

Kitchen, D. M. & Packer, C. 1999. Complexity in vertebrate societies. In: Levels of Selection in Evolution, (L. Keller, editor), Princeton, New Jersey: Princeton University Press, pp. 176-196.

# 9 COMPLEXITY IN VERTEBRATE SOCIETIES

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Individuals are the preeminent vehicles for selection. Yet individuals consist of a collection of genes, the physical elements of evolution. Does the transition from selfish gene to individual genome provide lessons for higher-order phenomena, in particular the relationship between the individual and the social group? Maynard Smith and Szathmáry (1995) argued that there have only been two general contexts in which such transitions may have occurred. First, eusocial species display an extreme degree of cooperation and division of labor, but they are in effect "extended genotypes" in which the genetic self-interests of each group member are highly similar. Thus, sufficient kinship permits specialization similar to the cells of a single superorganism (Seeley 1997; see also Keller and Reeve, chap. 8). Second, human cognition and language permits rational planning and a unique capacity for cultural transmission, enabling the development of an elaborate social organization beyond the reach of most organisms (see Maynard Smith, chap. 10).

Social evolution is often considered to have reached only these two remarkable pinnacles; everything else appears to be stranded on lower ground. But is the topography of vertebrate sociality really so uniform? Detailed studies of animal societies often reveal hints of true complexity, sometimes even giving the appearance of group-level coordination or a well-organized division of labor. Do these provide evidence of a higher level of selection that has superseded individual selection? Or has individual selection alone produced these novel levels of organization?

Although there is theoretical evidence that group selection can operate under certain strict criteria, fitness differences among groups will only rarely supplant the effects of differential individual fitness within the population (Williams 1966; Dawkins 1976). But can important evolutionary pressures be revealed by measuring fitness effects at the group level? Proponents of neo-group selection advocate that group-level adaptations have produced "emerging properties" that can only be understood from their effects on the relative fitness of different groups (e.g., Sober and Wilson 1997; Wilson 1997ab). They also urge the necessity of viewing the group as an entity in its own right rather than reducing everything to the sum of individuals. Strict individual selectionists, however, suggest that such complexity can best be understood by building from the simplest unit. If it is advantageous for individuals to form groups, individual selection will lead to adaptations that maximize personal fitness within the group and thus produce the complexities observed in nature. For example, certain physical structures may transcend the contribution by any single individual (e.g. termite mounds, weaver bird nests, acorn woodpecker granaries), but these are epiphenomena that result from individuals working for themselves and their kin rather than the result of a pre-planned blueprint (Maynard Smith and Szathmáry 1995).

One way to view these contrasting approaches would be to apply to vertebrate societies criteria similar to those that Maynard Smith and Szathmáry (1995) have suggested for the evolution of human societies: Rousseau's social contract *versus* Adam Smith's free market. According to Rousseau, society is designed to maximize benefits to the society itself, whereas Smith contended that society results from the behavior of individuals working for their personal benefit.

Our task for this volume was to determine how the most complex and apparently coordinated vertebrate social behaviors conform to this dichotomy of societal evolution. Many vertebrate societies are centered around cooperative breeding, and this pathway apparently leads toward eusociality in the same manner as naked mole-rats, termites and hymenoptera (Wilson 1971; Lacey and Sherman 1991, Sherman et al. 1995). Because strict eusociality is rare among vertebrates (see Alexander, et al. 1991), and the behaviors associated with cooperative breeding systems have been the subject of several recent reviews (Stacey and Koenig 1990; Emlen 1995; 1997; Solomon and French 1997), we have chosen instead to examine alternative examples of emergent properties in vertebrates. Predator avoidance, food acquisition, and resource competition all provide clear examples of complex, group-level behavior. Can simple rules of individual behavior account for these phenomena? Or do we see signs of a superorganism with near-perfect coordination, altruism, specialized division of labor, and advanced group-level decision-making beyond the sum of its parts? In each case, we characterize the complexity of the behavior, providing a plausible scenario for the evolution of the trait and exploring its maintenance at the observed level of complexity. Where possible, we discuss factors that may have prevented each trait from attaining an even higher level of complexity.

## **I. Predator avoidance.**

Predation has been an important force in the evolution of group living, primarily through the dilution effect (Treisman 1975). Individuals benefit from dilution whenever a predator can only capture one prey at a time and a group of  $n$  individuals is attacked less than  $n$  times as often as a solitary. But group living affords numerous other antipredator advantages beyond the sheer safety of numbers, including the confusion effect and corporate vigilance. Predator-avoidance behavior often shows a superficial resemblance to higher cognition or a coordinated division of labor. We discuss these phenomena within the context of evasion and vigilance.

**A. Coordinated evasion.** *A flock of dunlins flies low over Puget Sound; Mt. Rainier glows in the afternoon light. The dunlins fly along in a loose-knit swarm until a merlin swoops down from the sky, and the dunlins make a sudden sharp turn, bunching together and moving as one. A few stragglers stand out from the crowd, and the merlin catches its dinner.*

Such coordinated evasive maneuvers can appear choreographed, giving the impression of a supra-individual intelligence. Indeed, the idea that cognition involves an extensive group-level process such that the group literally has a mind of its own (Wilson 1997b) has been around for decades (e.g. Selous 1931). This impression may tell us more about the neurological attributes of the observers than of the birds themselves, however. Slow-motion film analysis of the dunlins' tightly executed maneuvers reveals a precise sequence of individual decisions. When first faced with an external threat, one to three birds react by banking toward the rest of the flock, and the remainder respond one by one, forming a synchronized "maneuver wave" (Potts 1984). This results from a pattern of neighbor following neighbor, not a direct response to the predator, and the individual birds react so fast that the sum of their actions appears to have a life of its own. Yet no higher level of organization is involved.

The proximate mechanism of this behavior, however, does not diminish its complicated group-

level effect. The response time between dunlin flock neighbors decreases along the front of the "wave" and becomes, on average, three times faster than the average startle response of a lone individual. This suggests that each individual synchronized its movement to coincide with the approaching maneuver wave propagating across the flock, giving rise to a "chorus line" (Potts 1984). A similar phenomenon is found in schooling fish where close proximity allows each individual to detect rapid pressure waves with their otolith and lateral line organs (Gray and Denton 1991). Individuals synchronize their movements with those of their neighbors (Pitcher and Parrish 1993), resulting in remarkably coordinated predator evasion maneuvers (Fig. 9.1).

The chorus line is possible because the animals' absolute speed of response is so quick that each group member can wait its turn and still escape the approaching predator. Otherwise they should follow a direct-response rule in which each group member flees as soon as it detects the predator. Neighbor-rules maintain integrity within the flock during evasion, and orderliness is individually advantageous by reducing the risk of collision and maintaining benefits from the dilution effect (Heppner 1997; Parrish and Turchin 1997). The chorus line will only be successful, however, in species where the maneuver wave can be reliably detected (Lima 1995; Lima and Zollner 1996) and the absolute reaction time is very rapid in comparison to the speed of the approaching predator.

What would a group-selected evasion tactic look like? In a world of like-minded individualists, each animal's only goal is to escape, but in a world where group interests supersede the needs of individual group members, the birds should try to minimize the risk that *anyone* is ever captured. Thus, individuals should maintain a precise location within the flock because novel movements could decrease the efficiency of the group's coordinated pattern (Schilt and Norris 1997). It is a common observation, however, that individuals attempt to move toward the center of the flock when threatened by a predator (Hamilton 1971; Romey 1997) and random movement patterns are continually generated by individuals within the group (Heppner 1997).

**B. Coordinated vigilance.** *In Tsavo National Park, a family of dwarf mongooses searches the grass for insects and spiders. The alpha male perches atop a nearby termite mound and scans the sky. As the chirpings of his family recede, he notices a subordinate female. A quick and efficient forager, she sits perched on another termite mound, digesting and watching the sky. The alpha male rejoins the pack, and everyone remains absorbed in a search for food. Startled by the shrill cry from the watchful female, the family safely joins the sentinel in her termite mound just before a pale chanting goshawk completes its futile plunge.*

Extreme examples of vigilance behavior involve an apparent division of labor with individuals taking turns as "sentinels." Several well-documented cases in birds and mammals indicate a highly coordinated system with at least one, but often only one, sentinel on duty most of the time (e.g. Gaston 1977; Rasa 1977, 1989a; Moran 1984; Ferguson 1987; McGowan and Woolfenden 1989; Hailman, et al. 1994). In Florida scrub jays, the occurrence of a single sentinel was more frequent than expected by chance (McGowan and Woolfenden 1989), and, in a study of captive meerkats, at least one individual played sentinel over 95% of the time (Moran 1984). The meerkats' coverage dropped to 70% immediately after the death of one group member — a decrease comparable to the time it normally spent on duty — though the survivors soon adjusted their guarding time to cover the gap. Substitutions between group members also seem to be well synchronized in these systems. In the scrub jays, one sentinel typically relieves another within the same minute (McGowan and Woolfenden 1989), whereas sentinel exchange in dwarf mongooses involves a consistent sequence of individuals (Rasa 1977, 1989a).

Vigilance has traditionally been considered to involve some form of altruism: animals must forego foraging time to scan for predators, and vigilant individuals may inevitably alert their companions of an impending attack (Pulliam 1973; Pulliam, et al. 1982; Parker and Hammerstein 1985). Thus the coordination observed in these sentinel systems implies a degree of active cooperation, indicating a group-level emergent property. More recent approaches to predator-detection behavior, however, have all emphasized an inherent *individual* advantage to being the first to spot the predator (e.g. FitzGibbon 1989, 1994; Packer and Abrams 1990; McNamara and Houston 1992; Caro, et al. 1995; Godin and Davis 1995; Bednekoff and Lima, unpubl.).

Although their elevated positions might make them seem more exposed, sentinels probably gain direct benefits from their behavior. Sentinels refrain from all other activities besides vigilance (e.g. Moran 1984; Wickler 1985; Hailman, et al. 1994), their posts provide an improved view of the surrounding area (Rasa 1986, 1989a; Hailman, et al. 1994), and they may be situated close to shelter (Rasa 1989a, but see Rasa 1987). Thus, active vigilance may pay more than continued foraging once an individual has reached its gut capacity, and any asynchrony in feeding requirements among group members would give the appearance of a coordinated division of labor. If this is the case, rather than look for evidence of cooperation, we should look for factors that lead to feeding asynchrony.

Animals with different nutritional requirements or foraging efficiencies will be expected to approach satiation at different times (Gaston 1977; Bednekoff 1997). Perhaps the first sentinel of the day was the last individual to have fed the night before or is the most efficient forager in the group. The staggered energy reserves of individuals would affect the relative payoff of vigilance behavior and the time at which they switch to this task. Some individuals may be more efficient foragers (e.g. adults vs. juveniles) or may have lower energy requirements (e.g. males vs. pregnant or lactating females), thus explaining why adults are more often sentinels than juveniles (e.g. Rasa 1977; Hailman, et al. 1994), and why males are sentinels more often than females (e.g. Rasa 1977, 1989a; Moran 1984; Hailman, et al. 1994). Consistent differences between individuals could also explain why the sequence of exchange between specific group members occurs with such regularity (Rasa 1977, 1989a).

However, an organized sentinel system cannot result from asynchronous requirements unless foragers benefit from the vigilance of the sentinel and sentinels can resume foraging when it is their best option to do so (Bednekoff 1997). Each animal's decision depends on what everyone else is doing: an individual can devote relatively more time to foraging (rather than vigilance) as long as there is at least one sentinel and the sentinel's response to an approaching predator is reliable and easily detected by other group members.

Why do sentinels signal an advancing predator? An alarm call might be the inevitable by-product of a startle response, a signal that encourages the predator to attack a different individual (e.g. FitzGibbon 1989; Caro, et al. 1995), or a means of manipulating other group members (Charnov and Krebs 1975). Besides protecting close kin (Hamilton 1964; Sherman 1977), animals may receive a strong benefit from the dilution effect and therefore benefit from protecting necessary companions (Lima 1989).

Assuming that sentinels enjoy even a minor improvement in predator detection compared to foragers, Bednekoff (1997) has shown that a coordinated sentinel system can arise purely through individual advantage. Bednekoff's model incorporates three factors: (1) At each time-step, individuals choose between foraging and vigilance, depending on their own energetic reserves; (2) individuals switch tasks at each time-step according to the foraging/vigilance behavior of other group members; (3) predator-detection information is effectively transferred from the sentinels to the foragers.

Consider first a group in which everyone forages, and no one is vigilant. Once one individual

has attained an adequate energy reserve, it can benefit more from behaving as a sentinel rather than continuing to forage. The remaining group members now enjoy considerably less risk of predation so that they only benefit from acting as sentinels if their energy reserves are sufficiently high (Fig. 9.2). Once the lone sentinel's reserves have fallen below the threshold, it resumes foraging, but its role is filled by any other group member with adequate reserves to become the lone sentinel. As a result, coordinated sentinel behavior can confer a selfish advantage as long as individual priorities can be satisfied asynchronously (Bednekoff 1997).

Sentinel behavior shows an irregular taxonomic distribution. What ecological differences might account for the presence of a coordinated vigilance system in one species and its absence in a related species or in a different population? Sentinels might be more likely in a population or species in which (1) elevated lookout posts provide a genuine predator-detection advantage (Bednekoff 1997), (2) food supplies are adequate (Gaston 1977; Bednekoff 1997), and (3) predator densities are high (McGowan and Woolfenden 1989).

Dwarf mongooses in the Serengeti are an example of the latter point as they do not display the complicated and coordinated sentinel behavior seen in the Tsavo population. Predation pressure is much higher in Tsavo than in the Serengeti (Rasa 1986, 1989b; S. Creel, pers. comm.), and the behavior of one particular raptor species apparently determines the payoffs from coordinated guarding. In Tsavo, the pale chanting goshawk uses the cover of trees and bushes to ambush from behind the traveling pack and exerts a potential predation pressure almost ten times higher than any other species (Rasa 1983, 1989b). This apparently explains why the mongoose sentinel focuses its vigilance 180° away from the foraging direction of the pack (Rasa 1989ab). In the Serengeti, however, pale chanting goshawk do not attack dwarf mongooses, and the mongooses never emit alarm calls in their presence (S. Creel, pers. comm.).

Sentinel behavior seems to have arisen from a simple system of mutual benefit: well-fed animals bide their time looking out for predators, while the remaining group members exploit their companion's vigilance. Individuals benefit from specializing in one behavior at a time but are not locked into a particular caste as in eusocial insects. Although dwarf mongooses show some of the most elaborate forms of sentinel behavior, this system is highly facultative, so the sentinel system is unlikely to provide a platform upon which group-level adaptations could be built.

## II. Cooperative and collaborative hunting.

*A pride of lions sleeps near a waterhole as a reedbuck advances to drink. Stretched out on her side, one of the lions spots her prey, waits until it lowers its head, then rolls onto her chest, every muscle tense. The reedbuck looks up; the lioness stays frozen. The reedbuck walks toward the water, and the lioness starts her slow careful stalk, using every shred of cover. Head up. Freeze. After 10 min she is within 15 m; the rest of her pride sleeps soundly. The reedbuck starts to drink; the female pounces and bowls it over. Woken by the scuffle, her pridemates run to join her. She snarls and attempts to swat them away while keeping her jaws clamped firmly on the reedbuck's throat. Undeterred, her hungry companions rip open the prey's abdomen and eat most of the entrails and muscle. Finally, the hunter relinquishes her grip and stands panting in the heat of the day — the last member of the group to feed.*

Group hunting frequently captures the popular imagination, and anecdotes abound of highly organized hunters working to seize a large dangerous prey. However, recent theoretical work has refocused attention on the conflicting costs and benefits for each individual in a hunting group, and empirical evidence is accumulating that shows truly *collaborative* hunting is far less widespread than

previously supposed (Busse 1978; Packer and Ruttan 1988; Scheel and Packer 1991). Nevertheless, numerous species clearly do cooperate in specific situations. How can we account for this diversity, and to what extent does cooperative hunting indicate some higher level of cognition (or some other form of emerging complexity)?

How do we define cooperation in this context? At its simplest, group hunting can be said to be cooperative as long as two or more individuals simultaneously pursue the same prey animal. Cooperation will evolve as long as each individual gains a higher payoff by participating in a group hunt rather than by scavenging from a companion's kill (as in the above vignette). Beyond this mere simultaneity of prey pursuit, group members may actively *coordinate* the hunt by modifying their behavior according to the tactics of their companions.

**A. Simultaneous/cooperative hunting.** When a prey item is large enough to feed several foragers and the effort of prey capture incurs an inevitable cost, the advantage of joining an ongoing hunt depends on the extent to which an additional individual can improve its companions' chances of successful prey capture (Packer and Ruttan 1988). If one individual can capture the prey by itself, the contribution of a second hunter may be too low to overcome the costs of hunting, and the second animal's best option would be to "cheat" and hence wait on the sidelines until the prey has been captured. However, if prey capture is difficult, each additional hunter may make an important contribution, and simultaneous hunting can evolve even in the absence of kinship or long-term relationships.

Using data from a variety of animal species, Packer and Ruttan (1988) tested these predictions indirectly, using data on group-size specific hunting success as evidence of cooperation. In most species where individual hunting success was high, groups performed no better than solitaires, but in species where solitaires suffered poor hunting success, larger groups performed at rates that were consistent with a simple model of simultaneous cooperation (where the success rate of a group of  $n$  individuals,  $h_n$ , is given by  $h_n = 1 - (1 - h_1)^n$ , with  $h_1$  = success of a solitary, and thus  $1 - h_1$  = failure of a solitary and  $(1 - h_1)^n$  = the chance that everyone fails simultaneously).

Subsequent studies have confirmed that groups generally do cooperate when individual hunting success is very low (e.g. Elklöv 1992; Fanshawe and FitzGibbon 1993). The most detailed data come from studies of African lions. In Serengeti National Park, individual lions often "refrain" from group hunts, but refrain (i.e. cheat) least often during hunts of prey species that are most difficult to capture (e.g. Cape buffalo, Scheel and Packer 1991). In Etosha National Park, individual hunting success is far lower than elsewhere, and these lions show a much greater degree of cooperation (also see below). The hunting success and grouping patterns of the Serengeti and Etosha lions as well as data from a third study in Uganda (Van Orsdol 1981) is compared in Fig. 9.3.

The Etosha lions showed the greatest improvement in hunting success with increasing group size (Fig. 9.3a). Only in Etosha were pairs more than twice as successful as solitaires, and trios were more than three times as successful (Fig. 9.3b). As might be expected, the Etosha lions spent considerably more time in groups than did the other populations (Fig. 9.3c). The root cause of these differences appears to be the harsh conditions of Etosha where prey abundance is very low and the lions are forced to specialize on prey species that are very difficult to capture (East 1984).

Before considering more complex forms of group hunting, we want to make two points. First, it is surprising how often "cooperative" hunting seems to consist merely of several individuals hunting simultaneously. Additional hunters rarely contribute to the success rate of larger groups more than is predicted by the simple multiplicative model of  $h_n$  as outlined above. Second, even when animals have actively cooperated to capture a large prey, their feeding behavior is often competitive and

disorganized (e.g. Kruuk 1972; Schaller 1972). Thus, their cooperation is context specific and does not lead to an overall increase in social complexity.

**B. Coordinated/collaborative hunting.** Hunting partners sometimes respond to each other's behavior, either recruiting additional companions in anticipation of a hunt or coordinating themselves during the hunt itself.

**1. Active recruitment of hunting partners.** Zebra stallions vigorously defend their families from spotted hyena, requiring the hyena to hunt them in large packs. Human observers can reliably predict when spotted hyenas are about to hunt zebra even if other prey species are nearby and no zebra are in sight (Kruuk 1972; Holekamp, et al. in press; L. Frank, pers. comm.). Before embarking on a zebra hunt, the hyenas assemble at "pep rallies" where they perform greeting ceremonies, scent marking, defecation, and social sniffing. Then one to two females often lead the group on long treks, ignoring easier-to-catch prey (such as wildebeest) in their path. Once they reach a zebra herd, they engage in a simultaneous (but not coordinated) hunt.

Although hyenas may appear to be making a group-level decision, these pep rallies arise from the fact that individuals in large hunting groups can expect to obtain a greater reward *per capita* by selecting zebra rather than wildebeest. Many more hyenas scavenge from a carcass than participate in prey capture, and zebra weigh around 40% more than wildebeest. Thus, even though hyenas form significantly larger groups when hunting zebra rather than wildebeest, feeding group size is comparable for both prey species. Hence, in areas of higher hyena density (and limited hunting opportunities each day), individuals gain higher payoffs by forming hunting parties large enough to catch the larger prey (Kruuk 1972; Holekamp, et al. in press).

Again, it is significant that even though hyenas actively encourage the formation of large groups, their coordinated behavior breaks down once they pursue a specific prey animal. Mutual benefit encourages mutual participation but not any clear-cut division of labor.

**2. Division of labor during group hunts.** Stander (1992ab) described a remarkably stereotyped system of hunting behavior in the Etosha lions. These animals mostly hunted a single prey species, springbok, which was so small that the lions needed to capture several prey each day. Hunting in a homogeneous habitat, pride members fanned out to surround their prey, and certain individuals consistently approached from the left, others from the right, while the remainder approached directly. These "wings" and "centers" showed clear preferences and generally only altered their position if their group composition changed on a particular day. Most interestingly, hunting success appeared to depend on whether the lions were able to hunt in their preferred positions, suggesting that this division of labor conferred the sort of benefits that might lead to true specialization (Maynard Smith 1978; Oster and Wilson 1978).

In the Serengeti, complex hunting strategies are occasionally observed (e.g., Schaller 1972), but because these lions live in a more heterogeneous landscape and typically hunt several different species each day, their hunting techniques are more haphazard, and they often fail even to hunt simultaneously (Scheel and Packer 1991). The Etosha lions, on the other hand, probably needed to coordinate their cooperation owing to the low success rates of solitary hunters, and the sheer repetition of stalking a single species of prey may have enabled each lion to learn a specific tactic that reflected an associated skill: Heavier females were more likely to be "centers", lighter females to be "wings." These Etosha prides lived in an extremely harsh environment and were unable to rear cubs during the study period (P. Stander pers. comm.), so it is noteworthy that their highly developed hunting strategies, having arisen *in extremis*, may have been invisible to natural selection.

Another example of coordinated hunting is provided by the chimpanzees of Tai National Park, Côte d' Ivoire, West Africa (Boesch and Boesch 1989). These animals typically show complementary actions such as driving, blocking escape paths, and encirclement, although no data are available on the consistency of individual behavior. The Tai chimps "collaborated" in 68% of group hunts compared to less than 20% in two Tanzanian populations. As in the lion comparisons, the Tai chimps show lower success rates when hunting solitarily, and they more typically hunt in groups than chimps in the other populations (even recruiting distant companions to the hunt). Boesch (1994ab) speculated that the greater degree of collaboration at Tai ultimately arises from ecological factors: The taller and thicker forest structure requires the chimps to work together to capture their arboreal prey. Boesch and Boesch (1989) also suggested that because chimps in this population are more consistently gregarious than their Tanzanian counterparts, they have greater opportunity to learn complex hunting tactics.

However, another interpretation of the Tai chimps' behavior is that these animals are less tolerant of scavenging by "bystanders" or "latecomers" (Boesch 1994b), and thus the individual who actually captures the prey gains a significant advantage. This leads to an important question. Is an apparent division of labor the result of each individual maximizing its personal chances of prey capture (Busse 1978), or do group members coordinate themselves to maximize the success rate of the entire group? Are individuals ever willing to reduce their personal chances of prey capture in order to maximize the success rate of their companions? This may vary from species to species. In chimpanzees, the successful hunter achieves the lion's share, but in lions (as typified by our vignette), the killer typically continues throttling the prey long after its pridemates have started feeding.

### III. Group-Group Competition.

*It has stopped raining. The young chimpanzee shakes himself off and resumes feeding. He occasionally scratches his chest and spits out a palm nut, which crashes through the fronds to the ground below, punctuating the dripping hiss of the forest. He is all alone in this narrow valley; his usual companions are somewhere off to the south. Then all hell breaks loose. Four males from a neighboring community charge toward the adolescent, he tries to escape, but two of the neighbors tackle him and hold him down. The other two take turns biting, kicking, and stomping on his neck, his back, his legs. They leave him broken and bleeding, dying on the forest floor, and return to their own territory where they climb a large fig tree and set off a chorus of hooting and screaming.*

Intergroup competition is widespread in vertebrates: Group territoriality occurs in carnivores (Kruuk and MacDonald 1985), rodents (Lacey and Sherman 1991), primates (Cheney 1987), birds (Davies and Houston 1981; Brown 1987; Black and Owen 1989), and fish (Clifton 1989). If groups fight to the death or for exclusive access to key resources, the self-interests of each group member will coincide with the interests of the entire group, as has been documented in coalitions of male lions (Grinnell, et al. 1995). These coalitions compete intensively for access to female prides, and they are typically only able to maintain residence long enough to father one to two cohorts of offspring. Unrelated partners will form lifelong relationships and cooperate whole-heartedly even in situations when their behavior cannot be monitored by their partner. However, this behavior is driven by the existence of larger groups of cooperative kin (which forces solitaries to team up in order to remain competitive) and is limited by the increasing degree of within-group competition in larger groups (the larger kin groups will tolerate reproductive skew, whereas unrelated companions will not) (Packer, et al. 1991).

Here we explore whether group-group competition has led to complex forms of cooperative behavior within each species. We then describe cases in which groups behave like individuals in higher-



order levels of competition.

**A. The complexity of "Us" against "Them."** The remarkable patrolling behavior and organized gang warfare of male chimpanzees (Goodall, et al. 1979; Goodall 1986) provides the best-known example of complexity in this context. Males seem to decide in advance when to make a foray to a territorial boundary. They seek out and stalk their quarry, usually a lone member of the neighboring community. The marauding males remain unusually silent and stealthy until launching a sudden attack, and those males who hold down the opponent make it easier for their companions to administer a *coup de grâce*. Of the few attacks that have been directly observed, specific individuals do not consistently show the same tactic (although certain individuals appear to be more actively aggressive). The caution with which they set out to maim or kill their opponent probably serves to minimize the risk of injury to their companions as well as to themselves. This is a dangerous task and is clearly an emergent property of group living: The entire group must keep themselves healthy in order to overpower even a single opponent.

Even in the case of group territoriality, however, individual costs and benefits may not always coincide, and intergroup conflicts may often involve a considerable degree of within-group decision making. When a large group greatly outnumbers its opponents, a lone defector might be able to gain the resource without paying any costs of territorial defense. Female lions compete against their neighbors for access to land, and larger groups dominate smaller ones (McComb, et al. 1994). Recent studies show, however, that not all individuals pull their weight when confronted by strangers: During playback experiments, certain animals routinely hang back during their approach to the territorial invaders (Heinsohn and Packer 1995). Others (nicknamed "friends in need") participate when their assistance would be most likely to influence the odds of winning the encounter. Still others ("fair-weather friends") participate most often when their group safely outnumbers the opposing group.

No theoretical model currently exists that can account for such a diversity of individual strategies during intergroup encounters, but these results emphasize the fact that individuals probably weigh personal costs and benefits before deciding to participate in a territorial dispute.

Nevertheless, some form of group selection will be expected to operate in this context. Successful groups may annihilate unsuccessful groups, and traits that promote individual survival will also promote survival of the entire group. Intergroup conflict therefore involves relatively little opposition between individual advantage and the good of the group. Because the outcome of these conflicts may depend on the emerging properties of group-level competition, the question remains whether a group-oriented perspective is necessary to explain the evolution of these properties or if they can best be understood by emphasizing individual fitness. Perhaps an individual-fitness approach similar to Bednekoff's models of sentinel behavior would reveal the factors necessary to produce a division of labor and other characteristics of group warfare.

**B. Higher levels of inter-group competition.** Resource competition is often restricted to disputes between members of the same group or struggles between neighboring groups. But individuals from separate groups may sometimes cooperate in competition against a common enemy (e.g. rock pipits, in which adjacent territory holders cooperate to evict potential newcomers; Elfström 1997), and entire groups may temporarily coalesce to form second- or third-order alliances. In fact, the spatially discrete social units of several vertebrate species actually consist of collections of matrilineal alliances, and thus more species show a multitiered social system than is generally recognized. These higher-order alliances are reminiscent of tribal societies in humans and involve some of the most intelligent

mammalian species, including primates, carnivores, elephants, and cetaceans.

Social complexity is increasingly seen as the driving force in the evolution of intelligence, with a large brain size being required to track multiple social relationships (Byrne and Whitten 1988; Barton 1996). Boehm (1992, 1997) argued that the quality of these relationships has also been important in the evolution of our own species, specifically in permitting the development of enforced egalitarianism. Thus the despotic tendencies of more powerful members of human society are countered by cultural traditions that create a powerful force for consensus and minimize the fitness outcome of such phenotypic variation. As outlined below, however, most multitiered vertebrate societies probably exist precisely because they are *not* egalitarian: each individual is ordered according to dominance rank and participates in ever higher levels of social organization in a nested series of group-ordered dominance relationships.

Primate troops and hyena clans show a complex social organization based on family-level alliances (Chapais 1992; Frank, et al. 1995). Mothers support their daughters in disputes against other families so that members of the same matriline enjoy adjacent rank in an overall hierarchy. But adjacently-ranked families will cooperate against subordinate matriline to maintain the status quo. Experiments in Japanese macaques (Chapais, et al. 1991) showed that a second-ranking matriline benefits by allying itself with the top-ranked matriline in order to prevent the formation of a "bridging alliance" between the first- and third-ranked matriline. By cooperating with the second-ranked matriline, the top-ranked matriline creates a state of dependency that forestalls a "revolutionary alliance" between the second- and third-ranked matriline. Despite these internal divisions, the entire troop or clan will cooperate during clashes with neighboring groups. In each level of complexity (summarized in Fig. 9.4), individuals apparently work together according to the usual rules of genetic self interest.

In Hamadryas baboons (Kummer 1968; Sigg, et al. 1982; Abegglen 1984; Stambach 1987) and African elephants (Moss and Poole 1983; Moss 1988; Poole, et al. 1988), discrete social groups show second-, third-, and fourth-level alliances (Fig. 9.4). The primary social group of Hamadryas baboons is the "unit group" which consists of a single adult male, several females, and their dependent offspring. These units often compete against each other, but then coalesce into "clans" that compete against other units or clans for access to females or food. Clans merge to form "bands," which in turn form "troops." Bands and troops compete against each other for access to waterholes and sleeping cliffs. Intertroop and interband encounters can seem quite organized, with males from each clan lined up side by side in front of their females and the subadult males advancing in the lead.

In elephants, the family groups aggregate to form "bond groups," and social interactions between these individuals are just as intense as between family members (after a separation, these individuals greet each other with trumpeting, ear flapping, trunk entwining and excited defecation; while apart, they seem to coordinate movements over long distance using low-frequency sound). Bond groups associate preferentially in a "clan," whose members interact frequently and greet each other by calmly putting their trunks in each others' mouths. Clans coalesce as a "subpopulation," whose members are intolerant of members from other subpopulations. These higher-order groups are most prominent during periods of food abundance but then disperse when food supplies diminish.

Elephant family groups (and, probably, bond groups) are matriline (Moss and Poole 1983), and males of the Hamadryas clans are suspected to be brothers (Sigg, et al. 1982; Abegglen 1984), but it is not yet known whether their higher-order alliances are also based on genetic relatedness. Even in the absence of kinship, individuals can benefit from preferential alliances because of the advantages of a clear-cut dominance relationship. As resources diminish, high-ranking groups may first align

themselves with known subordinates to evict competitors of unknown fighting ability, then the dominants can oust the subordinates when the resource is only large enough for a single group.

Not all multitiered systems are obviously despotic. In some social species, higher-order alliances may essentially involve a lottery in which groups cooperate with other groups without necessarily knowing who will win. For example, male bottle-nosed dolphins form stable first-order alliances of two to three individuals, which coalesce to form second-order alliances during competition for receptive females (Connor, et al. 1992). These second-order alliances will steal females from other groupings, and only one first-order alliance ultimately herds the female. Two members of the winning coalition may then mate with her simultaneously, and if there is a third male in the coalition, the identity of the "odd man out" changes from one takeover to another (Connor and Smolker 1995).

No paternity tests have yet been performed in dolphins, behavioral observations are sparse, and the kinship between coalition partners is unknown. It is possible, however, that these primary coalitions arise from mutualistic advantage. If each male in these alliances has an equal chance of fathering each offspring, then cooperation will pay as long as coalitions gain significantly greater access to females than do solitaries. A similar argument applies to the temporary coalitions of savanna baboons (Bercovitch 1988; Nöe 1990), in which pairs of males are much more successful at taking over oestrous females than are lone challengers. In the dolphins, the first-order alliance is truly analogous to an individual baboon, and their extraordinary levels of cooperation apparently stem from the difficulty of sequestering receptive females in this species.

Multitiered vertebrate societies show many important similarities to human social organization, and it is striking how many of these examples involve long-lived intelligent animals. However, most of these societies are readily understood in terms of a few simple rules of despotic and nepotistic behavior. Even in cases where higher-order alliances appear to be egalitarian, they are the product of a lottery, not a social contract.

#### **IV. Prospecting for new pinnacles of complexity.**

*The sun has set, and a herd of Cape buffalo moves away from the river, looking for a spot to bed down for the night. The bulls, cows, and calves chew their cud and occasionally call to each other. Suddenly, everyone is startled by a bright light in the sky. The herd springs into action. The bulls approach the disturbance and start thrashing the ground with their horns. The cows and calves trundle back down toward the river. An astonished biologist records the scene.*

*"My god, what' s that objectn the sky? A spaceship? Oh heavens, it' s landed, and those bull buffalo — they' ve started digging a trench! And the cows, the cows have constructed some sort of suspension bridge. They' re carrying their calves across to the other side!"*

*The door of the spaceship opens, and an alien voice announces, "We are Borg. You will be assimilated. Resistance is futile."*

The idea that a buffalo herd could organize a complex defensive response is even more ludicrous than the notion of a pompous space alien landing in the Serengeti. (We chose the Borg because they regularly threaten the characters of "Star Trek" with a group-level cognition. Individuals function as neurons within a collective intelligence.)

\* True group-level adaptations/cognition in any animal as intelligent as a mammal should be elaborate, conspicuous, and unequivocal. If insects can organize fungal gardens, warfare, and bridge building, we should surely see "emerging properties" at least as impressive in the vertebrates. In our survey of some of the most complex vertebrate social behaviors, we found little evidence of such group-level adaptations. Self-interested behavior could always be seen to mold the form of society not vice versa.

With the exception of naked mole-rats, we could find no example of a division of labor that involved a long-term specialization: Every individual could alternate between foraging and acting as a sentinel, between hunting as a "center" and a "wing," and between a variety of tactics during a gang attack. The Etosha lions showed the most persistent specializations, but even here specific individuals modified their behavior in response to changes in group composition.

Are most vertebrates "generalists" because their group-level responses are too rudimentary to require specialization, or is group-level cooperation relatively undeveloped because individuals are selected to be generalists? In the absence of eusociality, all these animals are capable of independent breeding, and each individual seems well equipped to solve a variety of problems. Cooperative group sizes are typically so small that reliance on a specialist might be disadvantageous. Imagine a musical quartet in which each musician can only play a single instrument; if one person dies, the surviving trio might be unable to perform properly. However, in ensembles large enough to be safely redundant (like an orchestra), the advantages of mutualism or the force of kin selection will generally be too weak to maintain a group-level degree of cooperation.

We also could find no example of group-level complexity that justifies the sort of "group mind" envisioned by Wilson (1997) and other neo-group selectionists. For example, Prins (1996) has suggested that Cape buffalo show "voting behavior," wherein several hundred animals assess each other's preferred destination before moving off as a single herd each day. Although group progression patterns may indeed involve some form of collective decision making, we see no reason to invoke anything beyond a simple set of individual decision rules (e.g., chimpanzee social organization: Te Boekhorst and Hogeweg 1994; task allocation in social insects: Pacala, et al. 1996).

Finally, we could find no compelling evidence that a vertebrate social system ever exceeds the sum of its parts. The coordinated evasion of dunlin flocks and fish schools is impressive only because each individual benefits from responding to the behavior of its neighbors. The most elaborate social organizations illustrated in Fig. 9.4 only require an ability to recognize a large number of individuals (rather than any form of group-level cognition). Though intergroup competition might be expected to provide the best possible context for group-level phenomena, group-territorial lions are hardly a paragon of cooperation, riddled as they are with "friends in need" and "fair-weather friends."

Outside of the possible exception of eusociality (with naked mole-rats providing the best known example in vertebrates; Jarvis and Bennett 1991), the landscape of vertebrate social evolution is dynamic but ultimately leveled by the forces of self interest.

### **Acknowledgments**

Scott Creel, Laurence Frank, Kay Holekamp, Cynthia Moss, and Philip Stander generously provided unpublished information. We also appreciated the insightful comments from Peter Bednekoff, Laurent Keller, David Sloan Wilson, and three anonymous reviewers.

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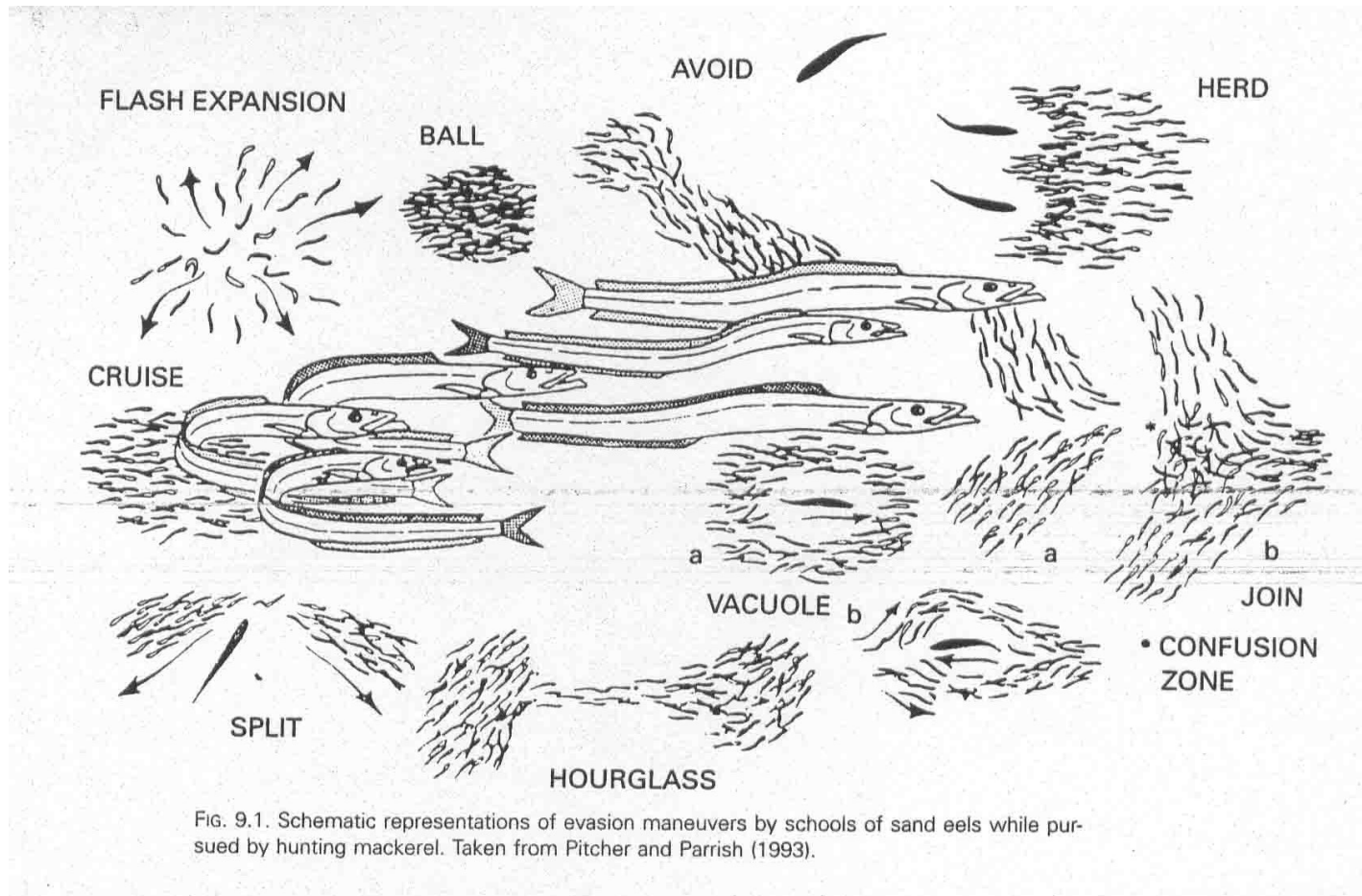


FIG. 9.1. Schematic representations of evasion maneuvers by schools of sand eels while pursued by hunting mackerel. Taken from Pitcher and Parrish (1993).

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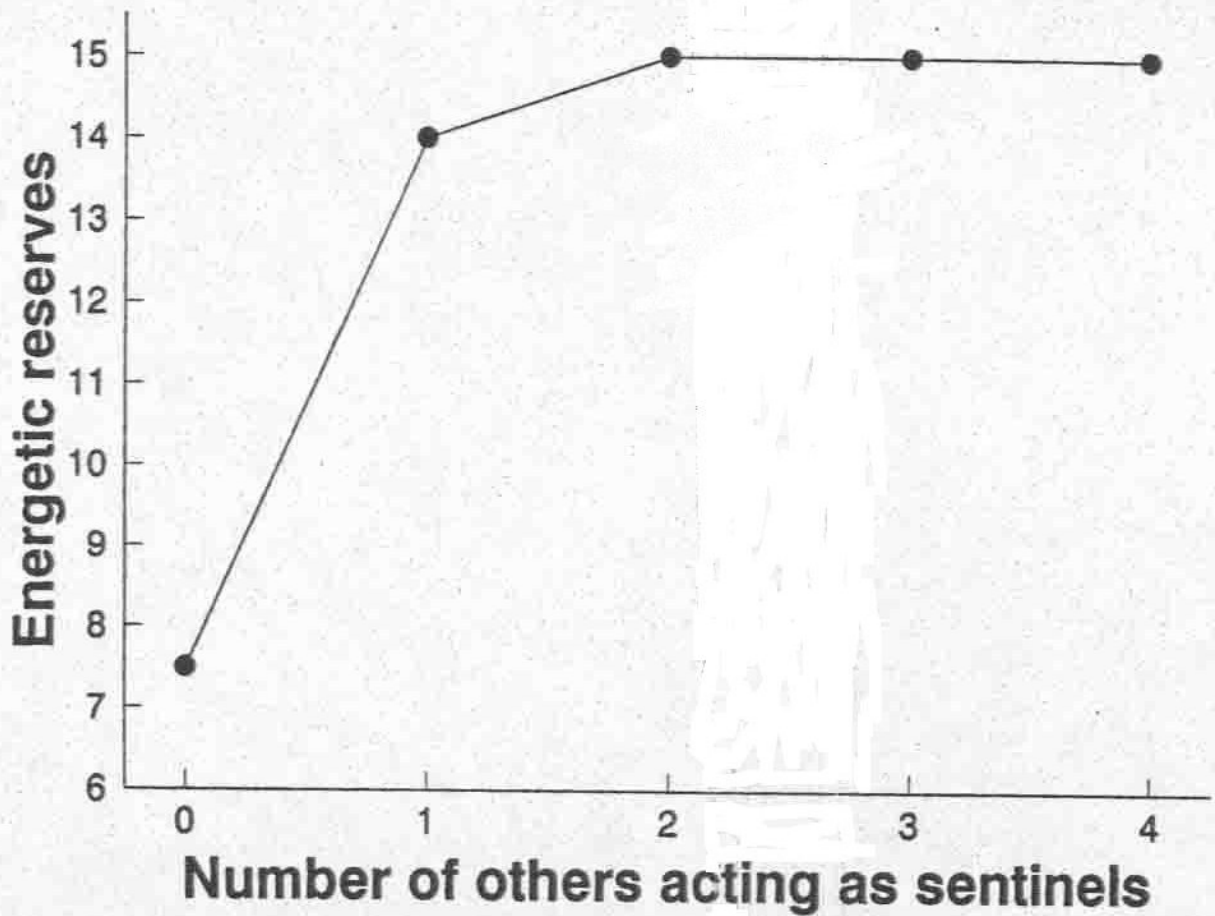
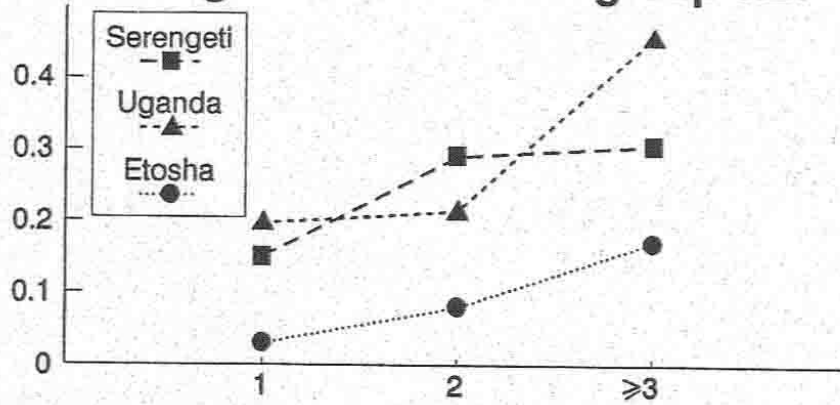
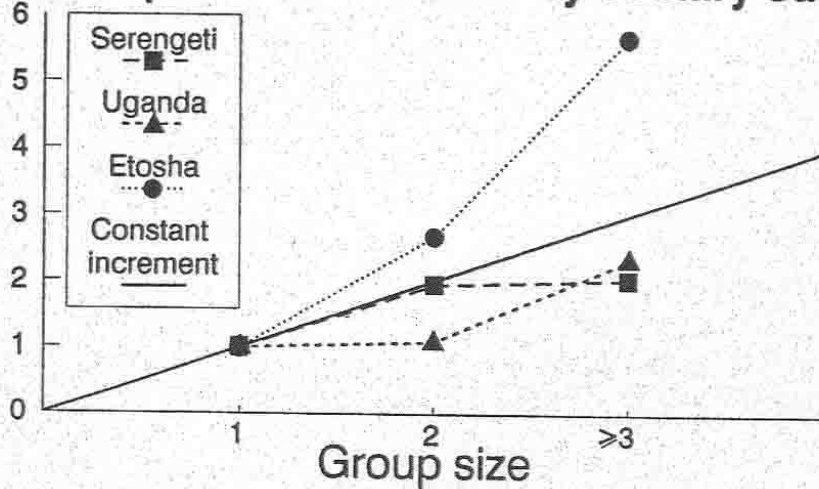


FIG. 9.2. Bednekoff's (1997; with permission of the University of Chicago Press) model of sentinel behavior. Bednekoff considered several different scenarios, but we only present the outcome when sentinels are the only animals to give an alarm call. Graph illustrates the optimal decision rule for a member of a group of five, given the number of other group members that are acting as sentinels. If an individual's current energetic reserves exceed the line, then it should become a sentinel, otherwise it should forage. The maximum possible energetic reserve is 15 in this model.

**A. Hunting success of each group size**



**B. Group success divided by solitary success**



**C. Time spent in groups of each size**

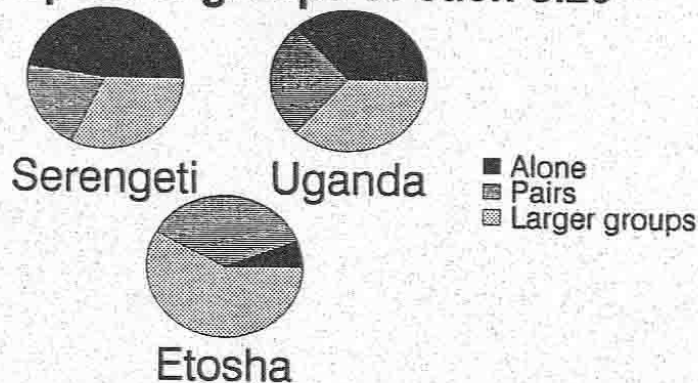


FIG. 9.3. Hunting success and grouping behavior in three different populations of African lions: Serengeti, Tanzania (Schaller 1972; Packer et al. 1990); Queen Elizabeth Park, Uganda (Van Orsdol 1981); and Etosha, Namibia (Stander 1992a,b). (A) Group-size specific hunting success. (B) Relative hunting success for each group size. (C) Proportion of time lions spent alone, in pairs, and in larger groups.

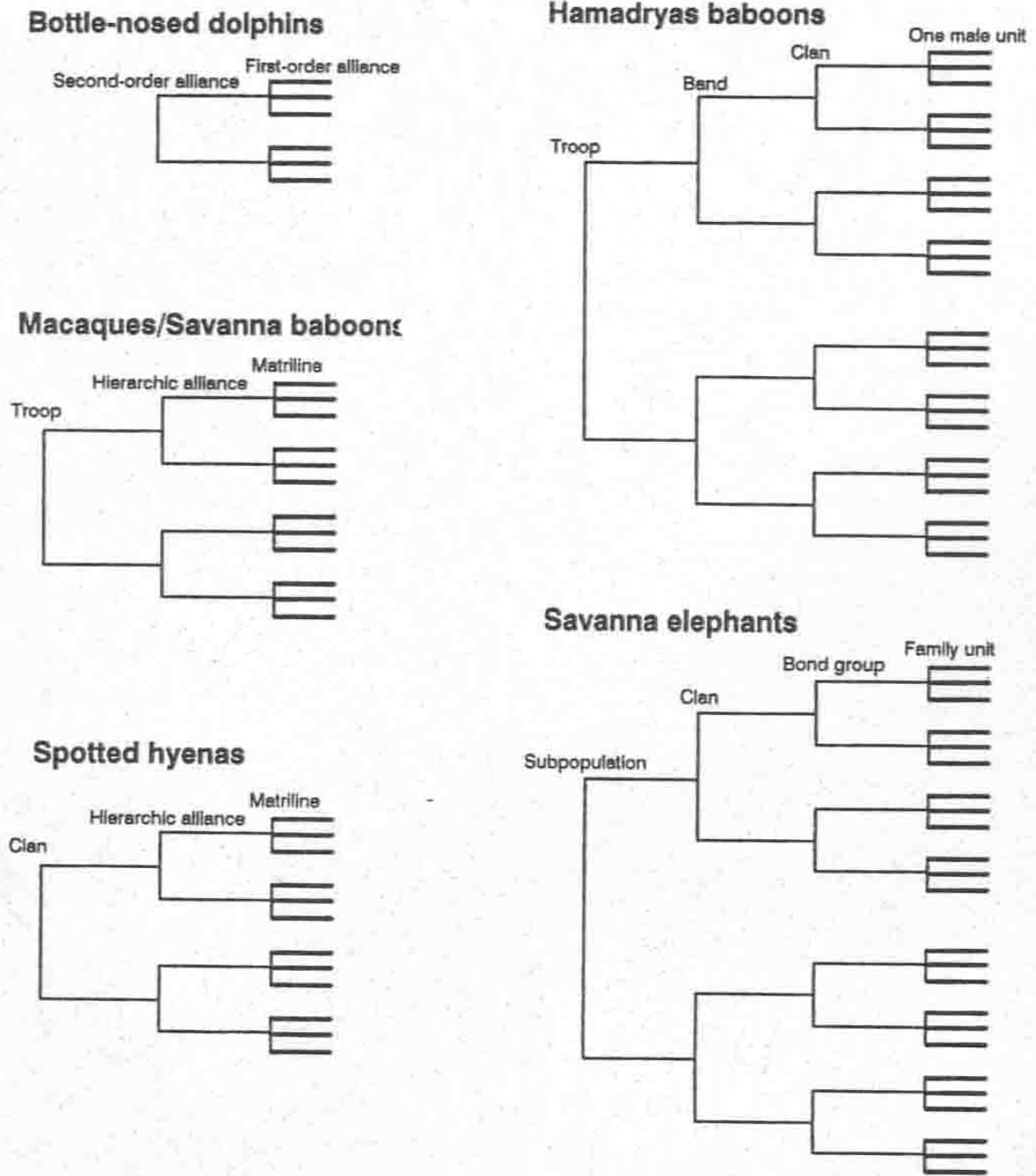


FIG. 9.4. Multitiered social systems exist in various vertebrate species. Horizontal lines indicate individuals or groups; vertical lines link cooperative partners.