

15 • Natural and sexual selection and the evolution of multi-level societies: insights from zebras with comparisons to primates

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INTRODUCTION

Animal societies derive from the social relationships that exist among its members (Hinde, 1983). Behavioural ecologists have traditionally focused on the core relationships defining a mating system as a means toward understanding the role of ecology in the evolution of sociality (e.g. Jarman, 1974; Bradbury & Vehrencamp, 1977). Typically, these core relationships emerge from the operation of both natural and sexual selection and how they differently affect the behaviour of females and males (Rubenstein, 1986; van Schaik, 1989). However, emphasis on mating systems has tended to marginalise the importance to social evolution of interactions and relationships that extend beyond the basic breeding unit. This is even true for the small subset of species with multi-level societies, where breeding units and other social subgroups are themselves organised into more complex social groups within a population. By examining how natural and sexual selection operate within multi-level societies, however, a more complete understanding of the function and evolution of sociality emerges than would by investigating the dynamics of mating systems alone (e.g. Dunbar, 1988).

Although the societies of many primate species are multi-levelled, the relative simplicity of societies of plains zebras (*Equus burchelli*) where only two tiers exist – the core breeding units and the herds they often comprise – can provide insights into the rules that give form to multi-level societies. In this chapter we begin by highlighting the environmental and sociosexual factors that shape zebra mating systems and herd dynamics. Then we show how characteristics of zebra herds emerge from individual cost–benefit decisions. Typically, forces of natural selection, because they operate on traits that promote survival via enhanced resource acquisition or reductions in predation risk, are thought to be most

important in shaping patterns of sociality (Jarman, 1974). Yet we show that while these forces play important roles in determining both core mating associations and the dynamics and structure of zebra herds, the forces of sexual selection, with their pressures to maximise mating success, also influence zebra herding behaviour by affecting the social decision-making processes of adult and subadult males. In particular, we show that the need for band, or ‘harem’, stallions to reduce the risks of cuckoldry by subadult bachelors plays the greatest role in determining when zebra core-mating units should coalesce to form herds. Overall, we show that higher levels of social organisation provide individuals with a source of potential social options for solving ecological and social problems that cannot be solved by adjusting relationships within core social groups. Higher-level connections between groups, however, only appear to remain viable when the relationships holding together the core social units themselves are not disrupted.

ZEBRA MATING SYSTEMS AND HERD DYNAMICS

EQUID MATING SYSTEMS

Our current understanding of plains zebra societies results from studying equid mating systems, of which the seven extant species display two general types (Klingel, 1974). In the African and Asiatic asses (*Equus africanus* and *E. hemionus*, respectively) and Grevy's zebra (*E. grevyi*), adult females and their most recent offspring range over large areas and form only temporary groups (Klingel, 1977; Woodward, 1979; Ginsberg, 1989). Breeding is not highly synchronised and breeding males defend mating territories for most of the year near resources needed by females. Plains zebra, mountain zebra (*Equus zebra*) and horse stallions

(*Equus caballus*) are also polygynous, but defend exclusive mating rights to small year-round harems of one-to-several females (Klingel, 1969a; Joubert, 1972; Groves, 1974; Feist & McCullough, 1976; Miller, 1979; Rubenstein, 1981; Penzhorn, 1984; Berger, 1986; Lloyd & Rasa, 1989). Females form social bonds with each other (Rubenstein, 1986; Rutberg, 1990), often living in the same harem for the majority of their reproductive lives (but see Berger, 1986), and they remain together even after replacement of the stallion. Interestingly, these females are not close relatives, as in most other mammals with stable female groups (Clutton-Brock, 1989), since both sexes disperse from their natal harems at 2 to 4 years of age (Berger, 1987).

Differences in the ecological environments inhabited by equids provide a first step towards explaining the basic dichotomy in their mating systems (Rubenstein, 1986). A fundamental tenet of behavioural ecology is that female movements and associations are driven primarily by the distribution of resources and the risk of predation – both forces of natural selection that shape individual survival and reproductive abilities; while male movements and associations result from the consequent distribution of females – both forces of sexual selection that affect the ability of males to secure matings with multiple females (Bradbury & Vehrencamp, 1977; Emlen & Oring, 1977). All equids are relatively large for ungulates, feed by grazing, and require water in addition to their food. Accordingly, individuals need to consume large amounts of grass and drink daily, for all individuals of the smaller-bodied species and the lactating females of the larger-bodied species (Ginsberg, 1989). The relatively open environments they inhabit and their lack of overt morphological defences can expose them to high rates of predation (Turner, 1992; Scheel, 1993). The asses and Grevy's zebra live in xeric environments where grass occurs in small patches distributed sparsely over a large area. Competition among females for grass presumably prevents their long-term association, and stable groups never form. In addition, the best grazing sites are often far from water (Rubenstein, 1989), weakening bonds between females with different water needs and abilities to travel (cf. lactating and non-lactating). Given the low density of females and their large home-ranges, males maximising reproductive success by defending either access to water or territories encompassing a variety of grassland types, will have at least some productive areas attractive to hungry females (Ginsberg, 1989; Rubenstein, 1994).

The other equid species, including the plains zebra, inhabit more mesic habitats where grass occurs in much

larger patches, is distributed more uniformly throughout a patch, and lies in closer proximity to water (Rubenstein, 1994). Consequently, the costs of competition among females are reduced, allowing groups to persist year-round. In addition, higher predator densities in mesic habitats result in greater anti-predator benefits from grouping. However, since female home-ranges are still large, males cannot economically defend the area needed by a group but instead defend the group itself (Klingel, 1969b; Joubert, 1972; Penzhorn, 1984). At least in the population inhabiting the Samburu-Buffalo Springs Game Reserve, a male's defence of his females from harassment by other males or the better access he can provide to contested resources produce reproductive benefits for females that may be the final elements favouring small, highly cohesive groups (Rubenstein, 1986; Linklater *et al.*, 1999). Studies of intraspecific variation confirm the importance of these ecological factors in shaping equid mating systems (Moehlman, 1979; Rubenstein, 1981, 1986; Ginsberg, 1989). A recent review by Linklater (2000), however, questions the tightness of the linkage between these ecological features and the nature of equid mating systems, but it does so by discounting the utility of precisely those studies that most strikingly highlight variations on the two major equid organisational themes. As new details emerge from more standardised comparative studies, alternative explanations determining mating systems based on additional factors, both past and present, may emerge. Yet until they do, habitat variation can be viewed as playing an important role in shaping the mating and social relationships that develop among equids.

ZEBRA HERD DYNAMICS

In contrast to most ungulates, plains zebra live in multi-level societies. A year-round 'harem' or 'band' of several adult females and their recent offspring, defended usually by only a single male, constitutes the basic breeding unit. Non-breeding, but reproductively mature, males also associate, forming 'bachelor' groups that range in size from two to more than 40 individuals. Both types of core social groups are common to equids (Klingel, 1974; Rubenstein, 1986) and other mammals (McCracken & Bradbury, 1981; Clutton-Brock, 1989), but a level of social organisation that is rarely observed in harem-forming species other than primates (reviewed by Stambach, 1987) is the formation of herds. Harems regularly associate in spatially cohesive herds that vary in both size, from two to over 100 harems (Fig. 15.1a), and in composition, containing harems and

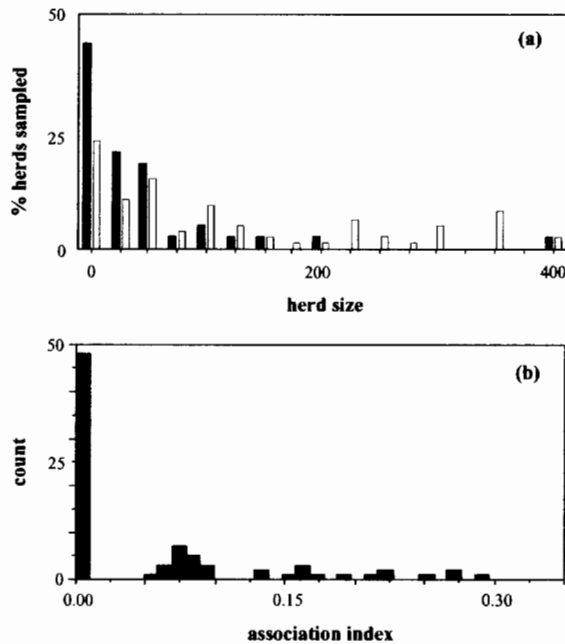


Fig. 15.1 (a) The frequency distribution of plains zebra herds by size in Ngorongoro Crater, Tanzania. Solid bars represent herds in the dry season; open bars represent herds in the wet season. (b) The frequency distribution of index of association among harems in Ngorongoro Crater, Tanzania. $IA = 2C/(A + B)$ where A is the number of times harem A is seen, B is the number of times harem B is seen and C is the number of times harem A and B are seen together.

bachelor groups or just harems. Preferential associations between pairs of harems – observed in different populations ranging from the species' northern limit in the arid Samburu ecosystem (Rubenstein, 1986) to the relatively lush grasslands of the Ngorongoro Crater (Fig. 15.1b) – create temporally stable subgroups within a larger herd and indicate a type of non-randomness to herd formation and structure. These observations, when considered together with the plains zebra's long life and the potential for close kin of either sex to reside in neighbouring core groups, suggest that interactions with individuals outside one's core group reflect a second tier of social relationships that critically shape the overall organisation of plains zebra societies.

Social relationships within a breeding group change over a lifetime. Individuals mature, gain experience and alter their competitive prowess and abilities to build alliances in a social context that also change with the comings and goings of competitors and allies alike, consequently affecting individ-

ual routes to breeding success (Pereira & Fairbanks, 1993; Feh, 1999). Similarly, the nature and types of relationships formed beyond the breeding group may critically affect the particular route an individual takes, as studies on the evolution of helping-behaviour have demonstrated (Brown, 1987). With respect to true multi-level societies, such as those of gelada (*Theropithecus gelada*) and hamadryas baboons (*Papio hamadryas*) (Stammach, 1987), the association of breeding units into higher-level social groups arises because these groups fulfil specific functions that breeding units alone do not (e.g. reduce predation risk in geladas (Dunbar, 1986), or facilitate mate or resource defence in hamadryas (Kummer, 1968; Sigg *et al.*, 1982)). These different functions could emerge from the fact that two societies, built from outwardly similar core mating groups (harems), and structured in both cases by kinship, are very different overall organisations – female-centric and matrilineal society in geladas vs. male-centric and patrilineal society in hamadryas. Thus, an understanding of the dynamics of social relationships within breeding groups may provide some understanding of a society's overall dynamics. Feedbacks between levels are likely to be important and yet remain largely unexplored. Studies on primate species with multi-level societies clearly show that two ecological forces – the 'top-down' force of predation and 'bottom-up' forces associated with vegetation – help determine the nature of higher-level societies that emerge. Yet a third factor – sociosexual forces – should also come into play. At least in a plains zebra population inhabiting the Samburu–Buffalo Springs Game Reserve at the northern edge of the species' range, the preferential associations that form among harems are long-lasting and appear to enable stallions more effectively to keep their females away from the advances of bachelor males (Rubenstein, 1986). By recording, in the Laikipia region of central Kenya, the size of herds (total number of individuals or number of harems), their composition (number of bachelor males relative to breeding males) and the ecological and social context in which they form, we have now been able to measure the relative importance of each of these three forces in determining the nature of zebra herds. By working on private lands, we sample zebra herds living in habitats that vary in overall structure as measured by the density of trees, as well as by the quantity, quality and diversity of vegetation. Moreover, predators range freely across ranches. Thus rapid changes in the numbers and types of predators threatening zebras are common. And lastly, Laikipia ranches vary in the way they legally crop zebras; some do not crop at all whereas others focus either on bachelor males or family groups, thus changing the local

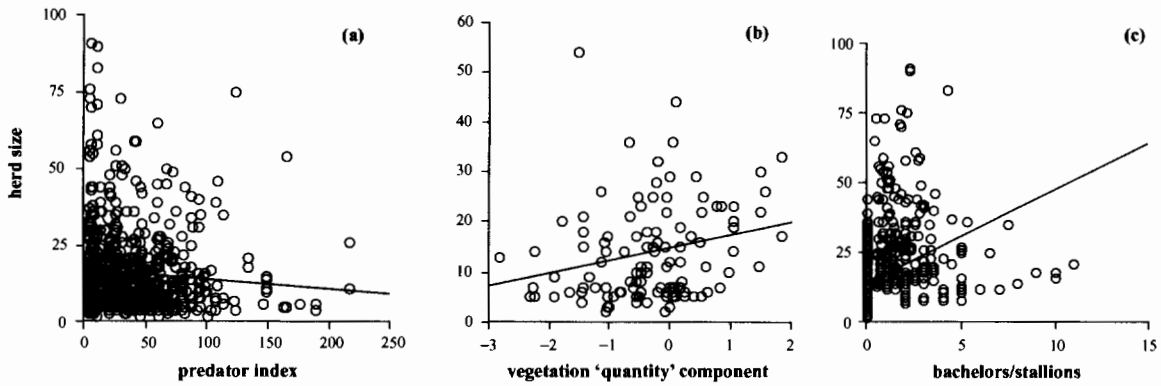


Fig. 15.2 Factors affecting herd sizes of plains zebra: (a) the impact of predator intensity: $y = -0.03x + 17.0$; $F(1, 684) = 4.3$; $p < 0.05$; (b) the impact of vegetation 'quantity': $y = 2.5x + 14.4$; $F(1, 105) = 7.8$; $p < 0.005$; (c) the impact of bachelor males nearby: $y = 2.6x + 10.4$; $F(1, 684) = 1024.5$; $p < 0.0001$.

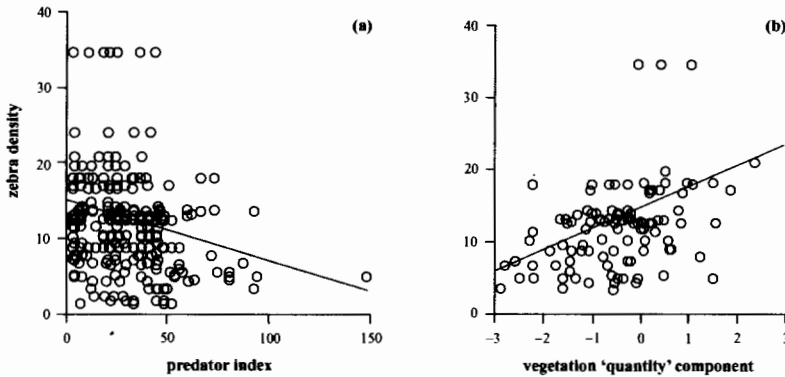


Fig. 15.3 Factors affecting the distribution of plains zebras across adjacent ranches in central Laikipia, Kenya: (a) zebra density on a ranch as a function of the number, type and impact of predators on the ranch (see text for details); (b) zebra density on a ranch as a function of the magnitude of the first-principle component of vegetation that was weighted by 'leaf density' and '% cover', both strong measures of vegetation 'quantity'.

ratio of bachelor to stallion males. Overall, variation is large with respect to all the dependent variables used in the General Linear Model we use to measure the relative importance of 'top-down', 'bottom-up' or sociosexual factors in determining herd size – as measured in terms of number of individuals or core social units; and composition – as measured in terms of bachelor-to-stallion ratios.

SOCIOECOLOGICAL PATTERNS IN LAIKIPIA

The overall analysis shows that all three factors play important roles in determining the dynamics of zebra herds. Although predation is often thought to be the most important factor in bringing individuals together to form groups (Alexander, 1974), our study shows the role of predation is only weakly implicated in determining the actual size of zebra herds (Fig. 15.2a). Yet this does not mean that predation is unimportant. As Fig. 15.3a shows, the risk of predation is a major determinant of where zebras tend to aggregate. Predators typically change location and vary activity throughout the day. Our predator index $PI = \sum [Abundance\ ith\ predator\ species \times Impact\ of\ ith\ predator\ species] \times [Habitat\ Visibility \times Diel\ Period]$, where the first part

of the expression represents Predator Incidence and the second part Context-Specific Risk, adjusts for these temporal and spatial changes and shows that as the risk of predation increases for a particular ranch, zebra numbers decrease. Thus as predators move into an area, zebras move out.

Once zebras assemble in a particular region – and the quantity of vegetation is a strong draw (Fig. 15.3b) – vegetation characteristics and the number of bachelor males in the vicinity of a harem all influence herd size (Fig. 15.2b, c). Of the three vegetation measures we computed using principle component analysis – ‘quantity’ ‘quality’ and ‘diversity’ – only ‘quantity’ matters. As the abundance of vegetation increases, so does herd size (Fig. 15.2b). Clearly, high levels of food regardless of its quality or diversity facilitate the coming together of core breeding groups. Apparently, the local abundance of leaves lowers competitive interactions as individuals increase spacing to reduce interference while grazing. But as Fig. 15.2c reveals, even more important in shaping herd size appear to be the effects of sociosexual pressures. As the number of bachelor males to breeding stallions in an area increases, so does herd size (Fig. 15.2c).

In order to determine the relative strength of these factors, partial correlation coefficients were computed and, as Table 15.1 illustrates, the strongest determinant of herd size is the ratio of the number of potentially cuckolding males to stallions in the vicinity of a herd (complete General Linear Model results appear in D. I. Rubenstein, M. Hack & D. Mazo, in preparation). Interestingly, while the ‘bottom-up’ factor associated with biomass still plays a role, a sociosexual variable plays the strongest role in determining the size of zebra herds. When the same analysis is performed for herd composition, as measured by the proportion of a herd that is composed of harem vs. bachelor groups, it is again a sociosexual variable that has the strongest effect (Table 15.1). In this case, however, it is the number of females in the herd that determines how many bachelor males will also be there. Thus overall it appears that the twin forces of sexual selection – male–male competition and female attraction – play the dominant roles in determining both the size and composition of plains zebra herds.

HERD CHARACTERISTICS AND DECISION-MAKING

Context-specific correlations are useful in suggesting how selection operates to generate particular patterns. Detailed behavioural measurements, however, often reveal how trade-

Table 15.1 *Partial correlation coefficients for herd size and composition versus the six dependent variables in each General Linear Model.*

Herd size vs:	Herd composition vs:
Zebra Density = 0.09	Zebra Density = -0.14
PC1: ‘Quantity’ = 0.18	PC1: ‘Quantity’ = 0.18
PC2: ‘Quality’ = -0.09	PC2: ‘Quality’ = 0.01
PC3: ‘Diversity’ = -0.07	PC3: ‘Diversity’ = 0.06
Predator Index = -0.09	Predator Index = 0.01
Bachelors/Stallions = <u>0.53</u>	No. Females = <u>0.26</u>

offs are handled and decisions are actually made. By recording the proportion of time that individuals spend foraging and then recording bite-rate during feeding intervals, we compute hourly intake rates. When these are compared across social contexts we can gauge how well individuals are performing in each. Figure 15.4 reveals how intake rate for individual males and females changes as both herd size and composition are altered. Even though males graze about 10 per cent less than females, both males and females feed most efficiently when the harem with which they are associated is alone on the landscape. As harems merge to form larger herds, both males and females experience slight reductions in foraging success but these declines are not statistically significant. In general, the presence of neighbours diminishes bite-rate slightly (Rubenstein, Hack & Mazo, in preparation), and although females spend the same proportion of time grazing as they do when a harem is alone, males end up re-deploying much of the time they normally spend vigilant, and some of the time they spend grazing, to socialising – displaying, fighting, but also mutually grooming – with other breeding stallions. Thus from the perspective of the females, there appears to be little difference in overall intake rate (bite-rate × hourly proportion of time grazing) between being in a herd of one or more harems. The same appears to be the case for males.

Herds, however, also vary in composition, and this is where sexual differences in foraging success appear. When a solitary harem is joined by a group of bachelors, the defending stallion spends virtually all of his time interacting with the intruders (Rubenstein, Hack & Mazo, in preparation) and this significantly reduces intake rate (Fig. 15.4). Not only does he leave his females and join the all-male group, he then proceeds to move among the males performing ritualised displays of dominance until each shows submission.

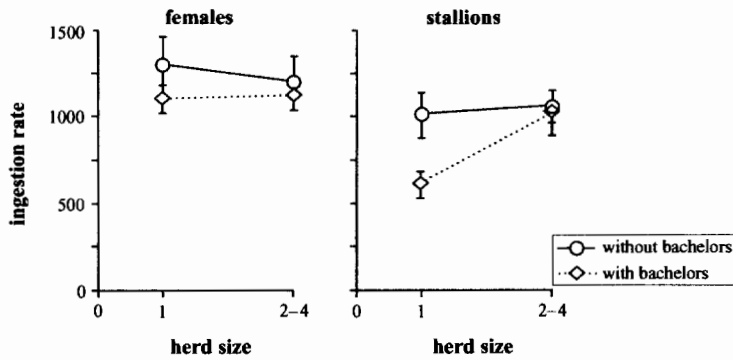


Fig. 15.4 Foraging intake rate for males and females in different social settings. Means and standard errors are shown. Solid line denotes social conditions without bachelor males present, whereas dotted lines depict conditions when bachelor males are present. Neither females nor males show differences in intake rate (bites per hour) when in a solitary harem or in small herds comprising between two and four harems. Males, however, do forage less than females in solitary harems, but the difference disappears when in small herds. When bachelor males join herds, only males show diminished intake rates when herds consist of just one harem, but this reduction disappears when mixed herds consist of more than two harem groups (2-way ANOVA interactions: males $F(3,89) = 3.1; p < 0.05$; females $F(3,142) = 2.3$; NS).

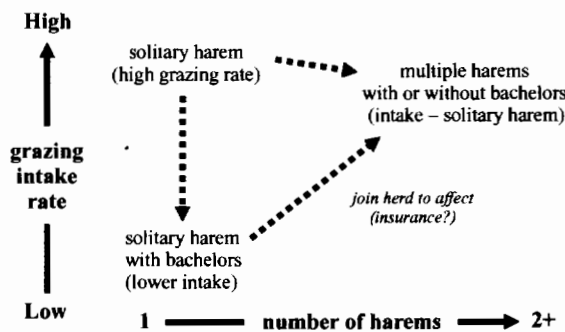


Fig. 15.5 Decision-making by breeding stallions. Stallion decision-making summarised by the impact of different social contexts on foraging success of females and their stallion, as illustrated in Fig. 15.4.

Occasionally, the males cease interacting in order to graze but they quickly return to low levels of jousting. Females, however, largely remain oblivious to these male escapades and continue grazing. As Fig. 15.4 illustrates their intake rate diminishes only slightly from that achieved when bachelor

males are absent. Thus it is the stallion that bears the brunt of preventing bachelors from interacting with his females. Given the high foraging cost of protecting against cuckoldry when alone, and the insignificant feeding costs of joining a herd and potentially acquiring the support of other male allies, it is not surprising that herds form.

In fact, patterns associated with intake rate (Fig. 15.5) suggest that herds should form even without the direct instigation of bachelor male incursions, since the costs in terms of reduced foraging efficiency for both males and females are so small whenever harems coalesce into moderate-sized herds. As our study takes place on many ranches where zebra cropping varies in intensity, as well as in terms of the age and sex-class of animals taken, we can compare the average size of herds that form on ranches where bachelor males are rare with those on ranches where they are abundant. On ranches where the bachelor-to-stallion ratio is high (~1.5), the size of herds consisting of only harems averages 17.1 ± 1.3 individuals (mean \pm S.E), approximately three harems, which is significantly larger than the herd size of 12.9 ± 0.9 individuals (~two harems) on ranches where the bachelor-to-stallion ratio is lower (~0.7) ($F_{1,256} = 6.7; p < 0.01$). It appears that as the probability of encountering bachelor males increases, stallions are more likely to form associations with other stallions to limit the threat bachelors pose. Herds thus appear to be a low-cost form of 'insurance' that serves the sexual interests of breeding stallions.

DECISION-MAKING BY BACHELOR MALES

ONTOGENETIC TRAJECTORIES

While harem stallions appear to adjust their behaviour to the risks imposed by bachelor males, bachelor males themselves are under evolutionary pressure to pass quickly, but

efficiently, through this subadult stage of their lives and surround themselves more permanently with females. To become successful breeders, what should 'clever' bachelor males do? Clearly, they must survive; staying in the game is essential. But growing quickly is also important. Without attaining sufficient adult physical stature it will be difficult for a stallion to hold on to females when sexual intrusions occur. But maximising survival and foraging success is likely to be mutually exclusive. Data from our Laikipia zebra populations clearly show that just as for herds composed predominantly of breeders, the size of bachelor groups increases as predation risk increases ($y = 0.91x + 0.9$; $F = 7.1$; $p < 0.01$; $r^2 = 0.10$). Yet where predator protection is likely to be greatest, foraging appears to be most limited (Rubenstein, Hack & Mazo, in preparation). Of seven solitary bachelors seen during our surveys, all were grazing when detected. For those in all-male groups, however, the percentage of grazing individuals drops to near 45 per cent, while for those in herds comprised of both bachelors and harem groups the percentage of bachelors seen grazing falls to just under 20 per cent ($X^2 = 39.6$; $p < 0.0001$; $df = 2$). Apparently, the need for safety and food are largely incompatible.

But to balance staying alive with gaining strength is not likely to be enough. Making the transition to breeding status requires acquiring a variety of social skills. Fighting requires strength but it also depends on agility and mastery of specific tactics designed to outmanoeuvre an opponent (Berger, 1986). Nipping, neck rolling, mock-biting, rump pushing, cutting and turning while running are activities practised repeatedly by bachelors when they are in groups. But mastering the tactics of fighting with other males is itself only part of the social 'tool kit' needed by a maturing bachelor. In equids, successfully breeding males establish strong, long-lasting social bonds with their mates (Rubenstein, 1994) and therefore must learn how to behave toward females to initiate and maintain these bonds. In wild horses, males without extensive experience of interacting with reproductive females frequently lose them to other males, or are less successful in their mating attempts (Stroeh, 2001). Therefore, the successful transition from non-breeder to breeder in plains zebra will require not only physical maturation and growth but the acquisition of critical social skills with both females and other males.

As bachelor males mature they often change social settings. As indicated above, they can be found alone, together with other males or in herds where both males and females are present. Presumably young male zebra vary their social setting because each provides different opportunities to grow,

acquire necessary social skills and survive. Moreover, as bachelor males mature, their requirements may change as their size or condition changes. Assuming that a bachelor is able to choose its preferred social setting independently of other males, which setting or combination of settings should it choose in order to maximise its future breeding success? How should this choice change with age, condition and experience? And does ecological context, in terms of food abundance and predation risk, affect a young male's choice?

MODELLING BACHELOR-MALE DECISION-MAKING

To help gain insights into how maturing bachelor males can best answer these questions, we apply a state-dependent dynamic modelling approach to the non-breeding period of plains zebra bachelor males. Observations on a variety of equid populations reveal that juvenile males disperse from their natal groups when 2 to 3 years old and then usually spend 4 to 6 years in bachelor associations, until physically and socially mature enough to sustain long-lasting relationships with females (see Feh, 1999). During this transition period young zebra males can be found alone, in groups of up to 25 other bachelor males or in mixed herds composed of harem and bachelor groups.

Each social context potentially offers different rewards and potentially extracts different costs. Being solitary should provide the highest foraging gain but also the highest risk of predation and the least opportunity to acquire social skills. Whereas all male groups offer predator protection, feeding rate declines as males engage in activities associated with acquiring male-related social skills (see Fig. 15.4). In mixed herds, predator protection is also great, although the extra 'anti-predator dilution' benefit of having more vulnerable youngsters around may be offset by an increased risk associated with peripheralisation induced by harem stallions. Foraging is probably at its lowest level, again because of peripheralisation to marginal feeding patches, as well as the result of frequent male contests; but in mixed herds the ability to acquire social skills is likely maximised. In such associations not only will bachelors interact with each other but also they will expand their contacts to include breeding stallions as well as their females. If these trade-offs are realistic – and preliminary observations suggest they are – then we can use the model to determine which herd-related developmental strategies are best under particular ecological conditions.

In our model (complete development in Rubenstein & Hack, in preparation) we assume that a young male, after

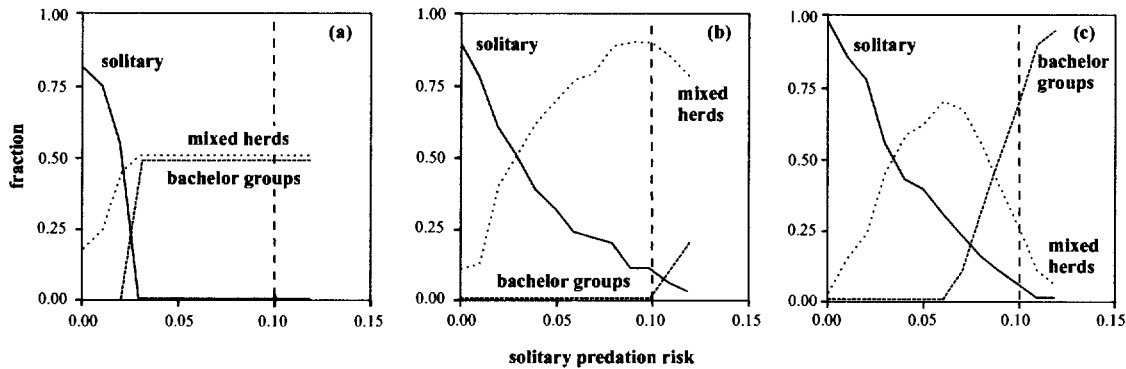


Fig. 15.6 Simulations of the stochastic dynamic-programming model on the optimal behaviour of bachelor males. In (a) and (b) predation risk is equal for all-male groups and mixed herds, and equals 0.04; and social experience gained is scaled at 0 for solitary bachelor males, 0.5 for those in all-male groups and 1.0 for males in mixed herds. Where (a) and (b) differ is in terms of weight gain: in (a) solitary males and males in all-male groups graze equally well and gain weight at a rate of 1, whereas bachelors in mixed herds do less well and gain weight at a rate of 0.5; in (b) weight gain remains the same for bachelors in all-male groups and mixed herds, but solitary males do much better and are scaled at 5. Where (c) differs from (a) and (b) is found in the risk of predation. In (c) bachelors in mixed herds suffer slightly greater risks of being preyed upon, and thus per-capita mortality increases to 0.045.

leaving his natal group, must survive four years as a non-breeder before being able to compete for his own females. During this transition period a bachelor must also grow in size and gain social experience with males and females in order to be competitive. To maximise his chances of success a bachelor may freely switch among social environments, and a male's state at the end of the non-breeding period – as measured by his body size and accrued social experience – determines his eventual lifetime reproductive success relative to the other members of his age cohort. In the model, we have divided the bachelor male's year into four time-steps of equal length corresponding to ecological seasons. Thus the maximum lifetime of a bachelor male is 16 time-steps. Each social environment it chooses entails a risk of predation, so survival to the next time-step is not certain. Also, the rate at which body mass and social experience increases varies with social environment. Because of stochastic events, individuals may differ in state upon arriving at the same decision point. As the iterations depicted in Fig. 15.6 illustrate, the values of the variables associated with each social context used in the model are easily scaled to reflect these trade-offs and adjusted to overall ecological conditions.

The dynamic-programming technique allows us to define the optimal choice of social environment at each time-step, depending upon each male's state values at that time-step. This is achieved by defining fitness in the present time-step (t) as a function of fitness in the next time-step ($t + 1$), contingent on the environmental choice made and the consequent changes in the state in which an individual enters time-step ($t + 1$). Since the fitness in time-step ($t + 1$) is already known for each possible state-value combination, the choice that maximised fitness at ($t + 1$) can easily be determined. How is the fitness at time-step ($t + 1$) already known? We start with the last, or terminal, time-step (T) and assign a terminal fitness value to each possible combination of state values considered. Some terminal fitness values are clearly unlikely since most males that survive to the terminal time-step will have accrued some social experience and gained mass. However, a large enough range of terminal states and their corresponding fitnesses are modelled so as to encompass all possible mass and social experience levels that a male might have accrued over the preceding 15 time-steps. To iterate the dynamic-programming algorithm, we work backwards through time starting at T , with known terminal fitnesses for each state, and determine the optimal action at the immediately previous time-step ($T - 1$) from each possible state at that time-step. Once the optimal actions are specified for each state at T , the fitnesses for each state at ($T - 1$) are also specified and they become the new values from which to determine the optimal action at each state in ($T - 2$). The process is iterated until the first time-step is reached. As such, dynamic programming results in a 'road-map' specifying the optimal action to take at each time-step and for each state in which an individual may be.

Figure 15.6 illustrates three simulations of bachelor-male tendencies under different ecological conditions. In the first two – (a) and (b) – predation risks associated with being in

either all-male groups or mixed herds are low and equal (per-capita mortality = 0.04). Again, in both iterations the ability to acquire social experience varies in the same way among social states, and is maximised at 1 for mixed herds, is halved for all-male groups and set to zero for solitary bachelors. In Fig. 15.5a relative mass gain is equalised and set at a maximum of 1 for both solitary bachelors and those in all-male groups; for bachelors in mixed herds, however, relative mass gain is reduced by half. In this iteration it becomes clear that when predation levels are low and, in particular, the risk for solitary individuals is less than 0.025, then bachelors should only be found alone or in mixed herds. And when the risk of being eaten gets very small for solitary individuals, the frequency of solitary bachelors found on a landscape should increase and they should dominate the landscape. What is most striking about the iteration depicted in Fig. 15.6a is that as long as the risk of predation on solitary bachelors is small and lower than when in any group (which would be the case if groups were easier to detect than solitary individuals), then the strategy for bachelors that gives them the highest terminal fitness is one in which they alternate between states. They should go alone to maximise growth rate for a time and then they should join mixed herds to maximise social experience. What they should *not* do is become a 'generalist' and form all-male groups that provide moderate pay-offs in both dimensions. Only when the solitary risk of being eaten reaches 4 per cent should bachelors become indifferent with respect to joining all-male or mixed-sex herds.

The importance of not seeking the middle ground is underscored in the iteration illustrated in Figure 15.6b, where weight gain derived while being solitary exceeds that which can be gained when in all-male groups. When being alone eliminates foraging competition and provides huge relative foraging gains, then the strategy of oscillating between two social environments – one where mass gain, and the other where social skills, can be maximised – is reinforced and extends into regions where the per-capita risk of being eaten when alone soars to 10 per cent.

The importance of predation risk cannot be underestimated. Under conditions when solitary bachelors maintain a large foraging advantage over those joining either type of herd, even a slight decrease of the survival rates to bachelors of joining a mixed herd tilts the balance toward all-male groups (Fig. 15.6c). If increased conspicuousness or less favourable positioning on the edge outweighs the dilution benefit of associating with more vulnerable youngsters, then under moderate levels of risk when solitary, the opti-

mal strategy is still to join mixed herds. But joining all-male groups is clearly becoming common, while wandering alone is becoming rare. By the time the risk of predation on solitary individuals reaches 10 per cent, however, virtually all bachelors do best by joining all-male groups.

Clearly, the simulations show that bachelor males are sensitive to maximising their survival prospects, weight gain and social experience. That they do so by changing social environments is not surprising. That they do so by specialising on one factor at a time, is. The switch to choosing a social environment that provides moderate gains in each dimension *simultaneously* becomes favoured only when the predation risk of being alone, or of being in mixed groups, becomes relatively high.

In our repeated censuses of ranches, we record the frequency in which bachelor males are distributed among these three social states. Overall, only 3 per cent of bachelors are seen alone. Most (67 per cent) are seen in mixed herds, while 30 per cent are seen in all-male groups (Rubenstein, Hack & Mazo, in preparation). Given that all but one ranch hosts at least one pride of lions and one clan of hyaenas, predation risk must be moderately high – at least 4 per cent for those in groups, and higher for those living alone. If the risk to solitary bachelors were to rise as high as 12 per cent – three times as high as being in a group – then the predicted distribution of bachelor males across social states would be roughly in accord with that of the iteration illustrated in Fig. 15.5b in which solitary bachelors experience a large foraging advantage by shunning competitors. Upon inspection, the actual distributions of plains zebra bachelor males are closer to the predictions of this iteration than one in which predation risk is lower for solitary males but higher for bachelors joining mixed herds than for joining all-male groups (Fig. 15.6c).

Risk of predation seems to play a major role in bachelor decision-making. Since predation risk varies with time of day and habitat-openness our censuses also reveal that bachelors are typically found alone when predation intensity scores were low (3.7), but in mixed herds when scores were significantly higher (5.1) ($F_{2,304} = 19.0$; $p < 0.0001$; $r = 0.12$). Moreover, in the one conservancy where predators are regulated and lions are not present, the presence of all-male bachelor groups is low (25 per cent) as predicted, but not significantly lower than on a neighbouring ranch (32 per cent) where predators are more abundant. Overall, predation appears to matter and adjusts the frequencies by which bachelors adopt particular social states, mostly in accord with the predictions of the model.

SYNTHESIS AND COMPARISONS LESSONS FROM ZEBRAS

The simple multi-level societies of zebras demonstrate that higher levels of sociality can evolve to solve social problems that core mating groups cannot. Core social groups, whether they are uni-male–multi-female ‘harems’ or closed-membership groups of bachelor males, lower the risks of predation. Moreover, harem groups, by virtue of the protective role of males, also provide enhanced feeding opportunities for females. But in certain environments, males in solitary harem groups cannot easily reduce incursions by bachelor males. Without attaining assistance of other breeding stallions, stallions would otherwise experience higher risks of cuckoldry.

Ecological factors, however, are not unimportant since they also influence, either directly or at times indirectly, the size and composition of herds. Zebras are sensitive to predation risk and seem to respond numerically by avoiding areas where predators are abundant. Yet at the same time they are drawn to areas where leaf biomass is high – just the places where predators hide. Apparently, plains zebra are in a dynamic ‘shell game’, since simply moving to maximise safety cannot be accomplished without sacrificing access to abundant supplies of food. Thus although predation risk does not directly influence herd size, once all other factors are held constant, predation pressure affects zebra densities, and density does directly affect herd size. Once zebras settle in a particular area, then vegetation abundance, more than any other feature of the landscape after controlling for all other variables, has a positive effect on herd size and composition. As leaf density increases, so does the size of herds, and the fraction of bachelor males that those herds comprise increases as well. But overall, the factor that has the greatest direct influence on herd size is the pressure of intruding, and potentially cuckolding, bachelor males. When their numbers are high, herds tend to be large. Apparently, a sexual problem is best solved socially, but at a level above the core social unit.

The actual decision-making process appears to be one of adjusting both proximate and ultimate costs and benefits among alternative social states. Breeding stallions appear to band together pre-emptively with their females to reduce the chances of successful incursions by bachelors and their ultimate, and potentially debilitating, reproductive consequences (Rubenstein, 1986); moreover, banding together with other stallions also reduces the proximate costs associated with foraging reductions that males alone incur when trying to reduce the chances of being cuckolded. Fortunately,

females in most herds with 60 or fewer animals suffer few reductions in foraging performance. Thus they are seemingly indifferent to being in a solitary harem or in a herd of moderate size. When such sexual conflicts of interest are eliminated, the pressure for stallions to aggregate is unopposed by the interests, or actions, of their females. In this particular context the forces of sexual selection operating on males do not come into conflict with the forces of natural selection acting on females, and the new social state is stable.

Stochastic dynamic modelling predicts that bachelor males should also alter their social environment, based on relative costs and benefits associated with alternative social states, but on a longer time scale than that of stallions. The eco-correlates analysis shows that bachelors are drawn to herds with many females (Table 15.1), but the model demonstrates that the attractiveness of herds is not likely to be universal. Over a time-horizon longer than that over which breeding stallions make decisions about social states, the model predicts the adoption of a diversified strategy of alternating between specialist tactics, each of which maximises gains in one dimension – physical or social growth – for short periods of time. This model predicts oscillations among social states, unless predation levels for solitary bachelors are very high or predation levels for bachelors in mixed herds are somewhat higher than those for bachelors in all-male groups. Actual distributions of bachelors among these alternatives match reasonably well the predictions of a stochastic dynamic-programming model the parameters of which assume that solitary males gain a strong, fitness-enhancing foraging advantage over social males, but that such solitary males also face predation levels three times higher than those in groups. Even with respect to developmental strategies that are under the influence of sexual selection, the model shows that factors of natural selection are likely to constrain options. Nevertheless, the modelling of social relationships within multi-level societies of zebras suggests that during ontogeny the acquisition of social skills should be as important as increasing body size. Since maximising the two-in-one social state appears difficult, changing social states, and in turn social relationships, are likely to be important features of male life histories.

PRIMATE COMPARISONS

The dynamics of higher-order primate social systems, especially those of baboons, correspond to those of zebras in many ways. Savannah (*Papio cynocephalus*), hamadryas and gelada baboons appear to exhibit strikingly different

patterns of social organisation. Savannah baboons typically live in multi-male–multi-female groups, whereas hamadryas and gelada baboons, both close evolutionary relations, live in harem groups comprising one male and many females. Yet as in plains zebras, both of these harem-based systems often show higher levels of social organisation since the harem groups often coalesce, forming herds.

Studies by Kummer (1968), Dunbar (1986, 1988), Stambach (1987) and Barton (2000) illustrate how these apparently different societies appear to be variations on a common theme; the entities that emerge are novel responses to different ecological conditions. Barton (2000) has proposed a model based on the interplay of five factors that can account for the differences among the species. He argues that two factors – *sexual dimorphism* (via the large size of males, making them socially important to females) and *male polygyny* (the tendency for males to bond to as many females as possible and exclude other males from joining) – are universal and influence the social structure of all baboon societies. Together, they provide a force that generates strong male–female bonds (e.g. ‘cross-sex bonding’; Byrne *et al.*, 1990) and encourage males to bond with as many females as possible, while segregating themselves from other males. But whether such a segregating tendency actually leads to isolated uni-male–multi-female core groups and fission–fusion herds typified by hamadryas and gelada baboons, depends on three additional factors that vary in strength with ecological circumstances. First is the *risk of predation*. This sets the lower limit to group size, which should increase as predation intensity increases. And as group sizes increase so should the number of males associating continually with females (Andelman, 1986; Altmann, 1990). Second is the *availability of food*. This sets the upper limit to group size, and when food becomes scarce the maximal size of groups should shrink. And third is the strength of *female–female alliances*. As the magnitude of intragroup contest competition increases, so should the strength of female–female alliances since such associations will determine the outcome of within-group competition. Barton’s model suggests that it is the balance between the strength of female–female and male–female bonds that ultimately determines whether or not baboons are organised into multi-male or uni-male core social units.

Whenever predation risk is high, groups should be large, but ‘bigness’ can come in two varieties. In one, large groups can be cohesive with strong female–female and female–male links, as typified by olive (*Papio anubis*) and annubis baboons. In the other, normally separate uni-male groups can create large groupings by forming bands in loose and

opportunistic associations. According to Barton’s model, what determines one from the other is the abundance and dispersion of resources. As the patchiness of food increases, alliances among females come to determine the outcome of contests for monopolisable resources. As a result, strong female–female bonds prevent males, who themselves are tied strongly to particular females, from removing those females from the cohesive group. Alternatively, when food is more sparsely and evenly distributed, contest competition is reduced and female alliances, along with the corresponding bonds that develop among females, tend to be weak. As a result, the segregating tendencies of males predominate. Bands or herd-like structures will still form when predation risk becomes high, but the solution to the predation problem is solved at a higher level than the core group.

This model accurately accounts for the fission–fusion nature of hamadryas society and it even explains the breakdown of the typical multi-male–multi-female groups of chacma baboons (*Papio ursinus*) when they inhabit sub-alpine habitats in South Africa. With feeding competition at extremely low levels in such habitats, many chacma baboons live in uni-male groups (Barton, 2000). Just like hamadryas baboons in the absence of predation, the chacma core units remain apart and are only reported to fuse into bands in regions where leopards are present (Barton, 2000).

Applying Barton’s model to account for the fission–fusion dynamics of gelada baboons is not as straightforward. Dunbar (1986) characterises the core harem groups of geladas as having both strong male–female and female–female ties. As such they would be predicted to live in large multi-male–multi-female groups. These female–female associations, however, are among close kin and they do not extend outside the core group. Hence, when harems coalesce into bands the extended female–female networks exhibited by savannah baboons are absent and, unlike savannah baboons, large aggregations of gelada baboons readily break up. Dunbar (1986) argues that coalitional support, even if limited in extent, is necessary when feeding competition does occur. Since gelada forage on grass-like lawns, he notes that such competition only occurs in large groups that routinely form only on open grasslands where predation risk is high. When foraging in less risky habitats, such as on grassy slopes, bands break up into segregated harem groups, and feeding competition is reduced. Thus the existence of even modest female alliances provides sufficient social flexibility on the part of geladas to either maximise foraging efficiency in relatively safe habitats by segregating to reduce competition, and by relying on coalitional support to do the same

in riskier habitats where safety in numbers also intensifies competition.

What is striking about Barton's model and its ability to explain how ecological factors interact to favour flexible social patterns and the evolution of higher levels of social organisation in baboons, is that with some minor modifications it can also account for the social dynamics of plains zebras. First, Barton's two universal factors apply to zebras as well. Males are important since they play a vital role in protecting females from harassment and give them extra time to forage; and males also strive to acquire as many females as possible. Thus strong male–female bonds are common and males in most harem–living equids avoid each other. Second, Barton's variable factors also come into play, but with some interesting twists. Unlike the strong bonds that exist between males and females, the bonds among females in most harem–living equids are weak. This pattern most likely emerges from the fact that equids forage by clipping vegetation and, unlike most baboons, rarely invest in digging for rhizomes or spending much time or energy in acquiring individual food items. Contest competition is thus rare, dominance hierarchies are weak and the need for female–female alliances is virtually non-existent. Moreover, food availability is high. Not only are grasses distributed relatively evenly on landscapes, but also the hindgut fermentation system of equids enables them to process food continuously. And, lastly, predation risk is high.

But it is on this point that the biology of equids and baboons diverges. Although a large array of group–hunting predators prey on zebras, the relatively large body size of zebras, their fleetness and the fact that males are highly vigilant mitigates the per-capita risk of dying for those zebras inhabiting closed-membership harem groups consisting of, on average, 10 to 12 individuals. And as the eco-correlate analysis has shown, the ability of zebras to range widely enables them to move away from predators fairly rapidly. Overall, the many counter-strategies of zebras living in closed-membership harem groups help keep per-capita predator risk relatively low. Yet predation risk would be high if core groups were smaller and less cohesive. For horses, the other harem-forming equid, bachelor males live in small open-membership groups (Rubenstein, 1981). This is quite different from zebra bachelor males. In both the Laikipia and Samburu populations, associations among bachelor males are strong, and groups typically range in size from six to nine individuals (personal observation). Therefore, it appears as if this species-specific transformation in the nature of bachelor–male relationships is a direct effect of current

predation pressures being greater for zebras than for horses. But what is most intriguing about this change is that although the eco-correlate analysis does not show a strong direct effect of predation risk on zebra herd size, predation apparently does exert an effect, only it appears to do so indirectly. Predation risk, by inducing bachelor males to live in large groups where long-term associations enable the development of coordinated action, appears to increase the risk to stallions of being cuckolded and of wasting valuable time and energy in trying to reduce this risk. As a result, stallions are driven to aggregate to lower these actual, or potential, costs. Because of the indirect way predation pressure acts on zebra herd dynamics through the sexual behaviour of bachelor males, the forces of sexual selection appear to play a greater role in shaping higher-level features of zebra societies than they do in shaping similar patterns of primate sociality. In primates, ecological factors shaped by the forces of natural selection appear to dominate.

CONCLUSION

Overall, zebra herds appear to form in order to solve social and ecological problems that emerge somewhat unpredictably. That sociosexual problems underlie the formation of herds should not be too surprising. Mediating complex sets of social tensions is not easily done and appears to require forming and dissolving social bonds involving conspecifics outside an individual's immediate social sphere. Higher levels of sociality – herds for zebras – clearly provide a diverse array of potential options to call upon when solving novel social challenges created by changing environmental circumstances. As long as bonds central to holding together the underlying core social groups are not jeopardised, multiple levels of social organisation will evolve. While the structure of some, such as those of hamadryas and even gelada baboons, may be relatively long-lasting, others, like the herds of plains zebra, may be more short-lived enabling rapid adjustments to short-term problems.

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