Social Behavior

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Introduction

No animals are completely asocial. All must come together at some point to breed. Few, however, are highly social coming together and interacting repeatedly. For those that do interact frequently, social interactions – both affiliative and agonistic – occur sometimes with relatives, sometimes with strangers, sometimes with members of the same sex, sometimes with members of the opposite sex; and sometimes with members of the same generation while at other times with members of other generations. The interactions themselves can be aggres- sive, cooperative, or even altruistic and can develop into strong relationships among particular individuals. Depending on the nature of these relationships and with whom they form, a variety of social systems can develop. Some may be made up mostly of kin or mostly of nonkin, some may be based on territorial separation or on the aggregation of competitors, some will exhibit monogamous as opposed to polygamous relationships between the sexes, and some will rely on the cooperation and help of nonmates in the rearing of offspring. This seemingly bewildering range of social diversity is shaped ultimately by ecological circumstances and patterns of dem- ography. But the very nature of a population's social structure itself will in turn affect the population's demography and its place in the biological community. It is these dual connections between social activities and the environment and the re- sulting feedbacks that mandates understanding both the cau- ses and consequences of animal sociality so that effective and efficient management or conservation policies can be de- veloped for protecting endangered species and for preserving biodiversity and ecosystem integrity.

From Social Behavior to Social Organization: Patterns and Mechanisms of Formation

Social animals form groups. While some are temporary, others are more permanent. Given that animals in groups incur

automatic costs of increased disease and parasite transmission as well as intensified competition, groups will only form when there are sufficiently large benefits to offset these costs (Alex- ander, 1974). Benefits largely come in three forms. First, ani- mals can develop forms of social behavior specific to stable groups that compensate them for the costs of group living. One such example is forming mutual grooming part- nerships 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 (*Hir-undo pyrrhonota*) that transfer information about the locations of rich but ephemeral feeding sites or troops of monkeys that drive smaller troops away from feeding trees. And third, ani- mals in groups can reduce their risk of being preyed on 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. Ex- amples include the scattering of fish in schools, or the gath- ering of young inside a ring of adult musk oxen (*Ovibos moschatus*) facing outward toward approaching predators with upturned horns.

Depending on the nature of the social relationships that develop among individuals, groups take on particular organ- izational forms (Emlen and Oring, 1977; Rubenstein, 1986). As Figure 1 illustrates, these relationships are shaped by the fea- tures of an individual's ecological and social environment. Particular distributions of food or water (bottom-up factors) and predators (top-down factors), in conjunction with the physiological demands of individuals differing in body sizes or reproductive states, will determine the frequency and magnitude of competitive and cooperative interactions that occur. The outcome of these repeated social interactions will shape overall time budgets and activity patterns. Because females maximize their reproductive success relative to other females by their ability to raise offspring to the age of independence, females are forced to efficiently solve the three ecological problems: finding

External constraints

Abundance_____ distribution

Needs

Food water safe sites

Female

Male distribution and abundance

Mating system

Internal constraints

Body size reproductive state

number of females for the longest periods of time. If resources are not only patchily distributed, but also the patches are large, widely separated, and fluctuate seasonally in abundance, then competition among females becomes so low that the for- mation of large groups is even more likely, provided that fe- males 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, one reproductive female at a time (''wandering'') or to pos- ition themselves at the intersection of female migratory routes and wait for females to visit them (''lekking''). In the first case, intense male– male competition generates a mating system based on ''male dominance polygyny,'' and in the latter case females are afforded the exquisite opportunity to simul- taneously compare many males before choosing with which one to mate! Whenever resources are sparsely but somewhat evenly distributed, high levels of competition prevent females from forming groups. As a result, individual females defend territories thus ensuring a regular supply of a renewing re- source. Since solitary individuals searching for members of the opposite sex will face increased predation risk, pairs often share territories and monogamy results.

This model accounts for the diversity of mating systems for many different groups of animals including insects, fish, rep- tiles, rodents, and many varieties of birds, ungulates, carni- vores, marine mammals, and primates. One of the best illustrations showing how environmental forces interact with

Figure 1 Model of ecological and physiological pressures influencing both intra- and intersexual relationships and showing how they shape social systems. Arrows depict social relationships. What type of society develops depends on details and perceptions of environmental conditions and interactions between males and females.

food or water; avoiding predators; or finding safe sites for young (Figure 1). The particular associations and distributions that develop will depend on the particular ecological and physio- logical circumstances that females experience. These associations and distributions in turn will shape male associations and dis- tributions, because male fitness is mostly determined by their ability to acquire mating access to disproportionate numbers of females. Especially for mammals, the mating system that de- velops becomes the core of a species' social system.

Ecological Challenges and Phenotypic Constraints

Resource distribution in time and space shapes animal social systems (Emlen and Oring, 1977). In environments in which resources are abundant but evenly distributed, competition is low enough to permit females to aggregate. 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. If resources, however, are more patchily distributed so that competition among females intensifies periodically, then female group sizes will vary and female associations become more transitory. Rather than de- fending unstable groups of females, males instead attempt to defend resource patches sought by females. Typically, in these systems of ''resource defense polygyny'' the most able males defend the best patches and thus gain access to the largest physiological constraints to shape a species' social system emerges from Peter Jarman's classic study of African antelopes (Jarman, 1974). 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 in- creased survival and reproductive prospects for particular species. He argued that the smallest bodied species, such as dik-dik (*Madoqua kirkii*), duikers (*Cephalophus* spp., *Sylvicapra* spp.), suni (*Neotragus moschatus*), and klipspringers (*Oreo- tragus 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 on them. As species increase in body size, both physiologically determined dietary needs and the way acceptable forage becomes distributed on the landscape changes. Since hiding or ''crypsis'' becomes

an untenable antipredator strategy for larger and more widely ranging spe- cies, forming groups becomes the best strategy for larger spe- cies to lower predation risk. Fortunately, with larger size also comes an ability to subsist on more abundant, lower quality vegetation. When food is patchily distributed, as it is for im- pala (*Aepyceros melampus*), reedbuck (*Redunca* spp.), and some gazelles (*Gazella* spp.), males defend the best patches that females prefer. When the vegetation is more evenly dis- tributed, 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 biggest species view large continu- ous swards of a landscape as acceptable, competition is vir- tually 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. A brief survey of mammals illustrates some of the more general patterns. For the equids the close association between food and water enable horse (*Equus caballus*) and plains zebra (*Equus burchelli*) females of different reproductive states to associate permanently (Rubenstein, 1986, 1994, 2010). 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 hemionous*), 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.

In felids, females remain separated when food is scarce and the habitats are densely wooded because in such circumstances individual prey can be caught and consumed before com- petitors can intervene. In more open habitats and where both prey and competitors are large and much more numerous, coalitions of females form to help hold on to kills until they are completely devoured. If these female coalitions are themselves large, then there is pressure for males to aggregate to control reproductive access to females. Thus, the only highly social felid is the savanna-living lion (*Panthera leo*), yet even in this plen- tiful landscape the leopard (*Panthera pardus*) remains solitary because it can safely catch its large prey in trees (Packer, 1986). For canids monogamy is the rule. But variations do occur with small-bodied foxes (*Vulpes* spp.) sometimes exhibiting polygyny and large-bodied hunting dogs (*Lycaon pictus*) and timber wolves (*Canis lupus*) developing polyandry (Moehl- man, 1986). Typically canids need help from nonbreeding foragers to help nourish lactating mothers. For the midsized jackals, such as the silverback jackal (*Canis mesomelas*), the helpers are young from previous litters that cannot themselves find successful breeding locations. For the smallest species, however, prepartum investment in young is relatively small for a female and thus her mate provides all the help that is nee- ded. In years when prey resources are very high, competition between mothers and their soon-to-be-fecund daughters is low and their daughters are not forced to disperse. As a result they provide neighboring males with additional mating op- portunities. For the largest bodied species, however, female prepartum investment is very high and they need all the help they can get. To enlist the support of other adult males that must hunt cooperatively to capture large prey, a dominant female not only kills the offspring of other females in the group, but also she mates with their mates so that these males behave as if they are the sires of the dominant female's young. Hence, depending on size-determined metabolic investments and needs, social systems of canids can vary from polygyny to polyandry and sometimes use the services of juvenile or adult nonbreeders to help rear offspring.

Monogamy is also the rule in birds, with more than 90% of all species exhibiting social monogamy. Unlike in mammals, where mothers are typically able to take care of offspring on their own, bi-parental care is essential for producing young in most birds. However, this does not mean all pairs are faithful. Although more than 90% of birds are socially monogamous, an almost equal percentage of these seemingly faithful species are not actually sexually monogamous. Although rarer, other forms of mating systems also occur in birds. When resources are clumped, males defend those that are essential to females. For example, in many species of hummingbirds, males defend territories when flowers that females need are sufficiently clumped. Lekking is particularly common in birds compared to mammals. Some of the most recognizable avian species, like the ornamented birds-of-paradise, the bowerbirds and their decorated bower structures, and the dancing manakins lek. In these species, males cannot defend resources or fe- males, and so they aggregate in areas where females are likely to compete against each other for female attention.

Ecology not only shapes animal mating systems, but also in some cases, the social systems themselves. Many species of vertebrates live in complex societies where individuals delay dispersal and independent breeding opportunities to help other group members raise their young. In these ''coopera- tively breeding groups,'' dispersal decisions are typically in- fluenced by ecological factors. Limited resources, such as territories, nest sites, and even mates, prevent young indi- viduals from dispersing to breed on their own. Although the spatial distribution of resources on the landscape can influ- ence dispersal and helping decisions, temporal variation in resource abundance may also affect cooperative breeding be- havior. In birds, cooperatively breeding species tend to be found more often in unpredictable environments where rainfall and resources vary erratically from year-to-year. Having helpers-at-the-nest may allow cooperatively breeding species to buffer these uncertain times better than those species without these nonbreeding auxiliaries (Rubenstein and Lovette, 2007, Jetz and Rubenstein, 2010).

Kinship and Demography

Although the abundance and distribution of key ecological resources are important in determining the particular pattern of cooperation and sociality exhibited by a population, other factors such as kinship and demography also play significant roles. Since W. D. Hamilton formulated the concepts of ''inclusive fitness'' and ''kin selection,'' the magnitude of the costs and benefits associated with particular social behaviors that ultimately determine which strategy is the best, had to be adjusted by degree of relatedness between social partners. Al- truistic or cooperative behavior between relatives should be favored whenever Benefits4Costs x r where r is the degree of relatedness. For both

parents and offspring and among full siblings, r ¼ [1] for grandparents and grand offspring and among half-siblings, r ¼ [1]; and among first cousins, r ¼ [1].

Hence, the stronger the degree of relatedness among relatives, the more likely altruists are to enhance the reproductive op- portunities of kin while incurring costs associated with di- minished personal reproduction. Thus, in the examples presented here, it is not surprising to find that the coalitions

that form among lionesses when protecting kills and among male lions when protecting mating opportunities with females are formed most often among full siblings; nor is it surprising that the helper jackals recruit to rear additional offspring are themselves the full siblings of the offspring being raised. In general, strong kinship lowers the threshold for the appear- ance of altruistic and cooperative behavior and may sub- stantially affect the costs of living in groups, particularly in cooperatively breeding species.

Nowhere is this more apparent than in elephant societies (Archie *et al*., 2006) (Archie *et al*., 2006). As is the case in many mammals, elephants live in fission–fusion societies in which individuals, or the subgroups they inhabit, separate and merge from time to time. In African elephants (*Loxodonta africana*), up to 20 individuals and their young live in core family groups in which daughters remain after reaching sexual maturity, while males leave. Depending on ecological conditions, core groups can separate into smaller units or merge with other core groups to form bond groups. Extensive genotyping of individuals using molecular DNA markers show that not only do family groups typically consist of close genetic relatives, but also that bond groups are most likely to form when the oldest females of the core groups were genetic relatives.

But as many of these cases illustrate, high population density and the intensified competition elephants engender for finding suitable territories with sufficient food and habitable burrows are the factors ultimately responsible for favoring the establishment of coalitions of relatives or the recruitment of helpers in cooperatively breeding societies. Thus, demographic factors, such as population density as well as sex ratio and age structure that result from differences in phenotype-specific vital rates also shape patterns of social organization. And since these features of populations are often altered by human activities, understanding how they shape, and are shaped by, patterns of sociality is essential if conser- vation assessment and planning are to be effective.

Hypothetically, if mortality, for example, were age specific and higher for prereproductive females than males, then high breeding sex ratios (males/females) would result and mating relationships would generally become more polygynous. If the sex-specific patterns of mortality were reversed, however, then polyandry would become more common. Since some of these mortality concerns were responsible for the variation in canid social structure described earlier (*see* Ecological Challenges and Phenotypic Constraints), these mortality schedules can have important consequences. Similarly, if mortality rates were size specific and happened to be greater for larger males rather than smaller ones, then discrete size polymorphisms could arise in populations. This appears to be the case regarding the main- tenance of so-called alternative male mating strategies. Often the typical strategy adopted by older and larger males of de- fending harems or resources yields the most reproductive gains but it often incurs the highest costs as well. Because displaying, fighting, attracting the attention of predators, and delaying re- production while growing are all costly activities, males adopting not only less successful but also less costly tactics can also flourish (Rubenstein, 1980).

Maintenance of such alternative mating patterns is common among many species of insects, fish, amphibians, birds, and mammals. For example, in bluegill sunfish (*Lepomis macrochirus*)

males typically defend nest sites where they display, attract females with which to mate, and then fertilize and guard the eggs they lay. Since only the largest males have the ability to defend such nest sites, they must delay breeding in this fash- ion often for more than 7 years. As a result, smaller and younger males have evolved various cuckolding strategies that may in fact be equally successful evolutionarily. In one, the so- called sneak begins breeding at 2 years of age. Although very small, such sneaks are virtually all testes and because of their inconspicuousness can dive from the surface just as a mating pair release sperm and eggs. By exuding large volumes of sperm, some make it to the eggs and fertilize a few. In the other, males delay breeding for as long as do females. By being the same size and color as females, these males join the mating pair and apparently fool the displaying male into thinking that he is courting two females. Then as the original pair releases their gametes, he does too and thus fertilizes some of the females' eggs. For these two strategies to be equally successful alternatives, the costs and benefits of each must vary inversely with frequency. Although they sometimes do, as in the case of the bluegill sunfish, in other species they do not (Gross 1991; Brennan *et al*., 2008).

A variant on this theme is associated with sex change. For many species, especially among the fishes, individuals begin life as one sex and end life as another. In bluehead wrasse (*Thalassoma bifasciatum*), for example, most individuals begin reproducing as females while residing with one male. If he disappears, then the largest female changes sex and becomes the harem-tending male (Warner *et al*., 1975). Alternatively, in anemonefish (*Amphiprion* spp.), some individuals change from male to female. In either protandrous (male first) or protogynous (female first) species (Fricke and Fricke, 1977), the sex that is last is the one whose reproductive success is most influenced by body size, and this ultimately depends on the nature of the social system.

Clearly, a variety of environmental features influence the patterns of sociality that populations of animals develop. In many cases these patterns are flexible and species can vary in the system of social organization they exhibit depending on environmental conditions. Thus, although female burros and asses typically live in transitory groups whose membership changes, when populations move from arid to mesic areas, social relationships can change. As was found on an island off the coast of Georgia, with food and water both more abundant and less separated, females with differing needs can and do coalesce into permanent groups. Males, which in arid areas are forced to establish territories along routes to and from water, respond by defending these groups much like males of horses, their close kin, and harem-like societies emerge. In some species of birds where pair-bonds are the norm, cooperative breeding groups form via the retention of offspring during hard times. In these occasional, or ''facultative'' cooperative breeders, flexible social behavior is an important part of their social lives.

Egalitarianism and Despotism

In some societies, rewards are relatively evenly distributed among members, whereas in others they are not. When ani- mals compete for critical resources, differences in fighting ability often lead to skewed payoffs, with dominant indi- viduals securing a disproportionate number of rewards, which are typically related to reproduction (Hager and Jones, 2009). The degree to which dominants can control the actions of subordinates varies. If it is incomplete and the rewards to subordinates low, then subordinates will be induced to leave and dominants will suffer. Thus, dominants may be con- strained to concede some resources to subordinates. For males, skew is often related to mating opportunities and re- cent models suggest that when control by dominants is in- complete, the degree of skew will depend mostly on ecological factors and fighting ability (Reeves and Shen, 2006). In mee- kats, for example, reproductive success of subordinate group members increases with increases in body condition and years with high rainfall (Clutton-Brock et al., 2001). Thus, for highly social and cooperatively breeding species, the genetic diversity of populations and the diversity of behavioral strategies they exhibit are likely to change with changes in climate and en- vironmental features.

The existence of dominance hierarchies is a fact of life for most social species, and as noted above, play an important role in structuring societies, skewing payoffs, and when those payoffs are tied to reproduction, affecting the long-term evo- lutionary sustainability of species. But the degree to which dominance influences these outcomes depends on the costs of achieving and maintaining dominance ranks, since high costs often shorten life span and reproductive potential. Con- ventional wisdom based on many studies posits that domin- ants only experience high levels of stress in unstable societies. But recent work on baboons shows that even in stable societies life at the top can be stressful. While stress levels in baboons generally decrease with rank, alpha males exhibit cortisol levels equal to those of the most subordinate members of the group and are much higher than those of males immediately below the top male (Gesquiere et al., 2011). Given that life at the top is likely to be costly for social species in both stable and unstable societies, it is likely that as deteriorating environmental conditions exacerbate com- petition for resources and mates, the longevity of alpha males will be decreased, thus altering the genetic diversity of popu- lations and perhaps their demographic potential as well.

Organization and Networks

Social organizations are often characterized by general char- acteristic such as the number and types of mating pairs or the stability of relationships. But such qualitative characterizations can often be misleading and hide subtle differences in the function or causation of societies. As a result, tools from network theory are being used to quantify the overall structure of societies and the degree of ''centrality'' and extent of con- nectedness (termed ''betweeness'') that individuals display within societies. The use of such quantitative measures is particularly important for fission–fusion societies where in- dividuals often form many different types of relationships. In equids, for example, both Grevy's zebras and Asiatic wild asses live in societies in which males generally live apart from each other and defend territories while females move among ter- ritories singly or in groups that regularly change membership.

When networks of proximity based on who has been associ- ating with whom are constructed, the graphs they produce are very different (Figure 2) (Sundaresan et al., 2007). Inspection shows that just about every wild ass is connected to every other wild ass and that individuals are organized into one large community. In Grevy's zebra, however, more com- munities (called ''connected components'') exist, even though within each community every individual is connected to every other individual. In general, individual Grevy's zebras show higher levels of centrality than onagers because the number of close associates (termed ''degree'') is greater in Grevy's zebras than in wild asses. In addition, ''cliquishness'' of Grevy's is greater than wild asses because the close associates of par- ticular Grevy's zebras are more likely to be close associates themselves than in the wild asses.

By computing these and other metrics, social network an- alysis provides a means of quantifying a variety of different features of society. And by doing so, social network analysis can help assess how social structure can cope with, or perhaps evolve in response to, environmental factors. For example, the metrics described in the previous paragraph reveal that Grevy's zebra society is characterized by more modularity than that of wild asses and that this difference corresponds to a difference in the uncertainty of resource availability and levels of pre- dation that each species experiences. Whereas wild assess live in environments in which humans have extirpated predators and have provided many predictable watering points, Grevy's zebras face mobile predators and large fluctuations in rainfall due to periodic and unpredictable periods of drought. Net- work modularity appears to help prevent the loss of important information for coping with environmental fluctuations.

From Social Organization to Ecological Impacts

Despite the fact that some species exhibit social flexibility and that there exists significant ''environmental determinism'' in the development of patterns of sociality, knowledge is only now emerging about how changes in social systems impact important vital rates, alter interspecific competitive abilities, and shape a population's growth rate and genetic structure. Never before have the social systems of so many species been forced to respond to human activities, most of which lead to reductions in population size, through overharvesting, frag- mentation of landscapes or habitats, and changes in the earth's climate. How are we able to predict which species will respond and how will a species' response impact its long-term growth and the health of the ecosystem in which it resides? When we intervene will we do so with a sufficient under- standing of what the consequences of changing social be- havior and social systems are likely to be? For example, will we know when a species switches from a monogamous to a polygynous social system and whether its growth rate or genetic diversity will increase or decrease? Will we know whether it will be more or less able to withstand selective harvesting or habitat fragmentation? Such

consequences of differing patterns of sociality must be understood before en- dangered species or their habitats can be protected. At least for free-ranging horses attempts to limit population growth using immunocontraception has led to a cascade of unintended

consequences that have altered group stability and mating patterns (Madosky *et al*., 2010) as well as the length of the breeding season and long-term male–females social and re- productive relationships (Nuñez *et al*., 2010).

Consequences of Social Change

Many examples are now appearing of human induced changes in species' social systems. One population of feral horses in- habiting a barrier island off the east coast of USA has been impacted twice by human activities and both the times major changes to social behavior and social organization resulted in large-scale changes in the population's vital rates. The first instance occurred when dredging of surrounding ship chan- nels altered currents and sediment deposition around the is- land. Before the emergence of hundreds of hectares of a new continuous sward of grassland, the island's horses exhibited two types of social organization. Where the vegetation was abundant and evenly distributed, females formed permanent membership groups and associated with a single male. Such harem groups were stable and males protected their females from harassment by intruders and rarely herded their own females. Where the preferred high-quality vegetation was broken up into patches of variable size by extensive ridges of sand dunes, females were not able to aggregate into perman- ent membership groups. As a result, males wandered in search of reproductively receptive females and, when doing so, har- assed females and limited their ability to forage. Not sur- prisingly, the body condition and reproductive success of the harassed females was much lower than that of females bonded to males. After the emergence of the new sward of grassland in the region where females lived in the fission–fusion type of society, females were able to aggregate and males were able to establish harems and the growth rate of the entire population increased markedly. Thus, when the abundance

and distribution of key ecological resources alter social sys- tems so that they more closely resemble a species' typical system, vital rates and the overall health of the population improve.

When the perturbation moves a population away from its normal pattern, as happened during the feral horse popu- lation's second brush with human activity, vital rates decline. As the horse population approached its carrying capacity, popu- lation control measures were instituted. During the initial round of management actions, more than 85% of the harem stallions were removed from the island. The resulting social disruptions were massive; many females were separated from their males and young, inexperienced bachelor males took over. Extremely high levels of harassment led to low reproductive rates despite the fact that overall density had also been reduced and food supplies were expanding. As these two disruptions illustrate, human activities that alter existing patterns of social relationships dramatically alter reproductive rates.

Similar outcomes occurred when large-scale El Niño in- duced climatic changes resulted in major adjustments to time and activity budgets of Alaskan red foxes (*Canis aureus*) (Zabel and Taggart, 1989). Before the 1982–1984 El Niño, many of the foxes on an island in the Bering Sea bred polygynously and produced litters of sizes equivalent to, and often greater than, those of monogamous pairs. After the El Niño and the re- productive failure of the large seabirds, the foxes shifted their diet to smaller, less abundant, and harder to catch prey. Dietary shortages were common, fewer foxes bred and pol- ygyny disappeared. Moreover, the litter sizes of these mon- ogamous pairs were smaller as well. Clearly, changes in social behavior in response to altered environmental conditions enabled some individuals to make the best of a bad situation. Overall, however, the health of the population suffered.

Major changes in the breeding patterns of elephants (*Lo*. *africana*) could result if climate changes alter the

patterning of grasslands in East Africa. Ordinarily group sizes and compositions change seasonally in response to changing abundances of vegetation. After the rains, when grasses grow rapidly on the extensive upland plains, small family groups of elephants aggregate into large matrilineal assemblages. With the flush of new vegetation many come into estrus and be- come reproductively active. At this time only the most dom- inant bulls come into musth, a heightened sexual and aggressive state. By aggregating, females incite male–male competition thus ensuring that they mate only with the best females. During the dry season, however, after the grasses on the plains stop growing and have been consumed by elephants and other ungulates, the elephants retreat to the swamps where other grasses and browse remain. The patchy nature of the habitat, however, prevents large groups of females from remaining together and the huge herds fission into smaller family units. In addition, few females remain to be mated and the dominant bulls go out of musth. Subordinates become sexually active at this time, but reproductive opportunities are limited. Thus, under a normal environmental regime two evolutionary consequences result: most males do not mate, but those that do are the most fit; and because genetic effective population size is affected by the number of males relative to the number of females mating, the effective population size of elephants is much smaller than the census population size. If global warming increases the duration and intensity of dry seasons, then selection for the best males will be relaxed but the effective population size of the population will increase, provided that elephants can sustain their high metabolic levels and maintain their high fertility and survival rates. With global changes in climate appearing in many different habitats, other examples of social readjustments that either change a species' evolutionary potential or that act as demographic shock ab- sorbers in the short run, but are unlikely to provide com- pensatory relief in the long run, are likely to become more common.

Consequences of Demographic Change

Many demographic changes leave their mark by altering crit- ical aspects of social behavior or by disrupting the develop- ment of important social relationships. As the elephant example illustrates, changing environmental conditions can change operational sex ratios thus altering a population's ability to maintain genetic diversity. But by changing sex ratios in other ways, humans can put populations at risk by making it difficult for them to grow in size. In lions, for example, trophy hunting, if it removed pride defending males and nomads in proportion to their abundances, would not se- verely affect population growth and effective population sizes would be maintained at normal levels. But if such hunting focused on pride males, then increased turnover would foster increased infanticide by take over males. While such di- versification of the gene pool might increase effective popu- lation sizes, it would certainly lower population growth rates because infant survival, which is already low, would plummet. Much clearly depends on whether or not the population is polygynous or monogamous and whether the perturbation will accentuate or reverse the pattern. Large-scale climate

changes could reverse and ameliorate the normal pattern as is likely to be the case in elephants, but selective hunting or poaching, as in the case of lions, could exacerbate an already critical situation.

Selective poaching could even make it difficult for popu- lations to recover once the poaching has been eliminated. Since hunting elephants for ivory meant that poachers sought the individuals with the largest tusks first, male numbers were reduced to dangerously low levels before large tusked females and smaller males were hunted. Because females prefer to mate with older males, lowered sex ratios and distorted age structures could make it difficult for all females to mate. As a result, population growth rates could remain low for histor- ically heavily poached populations.

Harvesting in fish might be accelerating already rapid population declines because of disruptions to normal social interactions. When harvesting is size selective and reduces the number of large females in a population, fecundity might be disproportionately reduced since ovary volume scales allo- metrically with linear body size dimensions; larger females have disproportionately larger ovaries and high fecundity. And as sex ratios increase, male harassment of the remaining fe- males may further reduce recruitment and population growth rate. When such size selective harvesting removes more males than females, sex ratios are reduced and females may become less choosy and more aggressive when selecting mates. While such changes in the intensity of sexual selection might not alter population growth rates, they might alter the genetic diversity of the population. Yet if males provide the majority of parental care and large males are removed from the population as if often the case in sports fisheries, then re- cruitment will be markedly reduced as unguarded eggs are cannibalized. The implications of overzealous size-selective harvesting in sex-changing fish or in fish that exhibit alter- native male mating behaviors appear to be equally severe. For species such as anemonefish in which the largest males change to females, removal of the largest females will force males to change sex at ever smaller sizes, thus producing fewer eggs. Population growth rates will be curtailed and the species will find itself at risk all because of overzealous aquarium traders. Migratory Atlantic salmon (*Salmo salar*) provide perhaps the clearest example of where human activities are changing the balance of male mating strategies within a population and hence the patterns of sociality. Atlantic salmon typically are born in fresh water and develop for 1–2 years before smolting and heading to sea to grow and fatten by feasting on a rich supply of marine invertebrates. Once they attain a certain size, they become sexually mature and return to rivers. There they travel long distances upstream until they reach clear and cool breeding grounds. Some individuals, however, never head to the sea. Instead, they remain in their natal streams and mature sexually at young ages and at small sizes. Such individuals are called parr and they never go through the smolting process that adapts them to a marine lifestyle. Under pristine environmental conditions, the fraction of the population that becomes parr is small since the reproductive gains of such a strategy are low. When competing for mates with larger more aggressive males, parr fare poorly. What matings they obtain are derived by ''sneaking'' among a mating pair and releasing milt at just the right time. Such events are rare and the mixing of milt is poor

so such ''sneak'' matings result in few young being sired. But the survival prospects of parr are high since they do not incur the risks of going to sea and, moreover, they begin breeding at a very early age. Thus, over a lifetime, reproductive success is moderate. But as human fishing increases and the netting of the older larger salmon intensifies, the relative lifetime reproductive success of parr is improving. Since the costs of migrating to sea and back again have increased dramatically, the long life span of parr give them a relative advantage. And given that com- petition with the larger males for mates is also being reduced, the chances of parr securing matings are also improving. Thus, it is not surprising that the composition of the population is changing as parr increase markedly in abundance. The impact on the long-term stability of the population is unclear. But the long-term impact on the balancing of mating morphs and sexual relationships is.

Consequences of Inappropriate Interventions

When humans intervene and develop management and con- servation plans they sometimes do so without accounting for important aspects of social behavior. As a result some disas- trous consequences have ensued.

Ignorance about the mating system of sperm whales (*Physeter macrocephalus*) has led to the implementation of harvesting plans that have almost led to their extinction. By using data from previous harvests in which the counts of males were much fewer than those of females, sperm whales were thought to exhibit a harem breeding system. Such a conclusion could only have been derived by assuming that sperm whales lived in permanent, closed membership groups. By making this assumption, the International Whaling Com- mission concluded that most males sighted would be su- perfluous thus disproportionate hunting of males would not limit the growth rate of the population; most of the males caught would not be necessary for fertilizing females.

Unfortunately, the social relationships of sperm whales are very different from those assumed. Females are the core of the society and do appear to live in permanent membership groups. But these groups often merge when diving for fish and divide labor between fishing

and tending the young that cannot dive deeply. Males are forced to leave their natal group when reaching sexual maturity, but they cannot accompany the breeding associations to the tropics. Instead they remain at the higher latitudes foraging in the cooler more productive waters. Thus, when males are hunted on the breeding grounds it is breeders and prereproductives that are taken. With breeding males severely reduced in abundance and the younger, subadult upstarts located thousands of kilometers away, many females are going unmated. As a result, the population is failing to recover and it will be years before the next generation of males is ready to start the population, already handicapped by such a low recruitment potential, on the road to recovery. Knowledge about sperm whale social relationships could have prevented the mistaken over-harvesting of mature males.

Another species in which ignorance about important features of social behavior is problematic is the black rhinoceros (*Diceros bicornis*). During the past 25 years, numbers have

declined from 65,000 to fewer than 5000 in 2011 because demand for their horns is so great. In an attempt at making rhinos less desirable, some nations have implemented a strategy of dehorning. Other nations have opted to translocate rhinos to extremely well-protected areas. Unfortunately, horns, and thus the value of rhinos, regrow quickly. But what is more troubling about the dehorning treatment is that it appears to disrupt effective maternal antipredator behavior. Although dehorned rhinos were no more likely to flee from predators than intact rhinos, the disproportionate disappearance of offspring being reared by dehorned mothers as opposed to intact mothers in areas with large numbers of lions and spotted hyenas suggests that horns play a vital parental and protective function. Dehorning, although initially thought of a cure for the disappearance of adults via poaching, became a contributing factor to the disappearance of young via pre-dation. Although dehorning might enhance adult survival in the short run, it would limit a population's growth potential in the long run.

A third example where ignorance hindered, but did not harm, a conservation program involved the reintroduction of Asiatic wild asses (*E. hemionus*) to habitats within its historical range. A goal of the Israeli government is to repopulate Judea and Samaria with biblical animals. Since the Palestinian race of the wild ass was extirpated by the Ottaman Turks at the beginning of the twentieth century, the onager was a prime candidate for translocation. The first reintroduction took place in 1982 with subsequent additions throughout the 1980s and increased the number of breeding females to 14. By the mid-1990s, however, the population had hardly grown and the number of breeding females totaled 16. What was not known at the time was that breeding success is bolstered by being reared in the wild and that onagers could facultatively adjust the sex ratio of the offspring they produced. In the Negev Desert, free-ranging onagers gave birth disproportionately to sons.

Trivers and Willard (1973) were the first to suggest that differences in the ability to invest in the successful rearing of offspring should lead to individual differences in the primary sex ratios of offspring. They argued that females with sufficient resources should invest in offspring of the sex with the higher variance in reproductive success. By producing well-endowed offspring of this sex, mothers would increase the number of grand offspring they were likely to have. In polygynous species like the onager, males are usually the sex with the greatest variance. Since onager females compete more on the basis of resource exploitation, or utilization efficiency, rather than via direct conflicts settled by social status, sex biases in offspring production were not expected. However, because age and experience affect utilization efficiency, differences in bodily condition and ability to invest in offspring were expected to exist among females in this onager population. Thus, it was heartening to find that middle-aged females – those in the best physical condition – gave birth to more sons than daughters. Conversely, those breeding for the first or second time gave birth to daughters as did older females nearing the end of their reproductive lives. The strategy the Israelis employed of translocating middle-aged females to the desert was sensible in economic terms since high risks were attached to releasing very young females and low future expectations were

associated with releasing older females. But had the Israelis released old females with yearling daughters they would have quickly accelerated the growth of the population. At the time, an understanding of how environments shape patterns of onager social behavior and the impacts that these behaviors would have on population dynamics was unknown.

The Kakapo (*Strigops habroptila*), a critically endangered ground-dwelling parrot native to New Zealand, represents another conservation story where sex-ratio manipulation may be critical to saving the species. Males, the largest parrot species in the world, are not only larger than females and better able to escape predators, but also females are particularly at risk of predation when incubating nests. In 1982, all remaining birds in the wild were brought into captivity. Of the 62 remaining birds in 2001, less than 30% were female and only six female fledglings had been produced since 1982. Owing to the supplemental feeding in captivity, most females were producing sons. After deciding not to boost female condition through supplemental feeding, the offspring ratio evened to approximately 50:50 and more daughters have since been produced.

Most animals exhibit some form of social behavior. Much of this behavior is intimately tied to the environment in which the organisms live. By understanding the relationships between environments and social behavior and between social organization and population processes, we should be in a better position to understand the problems endangered species are likely to face and what interventions to protect them are likely to be effective. In a time when global warming is a reality and human modification of the landscape is occurring at alarming rates, gaining a better understanding and appreciation for animal social behavior will help in preserving species and ecosystems across the planet.

Appendix

List of Courses

1. Behavioral Ecology
2. Animal Behavior
3. Social Behavior
4. Conservation Behavior

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