 8.1). For female horses having left their natal group for at least 3 years, only a few have failed to give birth during their lifetimes. The distribution of total births is bell-shaped, with 50% of the population giving birth to between two and six offspring during this period. Yearly foaling rate is similarly bell-shaped, with the average female giving birth approximately once every other year (Table 8.1). For plains zebras, moments of variance and skew are greater than those of horses for both the total number of young born and yearly foaling rate (Table 8.1).

Reproduction in males for both species is more variable and more skewed than for females (Table 8.1). Figure 8.4 shows the distribution of the total number of foals sired by male horses; similar distributions and moments are seen for male plains zebras (Table 8.1). In general, measures of male fertility are more variable and show more skew than measures of female fertility in both harem-dwelling equids (Table 8.1).

Factors affecting female reproductive success

Age

Many features of reproduction in horses and plains zebras are affected by age. On Shackleford Banks the fraction of females giving birth in any given year increases with age (Figure 8.5). Whereas only 27% of females less than 6 years of age have given birth, 55% of those older than 10 have done so. Moreover, the total number of foals produced during the 17-year period increases the longer a female lives (Figure 8.6) as does the number of offspring surviving to independence (Figure 8.7). In addition, as females age, their yearly

Table 8.1 Summary statistics of distributions of various measures of reproductive successes for male and female horses and plains zebras. Means, variances, and skews are calculated from the first three moments of the frequency distributions. For horses, statistics before and after management are presented.

	Males			Females		
	Mean	Variance	Skew	Mean	Variance	Skew
Horses (natural conditions)						
Total young born	4.92	24.83	1.96	3.76	6.14	0.59
No. surviving to independence	-	-	-	3.04	3.08	0.69
Yearly foaling rate	1.11	0.44	0.30	0.42	0.04	-0.48
Horses (after management)						
Total young born	2.08	5.51	1.16	2.05	0.79	0.74
No. surviving to independence	-	-	-	1.46	0.67	2.03
Yearly foaling rate	0.52	0.26	0.70	0.20	0.04	0.54
Plains zebras						
Total young born	2.34	2.07	1.00	0.84	0.66	0.54
No. surviving to independence	-	-	-	0.16	0.15	2.32
Yearly foaling rate	0.66	0.21	1.78	0.29	0.07	0.81

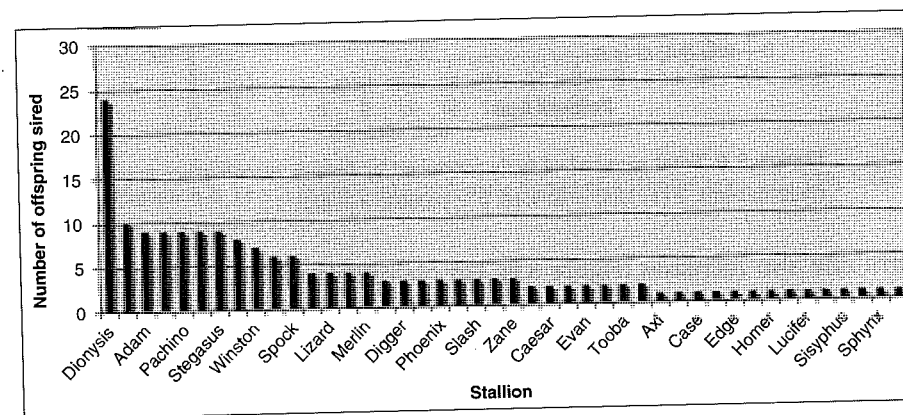


Figure 8.4 Distribution of the number of offspring sired by individual male horses over their lifetimes. Moments of the distribution found in Table 8.1.

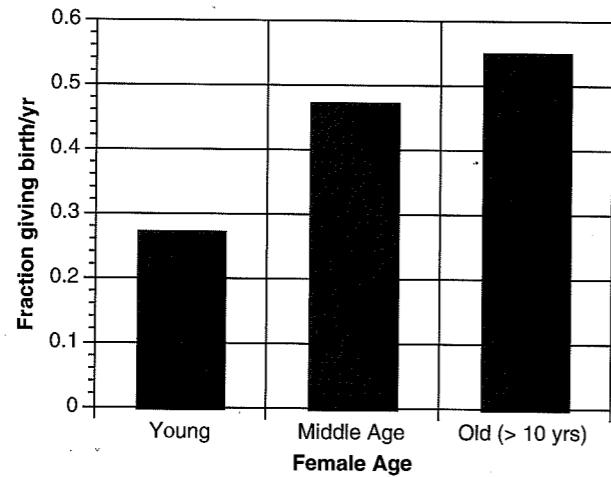


Figure 8.5 Fraction of female horses giving birth per year as a function of age. $\chi^2 = 24.7$, $p < 0.0001$; $df = 2$; $n = 610$.

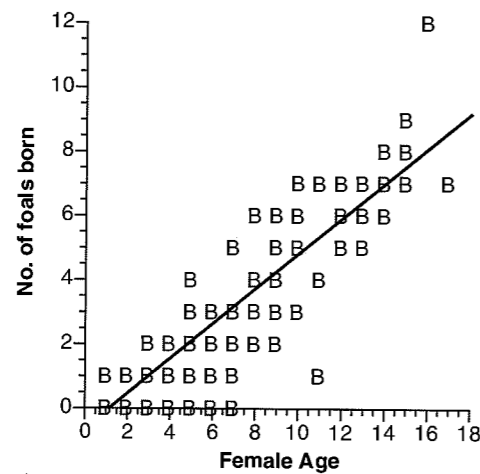


Figure 8.6 Total number of foals produced by female horses since leaving their natal harems. $F [1, 155] = 679.48$; $p < 0.0001$; $r = 0.91$.

birth rate also increases (Figure 8.8). For plains zebra females, age-dependent birth and survival patterns are similar (Table 8.2).

Rank

Although a greater proportion of high-ranking females give birth each year than middle- or low-ranking females (Table 8.3), rank is age-dependent ($\chi^2 = 18.9$; $df = 2$; $p < 0.001$). When residuals of total number of foals born, or

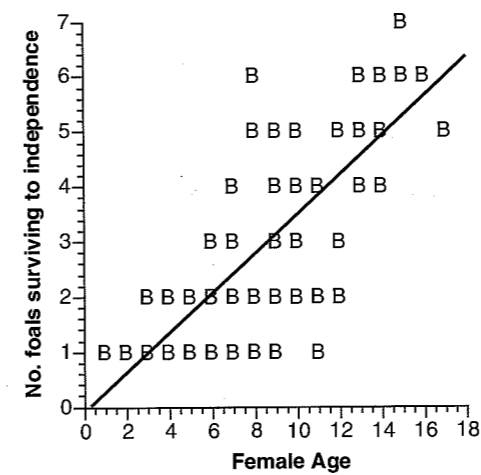


Figure 8.7 Number of foals surviving to independence at 1 year of age as a function of female age. $F [1, 97] = 175.96$; $p < 0.0001$; $r = 0.83$.

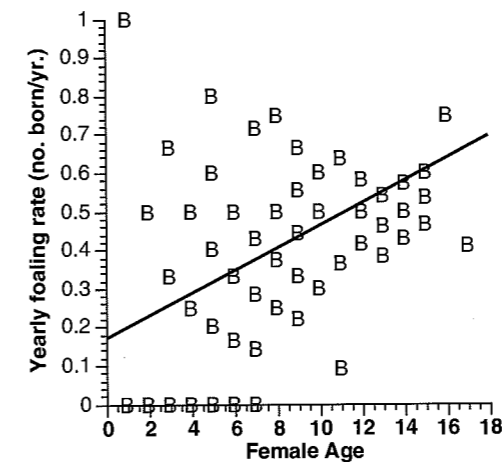


Figure 8.8 Yearly foaling rate by female horses of different ages. $F [1, 155] = 44.12$; $p < 0.0001$; $r = 0.47$.

total number surviving to age of independence, are compared for high-, middle-, and low-ranking females, high-ranking females outperform females of lower rank (Table 8.3).

Male rank also has a strong effect on both the total number of young produced and the total reared to the age of independence by females after accounting for age (Table 8.3). Females bonded to males of higher rank bear

Table 8.2 Age-dependent birth and survival patterns in plains zebras

x-variable	y-variable					
Female age	Birth rate		<i>F</i>	<i>df</i>	<i>p</i> value	<i>r</i>
	(mean)	(SE)				
Old	0.30	0.02	3.32	2,298	< 0.05	0.21
Middle	0.26	0.04				
Young	0.10	0.12				
Female age	Total foals born		<i>F</i>	<i>df</i>	<i>p</i> value	<i>r</i>
	(mean)	(SE)				
Old	0.92	0.05	6.58	2,352	< 0.002	0.25
Middle	0.68	0.08				
Young	0.21	0.13				

more young, and more of them survive to independence, than females associating with males of lower rank (Table 8.3).

Social stability

Since males vary in the degree to which they provide females with material rewards (Rubenstein 1986), females faring less well should switch groups in search of better conditions. Since older females have had more opportunities to change groups than younger females, residuals from the best-fit line of number of moves regressed against age were compared with residuals of the best-fit lines regressing total number of young produced, or surviving to 1 year of age, against age. In both cases, after controlling for age, females' reproductive success is inversely related to the number of different harems a female joins. Females moving frequently among males bear fewer young ($F [1, 152] = 11.99; p < 0.001$) and have fewer of them survive to independence ($F [1, 107] = 13.72; p < 0.0005$) than females bonded more tightly to males.

How long-term residency leads to enhanced reproductive success is related to reduced harassment by males. In general, females associating with higher-ranking males, or males rising in rank quickly, are herded and harassed less than females associating with lower-ranking males (Figure 8.9; Rubenstein 1994). And females that are harassed more tend to be females that are most likely to switch harems (Figure 8.10). How females determine with which male to associate after leaving a harassing male could be based either on cues learned from witnessing male-male contests (Rubenstein & Hack 1992) or from direct feedback of male herding tendencies after joining a new harem. If indirect cues were the deciding factor, then females should generally move from high- to low-harassment males on their initial foray. If such information

Table 8.3 Factors affecting female reproductive success in horses

x-variable	y-variable					
			χ^2	<i>df</i>	<i>p</i> value	
Female rank	Proportion giving birth					
High	0.61		10.68	2	< 0.005	
Middle	0.38					
Low	0.31					
Female rank	Residuals of total foals versus age		<i>F</i>	<i>df</i>	<i>p</i> value	<i>r</i>
	(mean)	(SE)	3.33	2.54	< 0.05	0.32
High	0.28	.25				
Middle	0.20	.31				
Low	-0.61	.27				
Female rank	Residuals of number surviving to independence		<i>F</i>	<i>df</i>	<i>p</i> value	<i>r</i>
	(mean)	(SE)	4.38	2.37	< 0.02	0.44
High	0.34	0.18				
Middle	0.21	0.28				
Low	-0.67	0.27				
Female rank	Residuals of foaling rate		<i>F</i>	<i>df</i>	<i>p</i> value	<i>r</i>
	(mean)	(SE)	1.03	2.54	< 0.5	0.19
High	0.08	0.04				
Middle	0.05	0.05				
Low	-0.02	0.04				
Male rank	Residuals of total foals		<i>F</i>	<i>df</i>	<i>p</i> value	<i>r</i>
	(mean)	(SE)	5.87	1.45	< 0.02	0.33
High	-0.016	0.15				
Low	-0.61	0.20				
Male rank	Residuals of number surviving to independence		<i>F</i>	<i>df</i>	<i>p</i> value	<i>r</i>
	(mean)	(SE)	3.27	1.26	< 0.08	0.32
High	0.01	0.24				
Low	-0.63	0.27				

is not perceivable or is unreliable, then the initial male chosen should not on average lead to reduced harassment. As Figure 8.11 shows, females often find themselves in a worse situation after their initial choice, and only after many moves do they find males that harass them less than their original partner.

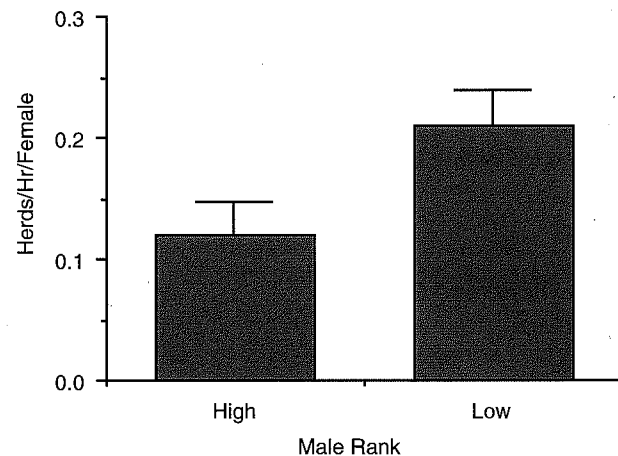


Figure 8.9 Rates of herding received by female horses in harems led by high- and low-ranking males ($t = 2.16$; $p < 0.05$; $df = 14$).

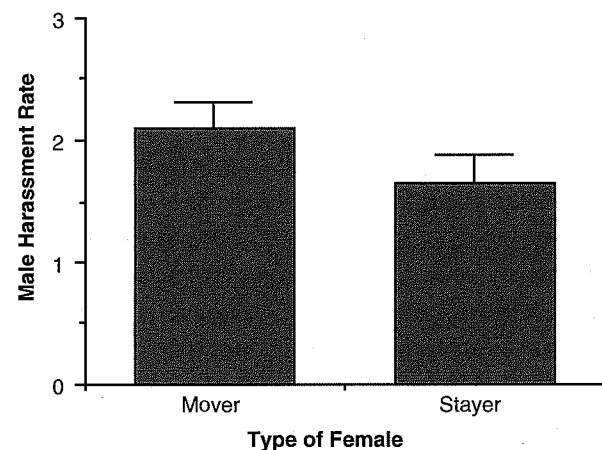


Figure 8.10 Rates of herding received by harem female horses that remain in the harem or ultimately leave ($t = 2.23$; $p < 0.05$; $df = 22$).

Factors affecting male reproductive success

Age

Both the number of total young sired by a male and his yearly siring rate increase with age. As males mature they accumulate more offspring over time ($F [1,60] = 173.9$; $p < 0.0001$; $r = 0.86$), yet they also tend to sire more offspring per year ($F [1,60] = 5.84$; $p < 0.02$; $r = 0.28$). Both measures of

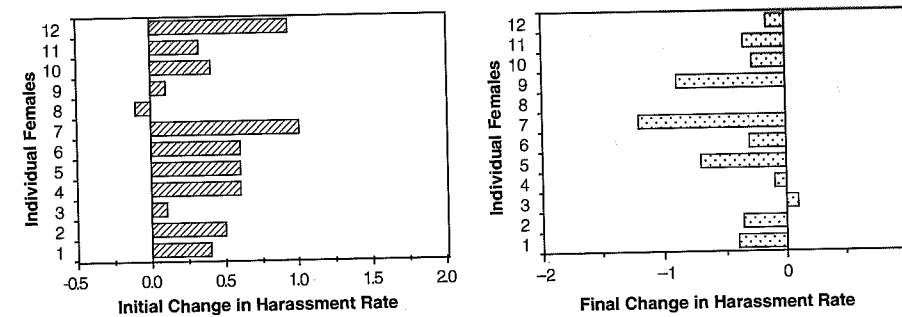


Figure 8.11 Paired comparisons of changes in harassment rates received by 12 female horses leaving their harems. Initial changes refer to differences in the rates they received from their original male and the male of the first group they joined (paired $t = 6.2$; $p < 0.005$; $df = 11$). Final changes refer to differences in the rates received from their original male and the male whose group they finally move to (paired $t = 4.24$; $p < 0.005$; $df = 11$).

reproductive success result from the fact that males accumulate females as they age. On becoming a harem leader, the number of females in the harem is smaller than in the year before they lose their harem (Table 8.4).

Rank

Dyadic interactions among Shackleford males yield clear-cut dominance rankings (Rubenstein 1994). These manifest themselves in two ways. First, for harems headed by single males, rankings are highly linear and second, harems headed by single males are always dominant to those led by two males. When the population of males whose rank remained the same throughout the study period is divided into thirds, males in the top third of the hierarchy sire more total offspring and have higher yearly reproductive rates than males in the middle or lower third of the hierarchy (Table 8.4). As before, these differences are the result of differences in the number of mares in a male's harem (Table 8.4).

When rank is assessed by type of harem, males that are sole harem leaders sire more total offspring and have higher yearly siring rates than males in dual-male harems (Table 8.4). Most multi-male harems (80%), however, are led by younger males that become single harem leaders later in life. When the effect of age is controlled for by plotting the residuals of total number of offspring sired or yearly siring rate against age, single-male harem leaders fare significantly better with respect to siring rate and slightly better in terms of total foals sired than multi-male leaders (Table 8.4). Even more striking is the fact

Table 8.4 Factors affecting male reproductive success in horses

x-variable	y-variable					
Harem longevity	Number of females		<i>t</i>	<i>df</i>	<i>p</i> value	<i>r</i>
	(mean)	(SE)				
First year	1.73	0.29	4.17	78	< 0.0001	0.82
Penultimate year	3.42	0.28				
Harem longevity	Number of foals sired		<i>t</i>	<i>df</i>	<i>p</i> value	<i>r</i>
	(mean)	(SE)				
First year	1.9	0.16	4.99	78	< 0.0001	0.20
Penultimate year	0.75	0.14				
Harem rank	Total foals sired		<i>F</i>	<i>df</i>	<i>p</i> value	<i>r</i>
	(mean)	(SE)				
High	8.3	1.62	3.60	2,28	< .05	.61
Middle	3.8	1.61				
Low	2.5	1.54				
Harem rank	Yearly siring rate		<i>F</i>	<i>df</i>	<i>p</i> value	<i>r</i>
	(mean)	(SE)				
High	1.58	0.15	8.02	2,107	< 0.0006	0.73
Middle	1.29	0.14				
Low	0.60	0.19				
Harem rank	Number of females		<i>F</i>	<i>df</i>	<i>p</i> value	<i>r</i>
	(mean)	(SE)				
High	3.88	0.33	6.98	2,107	< 0.002	0.58
Middle	2.78	0.31				
Low	1.96	0.23				
Harem type	Total young sired		<i>F</i>	<i>df</i>	<i>p</i> value	<i>r</i>
	(mean)	(SE)				
Single male	4.62	0.75	2.22	1,45	0.14	0.20
Multi-male	1.20	2.16				
Harem type	Yearly siring rate		<i>F</i>	<i>df</i>	<i>p</i> value	<i>r</i>
	(mean)	(SE)				
Single male	1.29	0.09	4.00	1,47	< 0.05	0.51
Multi-male	0.86	0.22				
Harem history:	Residuals of number of		<i>t</i>	<i>df</i>	<i>p</i> value	<i>r</i>
males leading both	foals sired					
harem types						
Single male	0.21	0.24	2.15	11	< 0.05	0.54
Multi-male	-0.45	0.19				
Herding intensity	Residuals of number of		<i>t</i>	<i>df</i>	<i>p</i> value	<i>r</i>
(number / hour)	foals sired					
Low (< 1/hour)	1.78	0.41	1.51	4	< 0.20	0.60
High (> 1/hour)	0.91	0.25				

that when the siring rates of males experiencing both roles over a lifetime are compared after correcting for age, siring rate is significantly higher for males when they become sole harem leader than when they share leadership with a partner (Table 8.4).

Social stability

Just as harassment rate affects female movements and fertility, it affects the stability of harems and male reproductive performance as well. Males that direct the movements of their females by overzealous herding experience higher female movement rates ($F [1,3] = 44.22; p < 0.007; r = 0.96$). And, although only a strong trend, when the population of single harem leaders is divided into high-intensity and low-intensity herders, the yearly siring rate of low-intensity males is almost twice as high as that of high-intensity males (Table 8.4).

Adopting alternative reproductive strategies or balancing selfish effort and the granting of concessions for access to critical resources are often thought of as different mechanisms that individuals use to reduce inequality and skew. For male equids this need not be the case. Male horses display a variety of routes to adulthood (Figure 8.12). The typical route involves leaving the natal group between 2 and 3 years of age and joining a bachelor group consisting of other non-breeding males. Bachelorhood is a period where males wander and socialize with other bachelors and harem males. Consequently dominance relationships begin to be developed with a significant portion of the male population. When a bachelor rises to the top of a group's hierarchy he begins to challenge harem leaders. In the typical route to adulthood about half of these high-ranking bachelors take over a harem intact (harem route); the other half form a bond with a young female dispersing from her natal group (monogamous route).

Two other less common alternative routes to adulthood are possible (Figure 8.12). In one, a young dispersing male forgoes joining a bachelor group, instead joining a harem group first as a peripheral male and finally as a secondary male (satellite route). This type of coalition illustrates how dominants sometimes offer concessions to retain the services of subordinates, as assumed by concession models of skew (Johnstone 2000). In the other, the dispersing male joins a bachelor group, but rather than spending time socializing and ascending the dominance queue, he forms a partnership with another recently arrived young male and together they leave the bachelor group and form a bond with a young dispersing female (polyandrous route).

The probabilities associated with each of these routes to adulthood are shown in Figure 8.12, and Table 8.5 combines these likelihoods with the

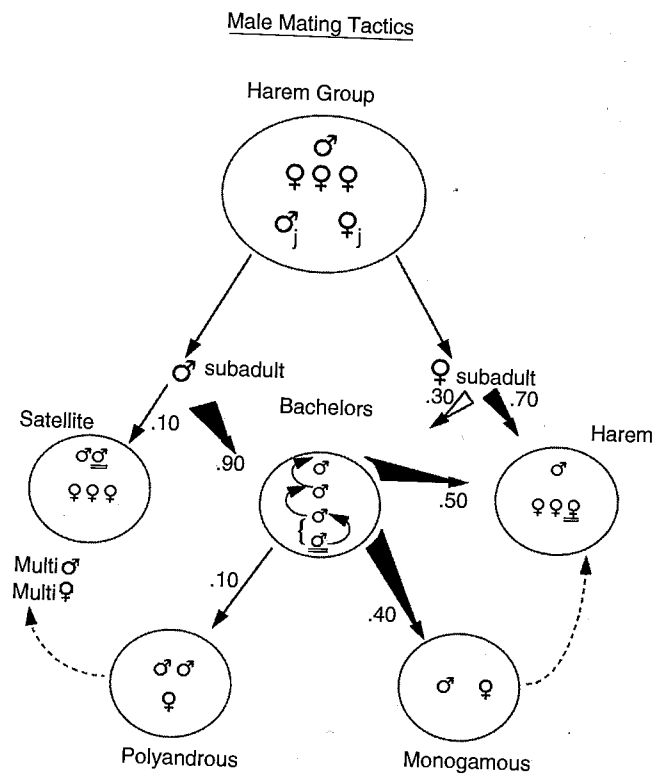


Figure 8.12 Pathways to adulthood of Shackleford horse males. All juveniles leave their natal groups. Females either join an existing harem group or bond to a high-ranking bachelor male. Males have four options available. They can follow the typical harem route by joining a bachelor group, rising in rank and taking over an existing harem. Or they can leave the bachelor group as an experienced young adult and bond with an emigrating female (monogamous route). Alternatively, they can join a bachelor group for a short period, leaving with a similar-aged low-ranking subadult and bond with an emigrating female (polyandrous route). Some males, however, forgo joining a bachelor group altogether and take up residence as a secondary male in an existing harem (satellite route). Probabilities of the various pathways are shown adjacent to pathway arrows.

reproductive values presented above to generate estimated lifetime reproductive success of males pursuing these different ontogenetic pathways. Not too surprisingly the typical harem route is expected to lead to the highest lifetime output. But what is striking is that two of the other trajectories are not far behind. And given that the patterns presented above show that there are large differences in both male and female reproductive success associated with

Table 8.5. Male reproductive payoffs

Reproductive component	Male mating strategy			
	Satellite	Polyandrous	Monogamous	Harem
Potential breeding years	10	8	8	6
Number of females	3 - >5	1 - >5	1 - >5	3 - >5
Inter-birth interval (years)	3 - >2	3 - >2	3 - >2	2
Number of receptive females	1 - >2.5	0.33 - >2.5	0.33 - >2.5	1.5 - >2.5
Percentage paternity	10 - >100	50	100	100
Yearly reproductive success	0.1 - >2.5	0.2 - >2.5	0.7 - >2.5	1.2 - >2.5
Lifetime reproductive success	10.3	7.3	10.4	12.8

rank of harem males, males adopting the satellite and monogamous routes are likely to perform as well as subordinates adopting the harem route.

The typical harem route derives its reproductive advantage because males take over an entire harem, usually containing a full complement of breeding females (4-6). As described above, females in single-male harems, especially if they are stable and the male is of high rank, have high yearly foaling rates and low inter-birth intervals. If takeover males are able to prevent other males from stealing these females and their harassment rate does not drive females away, then the expected reproductive success of takeover males will be great. But this route comes with an opportunity cost associated with time lost while rising in rank within bachelor society. It is precisely this cost that allows males adopting alternative routes to adulthood to flourish. Males adopting the monogamous route trade off time spent in acquiring dominance within bachelor groups with time spent increasing the size of their harems from one female to many. And while males adopting the satellite tactic reduce this opportunity cost to a minimum by associating with many reproductive females with almost no delay, their fertility is likely to be low initially since single harem stallions typically sire about 90% of a harem's offspring. While pairs of males adopting the polyandrous route also reduce the time to adulthood, they must share paternity, which will range from 10% to 50%.

Behavioral alternatives, inequality, and skew

Males

While this series of trade-offs makes it possible for alternatives to coexist, their existence reduces inequality in male reproductive success. If males did not avail themselves of these alternatives the reproductive disparity

among dominant and subordinate single harem stallions is likely to be even greater. Moreover, the behaviors that contribute to reducing reproductive inequality and stabilize these alternatives are the same behaviors that reduce reproductive skew. When males are challenged by other males for access to females, males must balance driving the challenger away and insuring that their females are not poached or do not stray. If only the typical route to adulthood existed, and males were only challenged by one stallion at a time, then balancing these competing demands would be straightforward: after a short period of assessment the subordinates would submit and herd their females away; if not, then dominants would escalate (Rubenstein & Hack 1992). Although herding females away from trouble solves a subordinate's immediate problem, the likelihood of female departures in the long run is high and thus provides the impetus for males to adopt alternative ontogenetic pathways. Since two-thirds of the alternatives entail young males attempting to get a head start on breeding by forming alliances either with similar age-mates (polyandrous route) or mature stallions on the decline (satellite route), the evolutionary stability of the alternatives depends on the behavioral dynamics that sustain these coalitions.

In both types of dual-stallion harems, the subordinate stallion is almost always first in approaching and engaging an intruder male. If his approach causes the intruder to retreat then little is risked and little energy is expended. Given his subordinate status, however, these initial contests usually escalate. Sniffing, squealing, and then biting, chasing, or rearing are commonplace (Rubenstein & Hack 1992). Since the intruder is far from his home area, the resident often has an ownership advantage and many (44%) of the contests end with the resident subordinate winning. But in slightly more than half of such contests (56%) the subordinate retreats, inducing the dominant male to join the fray. But this is where the two types of coalitions differ. In coalitions emerging via the satellite route, in virtually all contests (98%) the resident dominant wins. What is important to note, however, is that before the partner joined the harem, the solo stallion was losing encounters and was dropping in rank. By associating with a younger partner the situation becomes reversed. In the three instances of satellite coalitions forming, each original harem holder had been losing females. With the creation of these partnerships the harems began to grow again. In one instance the group grew from two to ten females. In coalitions begun via the polyandrous route, both males are usually in the bottom half of the breeding hierarchy. As a result, even with the dominant engaging the intruder first, resident dominants win less than half of encounters (38%) they assume. In no case, however, was a female ever abducted or seen to stray during a contest.

Clearly, coalitions of males protect against losing females while increasing the likelihood of winning, and perhaps even create long-term benefits by deterring future intrusions from neighboring males. For their services, subordinate males receive mating opportunities. In polyandrous-originating coalitions, subordinate males are rarely prevented (7%) from mating with estrous females. They are allowed to flehmen, inspect and lick female genital areas and, if the female doesn't kick while a subordinate is mounting or walk out from under him once he is mounted, then thrusting and ejaculation occurs without interference by the dominant stallion. In 96% of these cases the dominant male subsequently mates with the female. If the dominant mates first, however, the subordinate male usually attempts to mate but succeeds only 88% of the time. Thus sperm mixing is common and paternity sharing is likely (Ginsberg & Rubenstein 1990). Although the situation is similar for subordinate males opting for satellite-route partnerships, the percentage of mating attempts by subordinates is lower. Given that group size can be up to five times larger for satellite partnerships than polyandrous ones, absolute paternity benefits for subordinates in these two coalition types are not likely to be that different.

In over 17 years of studying the Shackleford horse population before population control began, only 12 coalitions formed and only three lasted until one partner died (Rubenstein 1982). As the above analysis shows, the expected lifetime reproductive success of these alternative strategies is predicted to be lower than that of the typical route to adulthood. Therefore it is not surprising that most coalitions disband after a few years. But while they last, what mechanism maintains them? Females generally do not stray far from a group even when in estrus. And given that the initiation and culmination of a successful mating takes between 2 and 5 minutes, it is unlikely that matings by a coalition partner will go unnoticed. That subordinates mate so often and without interference suggests that dominants are allowing them to do so.

While these behavioral events tend to support the idea that concession giving by dominants is a mechanism for maintaining the stability of groups, dominants continuously reinforce their dominance by initiating fights before, during, and after the breeding season. Maintaining rank differential within coalitions appears to be important, but whether it plays a role in conditioning inferiority in subordinates so that they initiate fewer matings, thus increasing inequality within the coalition, or whether it is part of the overall maturation process that leads to breaking up the partnership, is hard to determine. In one of the three cases of satellite-originating partnerships, the subordinate spent most of his time associating with all new females joining the harem as it grew. On a regular basis the dominant would disrupt these associations by chasing

the subordinate away. Eventually the subordinate left the coalition to take over a neighboring harem, and within a few days those females from the old harem with whom the subordinate had formed strong associations moved to his new harem. Thus it appears that dominants continuously reinforce their dominance over subordinates for good reason. Frequent low levels of aggression by dominants appear to limit freedom of movement by subordinates. But making subordinates "think twice" before attempting to mate also reveals that dominants are unable to enforce exclusive control of mating. Consequently, granting concessions and enforcing only limited control over subordinates – a form of selfish effort – appear to be operating jointly as Johnstone (2000) and Reeve *et al.* (1998) suggest and as Reeve & Shen (2006) explicitly capture in the "bordered tug-of-war" model.

Females

As we have seen above, reproductive inequality and skew also exists among females, even if the magnitude of these differences is smaller than among males. Since female rank affects reproductive success, dominant females have some control over the reproduction of subordinates. Yet subordinates stay. Why do they do so? In part they stay because they are tolerated by the dominants. Subordinates help limit the number of immigrating females joining harem groups (personal observation). Even in species where scramble competition is the norm, as it is in equids, competition will increase if groups get too large. Therefore, allowing subordinates to stay as an aid in preventing even more females from joining represents a cost to dominants. As predicted by concession models of skew (Johnstone 2000), granting residency appears to be a price that dominants pay to derive even greater gains. But do dominants actually have the ability to determine the optimal size of their harems? The answer is mostly likely no – and understanding why provides a more compelling reason why subordinates stay. Stallions typically stand near immigrating females, protecting them from approaches by other females and thus limiting the ability of resident females to force immigrants from harems. Because male rank and the social stability it provides affects female reproduction more than does female rank (Rubenstein 1986), when male and female reproductive interests come into conflict, females are caught in a bind. Consequently, they rarely confront males, and male interests tend to prevail.

The limited ability of females to control their own reproductive success is underscored by two unfortunate "experiments" that occurred on Shackleford Banks when two harem stallions inadvertently died during immobilization by another team of researchers. Since this immobilization was being carefully monitored, we were able to get detailed, fine-grained behavioral data on the

social behavior of the unguarded females. Almost immediately these groups were besieged by harem leaders and high-ranking bachelors. For up to four days these females fended off advances, but the intrusion rate was over 10 times higher than when their harem males were present. The percentage of time females foraged decreased from 72% of every hour to less than 40%, not only because of direct approaches by males, but because all female groups retreated to less frequented areas where forage was less abundant and of lower quality. After four days each group disintegrated.

This inadvertent perturbation to the normal social structure highlights the central role that males play in the lives of females. Their increased vigilance reduces their grazing time to 80% of that of their females, but it also buffers their females from extensive intrusions. As a result, females are provided with increased time for grazing and a means of enhancing their reproductive success (Rubenstein 1986). Our observations also suggest that frequent reciprocal and mutualistic actions that would be required of females to hold groups together in the absence of males are costly. Thus female-female transactions in which dominants would limit their aggression towards subordinates could in theory encourage group cohesion as predicted by concession models of skew (Johnstone 2000). But even if females attempted to grant such concessions to foster residency, their actions would be superseded by female-male transactions. But what form are these transactions likely to take?

Males have much to gain by keeping as many females as possible in harems. Subordinate males do this by adopting a "best of a bad job" strategy of herding females away from competitors rather than driving competitor males away from females (Rubenstein 1994). In the long run such behavior reduces subordinate harem size and ultimately reproductive success. Dominants, however, provide more stable and less stressful environments for females, where their reproductive success is enhanced. Dominants also attract more females than subordinates. For males, both factors increase reproductive success.

Skew dynamics

Understanding how males and females balance the tension between cooperation and competition provides insights into the processes determining levels of reproductive inequality and skew. For group-living species, reproductive skew emerges when three conditions pertain: dominants must be able to limit the reproduction of subordinates; subordinates must do better by staying than by leaving; and dominants must do worse if subordinates leave rather than stay. For horses all three conditions are met, but because of novel social dynamics. First, although competition among females is limited and involves "scramble" rather than the "contest" behavior, dominant females

control the reproduction of subordinates to a limited degree (Table 8.3). Second, subordinate females do help dominants by preventing additional females from entering the group and intensifying competition. And third, subordinates faring poorly sometimes do leave harems in search of better opportunities, but the process of integrating into new ones is difficult and not without costs (Figures 8.9–8.11). Thus for some subordinate females that are balancing the marginal gains of staying with leaving, concessions could tip the balance enticing them to stay and join in mutualistically beneficial behavior. But dominants do not appear to offer such concessions because males intervene to keep these subordinates – as well as many future subordinates – in their groups.

Since the size of harem groups that benefit polygynous males will usually be larger than those that benefit females (Armitage 1981, 1986), reproductive tension is created among males and females. While agonism by dominant females does induce some subordinates to leave when groups get large, aggressive herding by males usually overrides the actions of their dominant females. But if males are too aggressive, subordinate females receiving herding actions by stallions will leave anyway. Thus, to maintain large harems, dominant males must curtail excessive aggressive behavior. Ultimately, the ability of males to balance agonistic and affiliative tendencies towards females will determine how many, and which, females stay. Just as dominant males in multi-male harems maintain their coalitions by conceding reproduction while simultaneously engaging in occasional bouts of aggression to condition subordinates to limit reproductive competition, harem males will strive to maintain harems larger than preferred by their females by using aggression against females in limited and discretionary ways.

Rarely in animal societies are reproductive interests among group-living individuals of one sex mediated by interactions and transactions with members of the other sex. But it may be widespread in the equids. In plains zebras, herds form as harems coalesce (Rubenstein & Hack 2004). Harems come together because cuckolding pressure imposed by bachelors is high, higher than levels reached in horses. Presumably high levels of predation favor bachelor males forming long-term associations with a large number of males facing similar risks. When confronted with coordinated actions of many bachelors, harem stallions reduce their individual cuckolding risk by banding together and keeping bachelors on the edge of the herd (Rubenstein & Hack 2004). Clearly males benefit by forming herds, but they can only do so because female foraging success is similar whether harems are in or out of herds. To insure that females remain indifferent, males in herds incur reductions in time spent foraging above those incurred when their harems are alone on a

landscape (Rubenstein & Hack 2004). This represents a significant concession to maintaining herd stability.

Impact of management on reproductive inequality and skew

In 2000 the US National Park Service began managing the Shackleford horse population with PZP immunocontraception of females. Along with yearly removal of females, this kept horse numbers well below carrying capacity. One immediate consequence of these interventions was an increased birth rate and a release from density-dependence. What little competition for resources existed in the more natural state, the current state offers even less. Other consequences were seen with respect to changes in behavior. Young females, especially those coming into estrus for the first or second time, showed reductions in time spent feeding and increases in time spent standing (Rogers 2001, Constantino 2002). Males also showed greater tendencies to herd females, especially those having received contraception (Stroeh 2001). After six years of intervention, patterns of reproductive inequality and skew of males and females have changed. As shown in Table 8.1, the variance in the distribution of total births, yearly foaling and siring rate, and the number of young surviving to the age of independence have all decreased.

In many respects, the underlying factors affecting these measures of reproductive success remain unchanged after management. Age still has a major impact on the number of foals born during the 6 years ($F [1,42] = 8.15$; $p < 0.007$; $r = 0.40$), on the foaling rate ($F [1,77] = 56.79$; $p < 0.0001$; $r = 0.64$), and on the number of harem changes made by females ($F [1,70] = 8.95$; $p < 0.005$; $r = 0.33$). After computing appropriate residuals to account for the influence of age, female rank still affects the total number of foals born throughout the period as well as the annual foaling rate (Table 8.6). And while females associating with males of higher rank perform better reproductively than females associating with lower-ranking males, the effect is of reduced significance (Table 8.6). Since females receiving contraception continue to cycle throughout the entire reproductive season, genital inspection and harassment remains high for all males (Stroeh 2001). Consequently, differences in the way males of different ranks interact with females have been diminished.

Reducing both the variance and skew in the number of foals born or sired during this six-year period should increase effective population size, since more females will contribute similar numbers of genes to future generations and a greater proportion of males will sire offspring (Falconer 1960). Given that the US Park Service is holding population numbers between 120 and 130, supporting

Table 8.6 Factors affecting reproductive success in horses after management commenced

x -variable	y-variable		F	df	p value	r
Female rank	Total foals sired					
	(mean)	(SE)				
High	0.54	0.19	37.17	2,31	< 0.003	.57
Middle	-0.24	0.36				
Low	-0.43	0.18				
Female rank	Yearly foaling rate					
	(mean)	(SE)				
High	0.075	0.04	3.72	2,48	< 0.03	0.36
Middle	-0.003	0.07				
Low	-0.60	0.03				
Female rank	Residual numbers of mares					
	(mean)	(SE)				
High	-0.25	0.26	1.59	1,70	< 0.25	0.24
Middle	-0.27	0.47				
Low	0.32	0.23				
Male rank	Foaling rate					
	(mean)	(SE)				
High	0.27	0.05	2.92	2,19	<0.07	0.28
Middle	0.20	0.08				
Low	0.01	0.07				

inherent features of a species' social biology that reduce the loss of genetic diversity is important.

Discussion

In our populations of horses and plains zebras reproductive inequalities and skew occur for males and females. At least for male horses, variation and skew would have been greater had it not been for the opportunity for low-performing males to join groups of different types. Such variants are maintained because of the many ways in which adjustments in concessional and selfish effort can be made. In all multi-male harems, complete control by dominants is absent either because aging males are dropping in rank (satellite route) or because young partners begin their reproductive lives as inexperienced equals (polyandrous route). Both situations meet the assumptions of the

bordered tug-of-war model, and the relatively peaceful coexistence that emerges fits one of the model's predictions (Reeve & Shen 2006). If there are no strong ecological or social reasons for maintaining groups, the model predicts that the degree of strife within groups will be low. Given that joining bachelor groups is a ready alternative that only incurs a moderate cost of delaying reproduction for a few years, it is not surprising that fights among coalition partners are infrequent and of low intensity.

Coalitions among males are not limited to our horse and plains zebra populations. While coalitions are relatively rare in our study (< 10% of harem groups in any given year), they are common in other horse populations. On a nearby North Carolina island 50% of the harem groups were led by two males (Stevens 1990); multi-male groups comprise 12% of harem groups in the Great Basin (Berger 1986); 33% of groups in the Kaimanawa Range are led by multiple males; and 38% of the reproductive units in the Camargue horses contain two or more males (Feh 1999). Recently there has been much debate as to whether these multi-male units are coalitions formed by mutualistic or reciprocal relationships (Feh 1999, Linklater & Cameron 2000a). Linklater (2000) and Linklater & Cameron (2000b) claim that multi-male associations are not true coalitions in part because the authors assume that the reproductive success of males and females inhabiting multi-male groups must equal that of males and females in uni-male harems. Otherwise, they could not be maintained by selection. Game theoretic models that account for differences in phenotype (Parker 1984) offer many alternative predictions concerning reproductive payoffs that would permit multi-male social units to be maintained. And if males and females residing in them do so only temporarily as part of a complex life cycle, then the existence of such social variants is easier to sustain; as payoffs produced during one period are incorporated into measures of overall lifetime reproductive success their contribution is diluted.

Feh's field study (1999) and critique (2001) provide ample evidence that multi-male groups are functional coalitions. As a result, understanding the behavioral dynamics that hold them together can provide insights into how evolutionary forces generate skewed reproductive patterns. In accord with concession models of skew (Johnstone 2000), we have shown the degree to which both dominants and subordinates act selfishly and provide concessions that maintain these groups until balance among the payoffs changes. And change they will as phenotypes and environmental conditions change. Feh (1999) describes trade-offs associated with the different roles that are similar to those we find: subordinate coalition members take more risks and dominants rarely interfere with matings of subordinates, although they are aware that they are occurring. Feh also goes one step further and calculates the degree to

which dominants allow subordinates to mate. In the Camargue population, subordinates sire about 25% of multi-male groups' offspring, a value that is consistent with our expectations.

What makes our study unique is that we also explore the more complicated dynamics underlying unequal and skewed reproduction of females. While not as great as in males, female reproductive skew is also significant. Despite abundant vegetation and physiologies that make subsistence on low-quality food economical, agonism persists among females and dominance hierarchies emerge. That dominance affects reproduction demonstrates harem females invest in selfish behavior. Mutual support among females in keeping additional females from joining harems benefits females of all ranks, and shows that dominants are prepared to provide concessions to retain the services of subordinates. But group cohesion can only be maintained if subordinates also offer concessions to dominants at critical times. Such concessions are seen occasionally at watering points where access is extremely limited (Rubenstein 1994). Yet even though these conditions meet the assumptions of the bordered tug-of-war model, they are not the conditions that matter most in shaping skewed reproduction of females. Male preferences for even larger harems generate pressures to override the preferences of females. But in meeting their selfish needs, males could often drive away precisely those females they want to retain. Thus males are left balancing agonistic and affiliative tendencies with those of their females. As the model suggests, the optimal mix is likely to change with changes in group size as well as demography. Thus we expect that when there are many harems available rates of herding and harassment should decrease.

The bordered tug-of-war model predicts that when ecological conditions are harsh, group breakup will be constrained and destructive conflict within groups should increase. What makes equids special is that they are among the few grazers that experience little competition. Marmots (*Marmota* spp.) are also grazers, but they are less free to wander widely in search of forage since they are tied to burrows for safety from predators (Armitage 1981, 1986). Thus they should experience greater competition than horses and plains zebras and they should exhibit more strife among dominants and subordinates. This appears to be true for most of the socially monogamous species. The need to maintain warmth during hibernation apparently selects for small numbers of young and thus complete reproductive suppression of subordinates by dominants (Allainé 2000). Reproductive skew is less pronounced in the yellow-bellied marmots (*Marmota flaviventris*), even though all females compete for limited resources. Apparently females cooperate in keeping other groups of females from usurping parts of the home range (Allainé 2000), much as female equids cooperate to keep additional immigrant females from joining harems. In both species emigration

by females is possible, thus reducing skew, but in marmots, males appear not to be involved in adjusting concessional and selfish investments.

In our study we showed that the dynamics shaping sociality in horses operate in plains zebras as well. Dominance differences set the stage for inequitable and skewed reproduction in males and females of both harem-living species. The importance of male rank in balancing concessional and selfish effort is a thread in both species' social cloth. Yet in plains zebras this thread appears stronger where ecological conditions make it more difficult for males to maintain control of females and their reproduction. Incomplete control of reproduction necessitates transactions between dominants and subordinates in order to stabilize social orders. When these transactions involve individuals within and between the sexes it is not surprising that a variety of mating and social structures can coexist. This is especially true for horses, and should be searched for in other species where conflicts of interest among many phenotypes are common.

Conclusions

Inequality in reproductive success in horses and zebras exists in both sexes, although both variance and skew is greater for males than for females. Differences in age and status shape the distributions of reproduction for both males and females. Social stability also determines degree of skew. After controlling for age, females that change groups often breed less often than those that remain attached to particular males for long periods of time. And for males, greater reproductive success accrues to those that curtail harassment of females. Perhaps what is most striking about equids that form long-term breeding associations among males and females, as is the case in horses and zebras, is that the magnitude of skew is lower than could be expected. Such attenuation emerges because of two factors. One is that males can adopt a number of alternative reproductive tactics. Each alternative relies on concessions to subordinates that boost reproduction above what would be achieved at that age by adopting the typical tactic. Moreover, each alternative tactic enhances the reproduction of the concession giver over what he would have gained without joining the partnership. Similarly for females, concessions enable non-harem females to gain access to a dominant male while limiting the loss of reproduction that females already bonded to such an "attractive" male would incur if group size were to grow even larger. The other factor is that intersexual conflict reduces reproductive differences within the sexes because neither males nor females can completely enforce their self-interest. While males would prefer larger harems, which would enhance male skew,

the aggression necessary to effectively maintain large groups would most likely drive females away. And for females the ability to keep group size small by peripheralizing additional females, thus reducing female skew by allowing wandering females to be spread more equitably among males, is modulated by male herding. Thus, while phenotypic differences such as age and size and their distribution within populations play important roles in shaping patterns of skew, a variety of intra- and intersexual relationships that characterize harem-living equids also influence sex-specific patterns of skew. The extent to which the interplay between these forces shapes skew in other harem-living species, or even species exhibiting other mating systems, needs to be explored.

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