

■ Social Organization

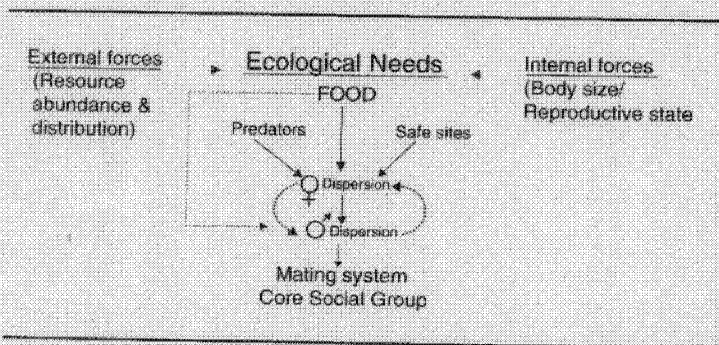
Herd Dynamics: Why Aggregations Vary in Size and Complexity

From Individuals to Groups

Apart from coming together to mate, most animals live solitary lives. Such a preponderance of asocial behavior should not be too surprising since as Alexander (1974) first noted, there are no automatic benefits of living in groups, only automatic costs. Typically disease and parasite transmission increase when individuals spend time together, as has been demonstrated in species from swallows to horses. Yet groups do form, and many are long lasting. Clearly, there are compensating benefits that can offset the automatic costs associated with disease and other likely detriments, such as increased competition for resources, including mates, and increased detectability by predators. Benefits mostly come in three forms. First, animals can develop types of social behavior specific to stable groups that directly compensate them for specific costs of group living. One such example is forming mutual grooming partnerships as do olive baboons (*Papio anubis*) to lower disease and parasite transmission. Second, by forming groups, animals can enhance foraging by being better able to find, acquire or defend food. Examples include colonial cliff swallows (*Hirundo pyrrhonota*) that transfer information about the locations of rich but ephemeral feeding sites or troops of monkeys who drive smaller troops away from feeding trees, or even lions (*Felis leo*) that defend kills to keep competitors away. And third, animals in groups can reduce their risk of being preyed upon by either increasing the likelihood of detecting predators, diluting their personal risks or by decreasing the likelihood that predators can make a kill; confusion and cooperative defense are mechanisms that provide such antipredator benefits. Examples include the scattering of fish in schools, tail flashing by white tail deer (*Odocoileus virginianus*), stotting by gazelles, or the gathering of young inside a ring of adult musk oxen (*Ovibos moschatus*) with upturned horns facing outwards toward approaching predators.

Whenever the sum total of all benefits exceed costs, group living will be favored by natural selection because such social individuals will sire more offspring and rear them to independence than asocial individuals. As genes for being social increase in frequency in the population, sociality will necessarily become the norm. In fact, groups will tend to be of similar

size in similar environments in part because the most favored groups will be those where benefits maximally exceed costs. But such groups are not inherently stable since any new member joining the group will lower the net benefits for all. Yet, given that the resulting net gain for each group remaining a group is still greater than that of an individual living alone, joining will continue until the difference between the net gain of living alone and living in a group of this particular size vanishes. At this size, the group becomes stable in



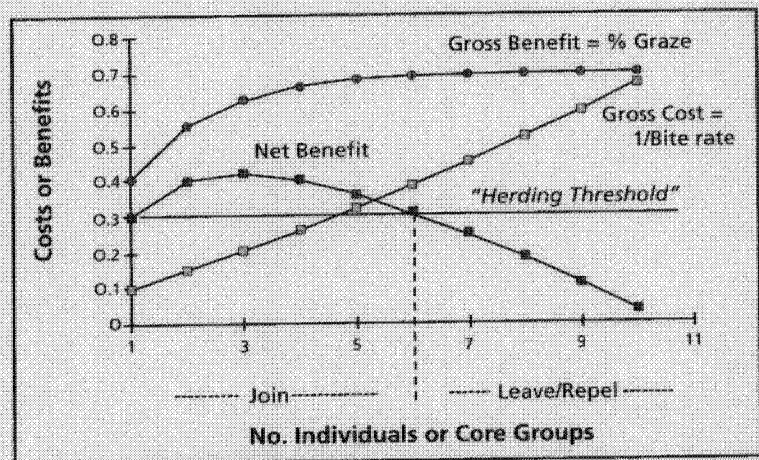
A framework showing how ecological and internal constraints determine mating systems and thus the structure of core social groups by first affecting distributions and associations of females which in turn affect distribution and associations of males.

Courtesy of Daniel I. Rubenstein

terms of numbers. Although "stable" groups are always larger than "optimal" sized groups, both hypothetical group types scale in similar ways as environmental conditions change, so either group type can be used to examine how environmental circumstances shape the dynamics of group living.

Groups take on particular structures depending upon the nature of the relationships that develop among their members (Rubenstein 1986). Particular distributions of food, water, predators, and safe sites produce different core social structures. Since natural selection favors females that leave more progeny than their peers, female distributions and abundances on particular landscapes will change as the distribution and abundance of key resources change. Such flexibility comes about because different ecological settings often select for specific types of behaviors that best enable females to satisfy their needs at the lowest possible costs. Once females have responded, their associations, and the distribution that develops on the landscape in turn, constrain what males can do. As males respond to the actions of females, with perhaps females adjusting their initial response to the subsequent actions of males, mating relationships develop and the core of a social system is born. (See the graph below.)

In environments in which resources are abundant, especially when they are evenly distributed, competition is often low enough to permit females to aggregate. Conceptually, if sufficiently large foraging or antipredator benefits can be derived by females that aggregate, and the groups that form are not too large, then these groups can be defended by single males and so-called "Harem Defense Polygyny" results. However, if resources are more patchily distributed so that competition among females intensifies, then female group sizes will vary, and female associations may become more transitory. Rather than defending unstable groups of females, males instead attempt to defend in advance of females arriving, resource patches sought by females (dotted line in the graph). Typically, in these systems of "Resource Defense Polygyny," the most able males defend the best patches and thus gain access to the largest number of females for the longest periods of time. If resources are not only patchily distributed, but the patches are large, widely separated, and fluctuate seasonally in abundance, then competition among females often becomes so low that the formation of large aggregations is even more likely, provided that females can range widely and follow the shifting locations of peaks in food abundance. Males will thus be forced either to follow these large groups competing for, and then tending, individual reproductive females one at a time (*wandering*), or to position themselves at the intersection of female migratory routes waiting for females to visit them (*lekking*). In either case, intense male-male competition generates a mating system based on "Male Dominance Polygyny," and in the latter case, females are afforded an exquisite opportunity to compare many males simultaneously before choosing with which one to mate! Whenever resources are sparsely, but somewhat evenly



Gross costs and benefits as typified by decreases in bite rate or increases in percentage of time spent grazing, and net benefits as computed by the difference between gross costs and benefits as a function either of the number of individuals in a group or the number of core social groups in a multilevel herd.

Courtesy of Daniel I. Rubenstein.

distributed, high levels of competition prevent females from forming groups. As a result, individual females defend territories, thus insuring a regular supply of a renewing resource. Since solitary individuals searching for members of the opposite sex, especially if small-bodied, will face increased predation risk, pairs often share territories, and monogamy results.

This conceptual framework can account for the diversity of core social groups that form for many different taxa, including insects, fish, reptiles, rodents, and many varieties of birds, ungulates, carnivores, marine mammals, and primates. One of the best illustrations showing how environmental forces interact with physiological constraints to shape a species' social system emerges from Peter Jarman's (1974) classic study of African antelopes. By showing how body size affected the ways in which different species perceived, and then responded to, the distribution and abundance of forage and predators of grasslands, Jarman showed why particular social systems increased survival and reproductive prospects for particular species. He argued that the smallest-bodied species, such as did-dik (*Madoqua kirkii*), duikers (*Cephalophus spp.*, *Sylvicapra spp.*), suni (*Neotragus moschatus*) and klip-springers (*Oreotragus oreotragus*) require limited amounts of high-quality vegetation. But given their small size, such food items often appear as if they are widely scattered. Faced with high levels of competition and intensified risks of predation, territoriality and monogamy appear to be the best strategies. Pairs generally live in wooded or shrub-rich areas where moisture enables vegetation to grow and renew itself well into the dry season. By signaling territorial ownership via scent rather than by means of sound or visual display, these small-bodied species reduce the chances that any of a large number of carnivores will prey upon them.

As species increase in body size, both physiologically determined dietary needs and the way acceptable forage becomes distributed on the landscape changes. Since "crypsis" (camouflage) becomes an untenable antipredator strategy for larger and more widely ranging species, forming groups becomes the best strategy for larger species to lower predation risk. Fortunately, with larger size also comes an ability to subsist on more abundant, lower-quality vegetation. When it is patchily distributed, as it is for impala (*Aepyceros melampus*), reedbeek (*Redunca spp.*), and some gazelles (*Gazella spp.*), males defend the best patches that females prefer. When the vegetation is more evenly distributed, which often results simply from the fact that larger species such as eland (*Taurotragus oryx*) and cape buffalo (*Synceros caffer*) can utilize even the lowest-quality items, larger groups form. Because the largest species view all types of vegetation populating continuous swards of a landscape as acceptable, competition is virtually eliminated, and many males associate with many females. With such high levels of male-male competition, defense of a small subgroup of females becomes impossible, and dominance defense systems develop.

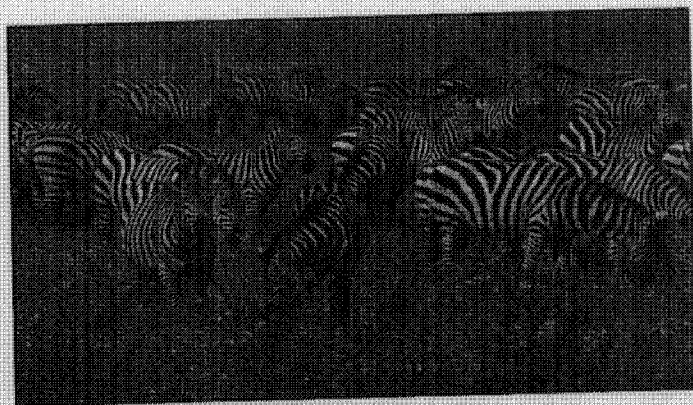
The same sorts of connections between changing ecological circumstances shape the types of sociality exhibited in other taxa. But, because ecological circumstances that are not too different from those described above generate novel social variants, it appears that strong biological interactions among internal and external constraints themselves become important determinants of sociality. Among the equids, for example, the close association between food and water enable horse (*Equus caballus*) and plains zebra (*Equus burchelli*) females of different reproductive states to associate permanently. Thus males are able to defend such groups and so-called "harems" form. When these two resources are widely dispersed, as for Grevy's zebra (*Equus grevyi*) and the Asiatic wild ass (*Equus hemionus*), females of different states are precluded by metabolic constraints from foraging together. As a result, males compete for territories along traveling routes that take females from feeding

areas to watering points (Rubenstein 1994). Differences in body size and the way they alter patterns of water dependency appear to be ultimately responsible for why two similar groups of species exhibit such fundamental differences in the strength of social relationships and hence core patterns of social organization.

From Groups to Complex Societies

Core social groupings that are built mostly upon mating relationships do not fully explain the diversity of social structures that develop among species. For many species, social relationships are limited to those with core social units. Consequently, such groups remain apart from other such units. Yet for other species, interactions and relationships develop among different classes of individuals beyond these basic units. As a result, some species live in large fission-fusion networks where either the nature or strength of relationships among individuals, or core social groups within which they live, change over time. In the latter case, multilevel societies develop in which core groups aggregate to form larger and more complex social networks. Some of the best examples of hierarchical social structuring are displayed by elephants (*Loxodonta africanas*) where female-led family groups aggregate during the rains but split during the dry season, or by gelada baboons (*Theropithecus gelada*) where herds of harems aggregate on the tops of plateaus where predation risk is high, but fragment on steeper slopes where the mobility of predators is more limited. Yet it is in the equids where the relative simplicity of the multifaceted social networks of both the plains and Grevy's zebras reveals how both natural and sexually selective forces interact to produce a multiplicity of social interactions that, in some circumstances, lead to multileveled societies.

As with elephants and gelada baboons, natural selection to maximize food acquisition and minimize risk of predation play important but small roles in determining whether large cohesive herds of harems and bachelor groups form in plains zebras (Rubenstein and Hack 2004). Populations are often large in areas where predators are absent, and where zebra density is high, the size of herds that form tend to be large. Similarly, as food abundance increases, so do herd sizes. But these effects are weak and pale when compared to the forces of sexual selection: Cuckolding risk brought about by the presence of bachelor males is hard to reduce when alone on a landscape. In areas where bachelor groups are large and the groups are cohesive, zebra herd sizes grow to be quite large. It appears that males tend to bring their harem groups together to insure that, if discovered by bachelor males, individual harem-"owning" males can more effectively drive the bachelors off before they can infiltrate his group and mate with those of his females in heat. Herds tend to be significantly larger where the relative number of bachelor males per breeding male is high. Interestingly, males are successful at forming these alliances only when females suffer no significant foraging or harassment costs when in herds. Since this occurs only when a moderate number



A tightly-knit herd of zebras grazing while walking.
Courtesy of Corbis.

of breeding stallions band together, limits to growth of herds exist. Thus by avoiding the creation of any intersexual conflicts, males are able to organize themselves to reduce the risk of losing exclusive control of mating. In essence, a second layer of sociality appears to have evolved to solve simultaneously both female and male problems that the fundamental set of relationships characterizing the core social group could not.

Although Grevy's zebras do not structure their extensive social relationships in simple multilevel tiers, the existence of multiple networks of relationships that develop, and that individuals modulate as circumstances vary, underscores the notion that complex societies develop to solve problems that simple one-dimensional social structures can not. Grevy's zebra females in particular have the options of bonding with many different classes of females as well as males. The details of how their oscillations among relationships as a function of "top-down" predatory, or "bottom-up" foraging, pressures change is only now emerging. But variation in the diversity of relationships is responsive to changes in population density and predation pressure. Thus for Grevy's zebras, individual decision making remains at all times more flexible than in plains zebras where, although females solve foraging and antipredator problems at the level of the core group, males can only solve problems of postmating competition at the level of the herd. In Grevy's zebras, females appear to solve their multiplicity of problems by changing the nature and strengths of their relationships at the primary level, in part because resource dependency is not similar for all individuals and thus constrains their ability to simultaneously solve different types of environmental problems with a society structured hierarchically.

From Phalanxes to Waves

Although group living, herd structure, and overall patterns of social organization are best accounted for by functional or adaptive explanations associated with ultimate consideration of reproductive success or even more proximate measures of more short-term behavioral costs and benefits, the actual shape of herds is best described by more mechanistic processes. Typically, models are constructed that imbue individuals on a landscape with particular attributes, and then these individuals act as particles or cellular automata responding to the actions of other such particles on landscapes with hypothetical environmental features. In most such models, forces of repulsion associated with competition and violation of personal space are combined with forces of attraction that reduce separation and the risks of predation. Debate exists over whether individuals are "aware" of all neighbors or are attending to only one or just a few neighbors located in detection "zones." Issues of detection ability get to the heart of how animals "know" what they know and provide an opportunity to enrich the study of animal decision making with important insights emerging from cognitive psychology.

Even with only simple assumptions about animal reasoning abilities, however, the results of simulations can predict the shape of herds that form on real landscapes and show how different modes of detection can alter energetic efficiency of herd dynamics (Gueron et al. 1996). For example, in cases where individuals exhibit hierarchical decision-making patterns in which individuals in particular zones evoke particular movements—first, moving away from neighbors that get too close ("stress" zone), second, moving freely according to idiosyncratic tendencies when repulsion has been overcome and a nearest neighbor is neither too near nor too far ("neutral" zone), and third, moving to a nearest neighbor when a nearest neighbor is not close enough for diluting the risk of predation ("attraction" zone)—stable herds form as long as all individuals are of similar phenotype. Moreover,

energetic savings accrue to individuals with "neutral" zones since acceleration and deceleration rates are low, and overall, the shape of these herds become wavy-front-like when moving slowly and columnar or phalanx-like when moving quickly, as is the case when wildebeest or zebras move across African savannas. However, for stability to be achieved when individuals vary markedly in phenotype, which can occur when females have different dietary or physiological needs, for example, then a fourth rule is required. Since different needs often lead to temporary separation, only by invoking a "stop" until discovered or a "speed-up" until a peer is found "rule," can long-term cohesion be maintained. While the use of such "toy models" to explore the ways in which global patterns of behavior can emerge from local interactions is only beginning, the ability to account for the complexity of herd shape and the energetics of group living illustrates the power of incorporating functional with mechanistic explanations to unravel the structural and shape dynamics of complex animal groups.

Conclusions

The dynamics of core groups and higher levels of sociality are driven by individuals joining together to minimize costs and maximize benefits. Such costs and benefits may be in similar or different currencies but the net result of forming groups is that individuals are better able collectively to solve problems posed by the environment. Female relationships in particular develop as they try to maximize the number of surviving offspring. Since male reproduction is much less limited by meeting ecological needs and much more governed by their need to sire more offspring than other males, if males can be enticed by females to help solve their most pressing problems, then it is likely that social relationships will be structured. In such societies the needs of all will be *simultaneously* satisfied as long as conflicts of interest among the sexes do not develop. When the limited, but strong, bonds of core networks cannot solve the sexually selected problems facing males, or even all the environmental problems confronting females, then the core social network itself may become more diversified, and the relationships more complex. In such a circumstance, individuals may modulate their relationships on condition-dependent bases in order to solve *sequentially* conflicting problems posed by complex physical and social environments.

Complexity of herds also emerges from the ways their shapes change in response to individual perceptions about landscapes. Not surprisingly, the decision making of individuals that leads to shape change is governed by "rules" that emerge from the forces of natural and sexual selection. Perhaps somewhat surprising is the fact that only a limited number of such rules can account for the emergence of complex patterns that characterize the shapes and energetics of real herds. Exploring the extent to which cellular automata type models can account for global patterns of behavior emerging from local interactions will provide important insights into herd structure and the dynamics of social organization.

- See also* Feeding Behavior—*Scrounging*
 Feeding Behavior—*Social Foraging*
 Social Evolution—*Optimization and Evolutionary Game Theory*
 Social Organization—*Alliances*
 Social Organization—*Home Range*
 Social Organization—*Territoriality*

Further Resources

- Alexander, R. D. 1974. *The evolution of social behavior*. Annual Review of Ecology and Systematics, 5, 325–83.
- Gueron, S., Levin, S. A. & Rubenstein, D. I. 1996. *The dynamics of herds: From individuals to aggregations*. Journal of Theoretical Biology, 182, 85–98.
- Jarman, P. J. 1974. *Social organization of antelope in relation to their ecology*. Behaviour, 28, 215–67.
- Rubenstein, D. I. 1986. *Ecology and sociality in horses and zebras*. In: *Ecological Aspects of Social Evolution*. (Ed. by D. I. Rubenstein & R. W. Wrangham), pp. 282–302. Princeton, NJ: Princeton University Press.
- Rubenstein, D. I. 1994. *The ecology of female social behaviour in horses zebras and asses*. In: *Animal Societies: Individuals, Interactions and Organisation*. (Ed. by P. J. Jarman & A. Rossiter), pp. 13–28. Kyoto, Japan: Kyoto University Press.
- Rubenstein, D. I. & Hack, M. 2004. *Natural and sexual selection and the evolution of multi-level societies: Insights from zebras with comparisons to primates*. In: *Sexual Selection in Primates: New and Comparative Perspectives*. F. M. (Ed. by Kappeler & C. P. van Schaik), pp. 266–279. Cambridge: Cambridge University Press.

Daniel I. Rubenstein

■ Social Organization

Home Range

The term *home range* is strictly connected to the study of local movements and space use of animals during their usual daily activities. The home range may be defined as “that area traversed by the individual in its normal activities of food gathering, mating and caring for young.” It should be underlined that home range is not *all* the area an animal traverses, but rather the area in which it normally moves; accordingly, occasional excursions outside its normal area should not be considered as part of the home range.

Unfortunately, home range is not the sole concept considering the local space use of animals. We have also to consider the concept of *territory*, that may be defined as “a more or less exclusive area *defended* by an individual or group.” However, it is often very difficult to ascertain the exclusive use of an area and to detect the keeping-out signals displayed. Moreover, the same species may be territorial in certain ecological contexts and nonterritorial in others. The degree of overlap between adjacent territories is also variable, and the very concept of territorial exclusiveness is far from adequate. Accordingly, the borderline between these two spatial systems is not as clear-cut as may appear from the above-mentioned definitions. However, the home range concept is used in a more general and comprehensive way than that of territory. In fact, spatial systems, whose exclusiveness has not been ascertained, are usually referred to as home ranges even though they may really be territories.

Radiotelemetry is a useful technique for the study of home ranges of vertebrates: Animals are caught, tagged with small transmitters, and tracked by researchers who detect signals by means of receivers. Transmitters can be radio-located using antennas to locate animals. The exact position occupied by a radiotagged individual at a given time is called *fix*. A major advantage of radio telemetry is that this technique records events in relation to time; radiotracking can show not only how often an individual visits each part of its range, but also what time of day it went there. Movement records from radiotagged animals fall into two main types. There are the short-term movements that animals make daily during foraging, courting, and general maintenance activity, and there are the long-term movements that are on a seasonal or even a lifetime basis. Note that while daily movements are generally