Zebra Sociality: Different Stripes for Different Types

Dan Rubenstein, the George Eastman Professor for 2003-4, writes about his work at the Mpala Research Centre in central Kenya, unravelling the ecology, social behavior and movements of zebras. With undergraduate and graduate students involved in the Program in African Studies at Princeton, where he is Professor of Ecology and Evolutionary Biology, as well as Kenyan research assistants, he has for 20 years been following the behaviour of over 1,000 individually identifiable zebras, recognizable by their unique stripes, across a variety of grassland and savanna landscapes in the semi-arid regions of central Kenya.

Animal societies come in many forms. In some, males and females are monogamous, bonding for long periods, if not for life, while in others polygamy rules, with females, males or both having many mates. And if this variety were not enough, even among the polygynous species where males acquire a number of partners, some males defend entire groups of females, others defend critical resources that attract many females to particular locales, and still others wander in search of females in estrus exploiting high rank to displace all other suitors when the time is right. Understanding why this bewildering variety of mating systems exists and then how these different patterns influence other facets of a species' social life lies at the heart of a branch of evolutionary biology known as behavioral ecology or 'sociobiology' and is the focus of my research on wild equids, especially zebras.

Why sociality, why zebras?

As a behavioral ecologist I want to understand why particular social relationships develop among individuals and why these relationships often take different forms in different species. Since social interactions take place as individuals seek safety or nutritive and reproductive resources, the distribution and abundance of these essential environmental elements will have a profound affect on determining the type of interactions that contribute to producing surviving offspring. In different environments the balance and variety of affiliative and aggressive actions appropriate for maximising reproduction, a measurable marker of the neo-Darwinian fitness concept of propagating as many genes as possible into the future, may vary. Determining how Darwin's 'hostile forces' ultimately shape a species' social structure by imbuing its constituents with traits of superior adaptive, or survival, value often involves comparing two or more species exhibiting social variations and inhabiting different habitats. This is where studying zebras come in handy; they afford a unique opportunity for unraveling the underlying rules that shape animal societies.

Zebras are special creatures. Apart from the fact that their shimmering stripes brighten the tropical savannas they inhabit, zebras belong to a rare group of mammals in which offspring of both sexes leave home before breeding. In most mammals offspring of only one sex remain in the natal range, taking advantage of lessons learned about finding resources and deriving support from allies whose reliability is strengthened by kinship. Most often it is female offspring that remain, since knowledge gained, and support received, affect their ability to reproduce more than males. But when both sexes emigrate, the strong social relationships that underpin the formation of stable 'core' social groups become more difficult to build because costs arising from competition for scarce resources are not diminished by genetic ties. Losing out to relatives sharing genes in common limits an individual's losses, since the additional offspring produced by victors provides some evolutionary compensation to the vanquished in proportion to the genes they hold in common. Thus, by

accounting for the evolution of different types of zebra societies in which members are unrelated, our studies have helped formulate a general understanding of the evolution of sociality.

All zebras are members of the same taxonomic family, the Equidae, sharing the same body plan and exhibiting the same underlying physiology and dietary needs. Because of these close evolutionary relationships zebras provide an exceptional comparative opportunity for untangling the impact of historical and ecological influences on social evolution.

By comparing the behaviour of two species with virtually identical evolutionary histories, any differences in sociality that emerge are most likely to be evolutionary responses to different environmental circumstances.

Social patterns and problems

Zebras exhibit two different types of social organisation. In one, typified by the plains zebra (*Equus burchelli*), unrelated females form long-term associations and live in so called 'harem' groups that usually include a single male and their pre-reproductive offspring. Since polygyny results, some males remain without females and these males aggregate into all-male 'bachelor' groups. Both types of 'core' groups travel widely, live in home ranges that overlap with those of other groups and often join together to form herds.

In the other, typified by the Grevy's zebra (*Equus grevyi*), females form groups but the associations are weak, changing weekly if not more frequently. Moreover, female associations with males are short-lived and males remain apart from each other defending large territories to which females come to graze and mate.

These variations on a polygynous theme generate a number of intriguing questions.

For one, why do the two species exhibit such fundamental differences in their 'core' social relationships and why do the plains zebras have a higher level of sociality? This additional social complexity emerges because harem groups themselves coalesce into long-lasting herds. But why this should be so is unclear, especially since another close relative, the horse (*Equus caballus*), also forms harem and bachelor groups, yet the core groups of horses do not form long-lasting herds.

For another, does an understanding of a species' society provide any insights that could improve management or conservation of their habitat?

This is not an abstract question. While over a million plains zebras inhabit broad areas of eastern and southern Africa, Grevy's zebra numbers have fallen to fewer then 2,500 and its range has been fragmented and restricted to small regions in north-central Kenya and southern Ethiopia. Is it possible that differences in social organisation exhibited by the two species affect their survival prospects, especially in areas where their ranges overlap, and where interactions among themselves and with livestock are common? And if sociality matters, is there anything we as scientists can draw upon to improve the conservation and management of these species?

Social solutions

What is striking about all equids is that females rarely compete for vegetation. In a very real sense they appear to behave as if 'a grass blade is a grass blade'. Regardless of abundance, females adjust their spacing to avoid interfering which each other as they try to consume as much food as quickly as possible. On average, females displace each other, usually with a 'wink and a nod', about once every 10 hours! Moreover, our analyses show that the percentage of each hour females devote to feeding and the number of bites they take every minute, remains unaffected by the size of the harem group, which rarely exceeds 10-12 individuals. Emphasis on females and what they do is the key to understanding the evolution of sociality in zebras and their kin, because it is females that face the arduous task of acquiring food, water and safety for themselves and their young. Males, of course, need these resources, too, but in an evolutionary sense males are 'judged' not by their bodily condition, but by their ability to gain more matings then other suitors. Therefore it is females that are under the strongest selective pressure to solve environmental problems posed

by nature, and it is their best response that ultimately gives shape to the society that emerges. How females distribute themselves on landscapes – scattered about when resources are sparse, or in groups if clumped and abundant – in turn constrain the responses of males and, when taken together, the sexual relationships that develop produce the 'core' social groups that are best adapted to particular environments.

At least for zebras, forage emerges as a permissive resource that facilitates, but does not guarantee, sociality. Our studies have shown that other costs, especially those associated with increased parasite transmission as measured by intestinal worm burden, are heightened by living in groups. Thus if group living is to evolve, offsetting benefits must accrue to females. Since zebras ferment vegetation after digestion there is no 'bottle neck' that slows food processing as in ruminant grazers. Consequently, zebra foraging is limited by the time they can devote to feeding and this is where the benefits of living in harem groups emerge. Spending time scanning for predators, taking care of young and maintaining clean coats all limit the amount of time that can be devoted to grazing. Dividing up time spent on these competing activities with other females would in theory produce savings, but sloughing off all vigilance activities to the male actually generates the greatest gains. Since males invest materially little in their offspring, they require fewer calories then females and, since they are already on the lookout for marauding stallions and cuckolding bachelors, the costs of becoming the 'designated lookout' are minimal. Moreover, given that males adopt these responsibilities for exclusive mating rights, transferring duties benefits all. Since not all males are equally good at providing protection, females exercise choice by voting with their feet, leaving poorer, lower ranking males and bonding to more efficient, higher ranking ones. Our analyses show that over a 15-hour day 'choosy' females that get their male right can increase daily grazing time by up to 1.5 hours. Clearly, males provide an essential service that translates into material gains and leads to the formation of closed membership groups. But this raises

A plains zebra and a Grevy's zebra (right)

an important question: if associating with males is so good, why don't Grevy's zebra females also do so on a permanent basis?

Long-lasting harem groups can only be maintained when grazing areas and safe drinking points are nearby. Grevy's zebras typically live in arid areas where water is sparse and because their size adapts them to withstand drought, not all females need to drink every day. As a result, non-lactating females, or those with larger and older foals, wander far from water in search of less denuded grasslands. Those with foals younger then three months of age, however, must drink daily and only wander short distances to nearby hilly areas for protection at night. Consequently, they seek out open watering places. But with forage sparse, they lose bodily condition. We know that such females would not choose to stay on these close cropped lawns even though their high nutrient content enhances offspring growth because, when a foal is killed, mothers abandon these sites and head for more distant areas where vegetation is more plentiful.

Adaptations to arid conditions create a tear in the social fabric that bind females of all reproductive states

together. With such bonds broken Grevy's zebra males face a problem not experienced by their plains zebra counterparts. Lactating females undergo a post-partum estrus approximately two weeks after giving birth and non-lactating females cycle every three weeks or so. Plains zebra males have exclusive access to both types, but if a Grevy's zebra stallion were to bond exclusively to either class of female he would forgo opportunities to mate with the other. What clever Grevy's zebra males do is follow neither, instead establishing territories where females are likely to spend much of their time. For dominants, territories surround access routes to safe water so that such males can socialise both with females lingering near water and with those travelling to and from grazing sites. With the best locations spoken for, subordinates settle for second best, defending territories in the better grazing area and hoping to secure matings if females linger long enough on the forage they control. At least both types of territory holders do better than bachelors who rarely associate with females and who only mate when on territory.

The above analysis shows how different mating, or 'core', relationships evolve to solve problems created by particular environments. That plains zebras exhibit another level of social organisation – herds – suggests, however, that some problems are not being met by the 'core' social relationships identified so far. What might these be?

Apart for some species of primates and elephants higher levels of sociality are not common in mammals. Typically, these additional levels help overcome ecological problems such as heightened risks of predation. Our recent findings, however, show that additional levels of sociality can also evolve to solve *social* problems. For plains zebras the dominant force determining the tendency to form herds is the magnitude of cuckolding pressure experienced by harem males. Vegetation abundance, but not quality or diversity, matters but only weakly, and the reduction of predation risk is not directly implicated at all.

We were able to detect this 'cuckolder' effect because our study takes place on private lands where limited culling is permitted under the auspices of the Kenya Wildlife Service. Since some ranches cull only bachelor males while others hunt only family groups, especially the breeding stallions, important variation is created in the ratio of bachelor males to stallions—our measure of 'intruder' or 'cuckolder' pressure. On ranches where bachelors are in large cohesive groups, stallions form alliances that effectively keep bachelors away from females. Typically this entails walling off bachelors so that they form a crescent around the edge of the herd.

What is fascinating about this process is that because the males are so successful in keeping intruders away, females behave as if they are indifferent to the presence or absence of bachelors. Fine-grained measures of bite rate show that females suffer a miniscule reduction in feeding when in moderate sized herds, with or without bachelors present, as opposed to being in a solitary harem. Males, however, experience almost a 50% reduction in feeding rate and it is only by banding together that they can amortise the cost of repelling intruders, recouping most of their lost foraging efficiency. Proximate feedbacks are thus acting as triggers, creating effective long-term evolutionary responses.

While indifference by females enables males to form coalitions, this does not mean females are passive players in this social game. Our most recent work shows that, much like females in Grevy's zebra herds, conflicts of interest among plains zebra females within harems over what feeding thresholds make joining herds economical means that males are unlikely to accrue all foraging gains potentially available to them.

In order to insure that 'averages' do not deceive and that each class of female gets her due, males become 'shock absorbers' in the system, taking on some of the costly activities that some females must shed in order to attain the feeding rate while in such a large herd that meets their particular needs.

These findings suggest that the answer to the conundrum as to why plains zebras but not horses, both harem-dwelling equids, form herds lies in the nature of bachelor

male associations. In plains zebras, bachelors live in large groups for long periods of time. In wild horses bachelor groups are much smaller and membership is temporary. Such a difference can change the magnitude of intruder pressure. But identifying such a pattern only pushes the problem back one stage: why are the bachelor patterns so different in these otherwise similar species? Although only conjecture, the answer must lie in the fact that predation pressure on the two species is very different. Only in zebra habitats do large predators persist. Where wild horses roam predators have largely been extirpated, and the costs of long-term associations among young ascending reproductive competitors are not offset by any other benefits. Thus the last piece to the social puzzle has been fitted. Although we found that predation pressure had no strong direct affect on the formation of herds in plains zebras, predation appears to act indirectly through intruder pressure by inducing stable groupings among bachelors, forging them into a powerful potential cuckolding force.

Conservation applications and human implications

Understanding the adaptive value of the social difference between zebras reveals how complex behavioural traits evolve. But understanding the rules governing social evolution and the ways landscapes shape behaviour can also provide important insights into why plains zebras are thriving while the Grevy's zebra are not, especially in areas where they coexist, and how 'pure' science can yield useful conservation applications.

Life on private lands can be challenging for zebras. Most landholders view zebras as vermin, competing for vegetation with livestock. Only landowners reducing their herds and investing in ecotourism support wildlife, including both zebra species and their predators. Thus if wildlife is to stay, it must 'pay' dividends to smallholders whose few hundred hectares rule out ecotourism, to group ranchers whose traditional pastoral practices leave too little forage for sustaining wildlife, as well as to the large commercial ranchers whose activities are generally wildlife-friendly. What is exciting is that our findings provide a number of insights into how such payoffs can be generated for these and other stakeholders.

One insight emerges from our determining whether or not government-sanctioned culling of plains zebras can be done sustainably. By constructing stochastic population projection models and tuning the demographic parameters to capture the crucial behavioral features of zebras described earlier, we have been able to forecast the size of zebra populations decades into the future. Without culling, the model predicts that the current Laikipia population of about 30,000 plains zebras (in an area of about 10,000 square kilometers) will rise to 35,000 zebras in 30 years, clearly a healthy situation. But even with indiscriminate culling – as long as it is limited to no more than to six per cent per year – the population tends to stabilise at about 25,000 zebras, still enough to placate the interests of ecotourists. More important, however, is our calculation that, even for smallholders whose lands rarely support more then 100 zebras, yearly income from selling carcasses would be increased by about 10%, a sizeable amount in this part of the world and one that is generated by the sustainable use of wildlife.

A second comes directly from our observations on the social and feeding behaviour of the two zebra species. By showing for the first time that plains zebras significantly lower the feeding rate of Grevy's zebras wherever plains zebras outnumber Grevy's zebras, we have highlighted a serious problem. Fortunately, our work also shows that there is a solution, but one requiring careful planning and coordination between government and private landholders. Since one of the goals of the Kenyan government is to replenish previously poached wildlife populations within National Parks, translocations from densely to sparsely, populated areas are under way. By documenting the existence of frequency-dependent competition we have suggested that removing plains zebras from areas where Grevy's zebras are abundant, but where their numbers are not increasing, should help reduce competition and increase Grevy's zebra birth

rates. In a pilot study where over 250 plains zebras have been moved from one conservancy to Meru National Park, recruitment by Grevy's zebras has indeed increased and offers the prospect that in the future, even 'excess' Grevy's zebras could be translocated to repopulate other parts of its historic range.

Conclusions

The central theme that emerges from our work is that features of environments have large impacts on behaviour and the structuring of animal societies. Females are affected most and thus play a fundamental role is determining which types of relationships develop for solving problems posed by nature. In zebras choosing a quality male can make a difference, but for some females in certain circumstances – those adapted to arid conditions – this is not always possible and variations on the basic social theme emerge. In today's world, where humans are dramatically changing environments, the implications of this message are likely to be profound since the ability of existing social systems to cope is being challenged. As our work shows, only a deep understanding of the fundamental dynamics of a species' ecology and behaviour can provide insights that could be used to alter human activities and give wildlife a fighting chance. But will the application of this knowledge make a difference?

The answer to this question can be 'yes', but only if all stakeholders are brought into the process. Recently we established a programme that employs local pastoralist communities to help gather data for determining whether or not existing livestock husbandry practices are curtailing the growth of Grevy's zebra populations on communal lands. By engaging communities in gathering data that may well show that current practices are harmful, we hope that whatever new practices emerge they would be cooperatively designed to be economically viable and ecologically sustainable. Already three scouts, one man and two women, from six communities are recording the abundance, the ages and sexes and even the activities of Grevy's zebras that they sight while carrying out daily activities. For the men, this means observing zebras while herding, so censuses on open landscapes and responses to the presence or absence of cattle are recorded. For the women, observations are made in more closed habitats while they collect firewood and water. Already, a novel finding has emerged: non-lactating Grevy's zebra females avoid livestock more then any other age or sex class. If livestock exploit the best grazing sites, as our vegetation analyses are likely to show, then avoidance of these areas by females having just weaned offspring and needing to replenish bodily stores could lengthen the inter-birth interval. This could be the 'smoking gun' lowering recruitment and it would have emerged by the actions of the pastoralists themselves. By making it profitable for pastoralists to take part in the process of understanding why the Grevy's zebra is endangered, we are building important connections that we hope will lead to sustainable solutions. This is ultimately the only way forward. Conservation action can only be sustainable if local communities believe in the goals of a project, understand the value of the emerging scientific knowledge and can put it to profitable use.