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Hyena societies

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Although the family Hyaenidae contains only four living species, and is therefore one of the smallest among mammalian carnivores, it is remarkable for its ecological and social diversity, which surpasses that of much larger families such as canids and felids. The four extant hyena species represent the last remnants of a family that was once large and diverse. At the peak of hyaenid diversity in the Late Miocene (12–6 million years ago), at least 24 different hyena species concurrently roamed Eurasia and Africa [1]. Miocene hyaenids included not only robust, bone-cracking forms, but also many species that were dog-like in their appearance and feeding ecology. Since the Late Miocene, the family Hyaenidae has declined in species diversity and geographic range, such that hyenas now occur only in Africa and the Middle East. Nevertheless, modern hyenas occupy a vast range of habitat types, including deserts, montane forests and open savannas. Furthermore, they fill a surprisingly wide array of ecological niches, ranging from specialized insectivore to large predator. In parallel with this ecological variation, hyena societies also vary considerably, ranging from monogamous pairs to large, complex groups.

The four living species in the family Hyaenidae (Figure 1) include the aardwolf (*Proteles cristata*), the striped hyena (*Hyaena hyaena*), the brown hyena (*Parahyaena brunnea*) and the spotted hyena (*Crocuta crocuta*). All of these animals are largely nocturnal, and all have hind legs that are somewhat shorter than their forelegs, giving their body profiles a sloping appearance (Figure 2). All of these animals communicate with one another by erecting their manes and tails, as well as through a rich repertoire of facial expressions [2]. They also rely heavily on chemical communication, and all hyenas mark their territories with deposits from anal scent glands. Here we will briefly describe the societies characteristic of the four living hyena species, consider the selection pressures that have shaped sociality in these animals, and inquire what we can learn by interspecific comparisons of social behavior among extant hyenas.

Aardwolf societies

The aardwolf is the only living member of a large clade of dog-like hyenas, but in contrast to its meat-eating ancestors, the aardwolf is highly specialized for feeding exclusively on harvester termites. This is the smallest of the extant hyenas; adults of both sexes weigh only 10 kilograms. Aardwolves are also the least gregarious of the living hyenas. They live in socially monogamous pairs, but both males and females are known to mate with individuals other than their social partners [3].

Despite this promiscuity, together with their social partners, aardwolves defend territories that contain enough termite mounds to support the pair and their juvenile offspring, and both males and females participate in care of the young. Although mates cooperate in parental care and territorial defense, individual aardwolves forage solitarily.

Striped hyena societies

Striped hyenas are primarily scavengers; their diet consists mainly of dried flesh and bones from carcasses of large vertebrates, supplemented by fruits and insects, as well as small vertebrates that these hyenas hunt themselves [4]. Striped hyenas, in which adults weigh 30–35 kilograms, usually forage alone, although multiple individuals occasionally gather at rich food sources. In this species, males are slightly larger than females, and males also appear to be socially dominant to females.

Striped hyenas are the least studied of the hyenas: their social behavior is poorly understood, but they are usually reported to be solitary [2]. It was recently discovered that small groups, composed of one adult female and one to three adult males, share a common home range and may be found resting together during daylight hours [5]. Females appear to mate both with group males and males that reside elsewhere. It is not known whether sires contribute in any way to parental care, but lactating females are usually found alone at dens with their cubs, and females appear to be solely responsible for care of young.

Brown hyena societies

Like striped hyenas, brown hyenas are primarily scavengers

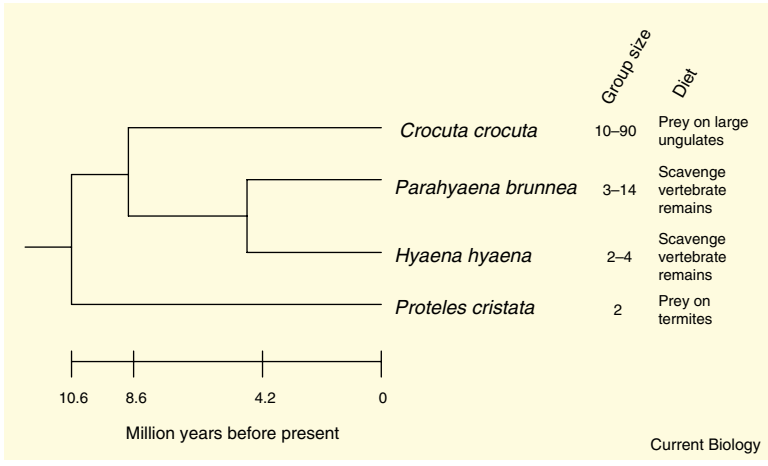

Figure 1. Extant hyenas.

A phylogeny of extant Hyaenidae based on [15] with species typical group sizes and diet.

that forage solitarily for carrion, and their diet is very similar to that of striped hyenas. However, sociality in brown hyenas appears to be more complex than that in striped hyenas. They live in small clans ranging in size from a single female and her cubs to approximately 14 animals [6]. Larger clans consist of extended families that include a female, her adult offspring of both sexes, and an immigrant male.

Males that leave their natal area either immigrate into a new clan or adopt a nomadic lifestyle. Females, but not males, breed in the natal clan, where they mate with immigrant and nomadic males. Females may nurse each others' young, although they give priority to their own offspring. Brown hyenas weigh roughly 40 kilograms. Social structuring within brown hyena clans appears to vary among populations, ranging from egalitarian groups to clans with well defined, sex-specific linear dominance hierarchies in which males are socially dominant to females [6]. Regardless, all group members cooperate to defend a common territory and also aid in rearing young by bringing food to the den.

Spotted hyena societies

Spotted hyenas live in multi-male, multi-female clans that range in size from 10 to 90 individuals [7]. Whereas the societies of aardwolves, striped hyenas and brown hyenas are all composed of relatively small family groups like those of other gregarious carnivores, the societies of spotted hyenas often contain many unrelated individuals. Thus, spotted hyenas exhibit a social system quite distinct from those of other carnivores. In fact, spotted hyenas live in large, complex groups having far more in common with many primate societies than with the societies of other carnivores.

Like troops of old-world primates, including baboons, macaques and vervet monkeys, spotted hyena clans are structured by strict linear dominance hierarchies in which an individual's position, or rank, in the hierarchy determines its priority of access to resources. In addition to using other sensory modalities for communication, spotted hyenas also express themselves to conspecifics with a vocal repertoire as rich as those in many monkeys. Also in common with several old-world primates, these hyena groups are matrilineal, and an individual's position in the hierarchy is determined by the social rank of its mother rather than by its age, size, or fighting ability.

Early in life youngsters of both sexes 'inherit' the social rank of their mother. However, while females remain in their natal group throughout their lives, virtually all males disperse after puberty to join a new clan. When a male immigrates into a new group, he enters as the lowest-ranking hyena in the dominance hierarchy; he behaves submissively to all hyenas he encounters in the new territory, regardless of their size, fighting ability or social rank. This creates a society in which adult females and their cubs are dominant to all adult male immigrants, and in this respect spotted hyenas differ dramatically from old-world primates. Although a male hyena loses his maternal social rank and its associated feeding privileges when he disperses, he must join a new group in order to gain access to sexually receptive females. Females strongly prefer to mate with immigrants, so they rarely mate with natal males, and almost all offspring are fathered by immigrant males [8,9].

For any spotted hyena living in a large clan, the task of learning one's rank within the group requires a large memory for individuals and interactions among them, as well as a significant capacity for social learning. Most of this learning occurs at a communal den, where all juveniles reside until they are 8–12 months of age. The communal den is a focal point of social activity for all group members, not just mothers and cubs, and most clan members visit it regularly. It is through interactions with clan-mates, particularly those involving maternal interventions and coalition formation, that cubs learn their social ranks within the group [10]. This process of rank acquisition is strikingly similar to that observed in old-world primates. While maintaining cubs communally facilitates social learning in spotted hyenas, communal rearing is not associated with alloparental behaviors such as provisioning, guarding, or allonursing, as it is among brown hyenas. Although alloparental behavior is characteristic of many social carnivores that rear young communally, factors such as intense feeding competition, a strict dominance hierarchy, and low within-group relatedness may preclude such behavior in spotted hyenas.

Unlike the three other extant hyenas, spotted hyenas are adapted for hunting medium- to large-bodied ungulates. They feed primarily on prey they kill themselves, though they will also scavenge opportunistically. A single spotted hyena can capture an adult wildebeest up to three times its body weight, but cooperation with other group members is required to capture larger prey such as zebra or buffalo [7]. Contrary to popular belief, hyenas usually hunt alone. Once a prey item has been captured, however, many group members typically converge on the carcass to feed. This leads to intense feeding competition, in which social rank determines priority of access to food.

Although feeding competition within groups can be intense, hyenas need help from group members to defend a territory and the food resources within it from neighboring conspecifics. Hyenas periodically patrol the borders of their territory, scent-marking intensively as they go. Neighboring groups will sometimes clash in 'clan wars' that typically occur if a kill is made near a territorial border. Females usually initiate and lead border patrols and clan wars,

though males also participate [11]. The frequency and intensity of territorial behavior appears to vary with hyena density, and is seldom observed when hyenas occur at low density, as in the Kalahari Desert.

Individual clan members must balance the demands imposed by feeding competition with those imposed by the need for cooperation from conspecifics during defense of territories or individual carcasses. Like the other extant hyaenid species and most other gregarious carnivores, spotted hyenas cope with feeding competition by spending most of their time dispersed in subgroups that are smaller than the clan itself. This type of social organization is known as a fission–fusion society. Among spotted hyenas, although all group members know one another, rear their young together, and cooperatively defend resources, the entire clan is rarely found together.

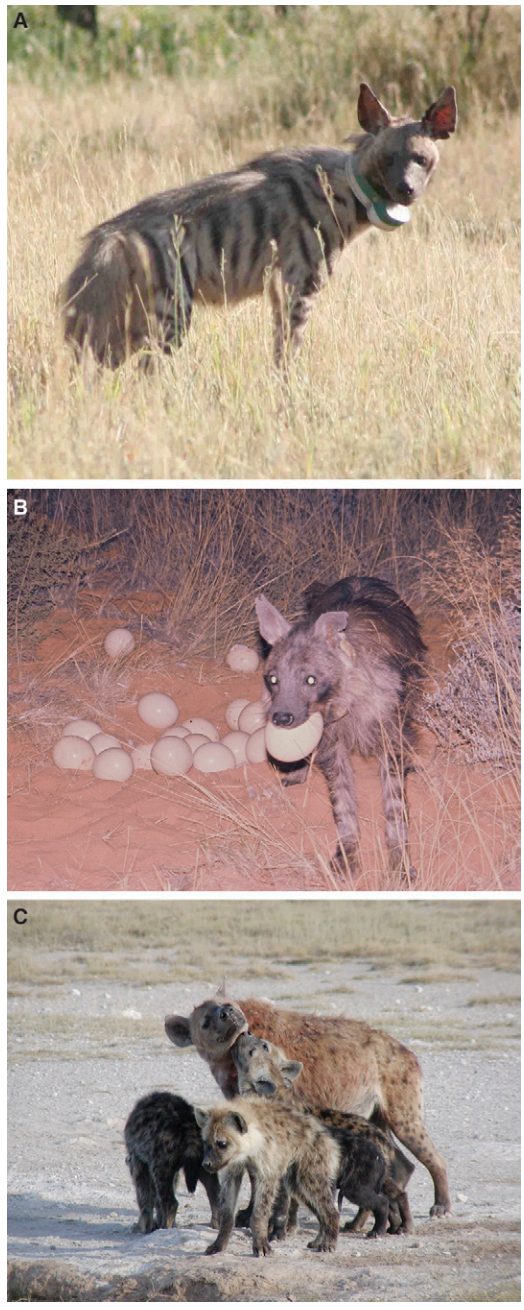

Figure 2. Three hyena species.
(A) A typically solitary striped hyena. This female has been fitted with a radio collar by researchers. (B) A brown hyena scavenges an egg from an ostrich's nest. Both brown hyenas and striped hyenas are primarily scavengers. (C) Spotted hyena cubs investigate an adult that has just arrived to the clan's communal den. Spotted hyenas are highly gregarious and the communal den is a focal point for social activity and social learning. (Photographs by: Aaron Wagner, striped hyena; Gus Mills, brown hyena; Heather Watts, spotted hyenas.)

Selection pressures favoring gregariousness in hyenas

Patterns of sociality in many carnivores are shaped by selection for reduced predation and/or selection for enhanced exploitation of food resources [12]. If predation pressure has been important in the evolution of sociality in hyaenids, then we would expect that those species most vulnerable to predation, usually those with the smallest bodies, would be most gregarious. Contrary to this prediction, gregariousness is positively related to body size among hyena species. Spotted hyenas, the largest of the extant hyenas, weigh up to 90 kilograms as adults, and they are also the most gregarious. This suggests that predation pressure has not been of primary importance in shaping sociality in this family.

Similarly, gregariousness among hyenas cannot be satisfactorily explained by the enhanced ability of individuals foraging in groups to find or capture food. For example, the diets of brown and striped hyenas are very similar yet their societies differ considerably. Indeed, these hyenas appear to associate with conspecifics despite their need to forage solitarily. It has been hypothesized that spotted hyenas live in groups because cooperative hunting allows these animals to capture larger prey animals or enhance their hunting success. Although cooperative hunting does increase the probability of success and allows spotted hyenas to capture larger prey animals, 75% of successful hunts are conducted by lone hyenas. Furthermore, only the largest and most challenging of prey species such as zebra, giraffe, and buffalo require more than one hyena for a successful hunt. This suggests that cooperative hunting was likely not paramount in the evolution of sociality, although assistance during hunts might represent a beneficial side effect of group-living among modern spotted hyenas.

Alternatively, the need to defend food resources from competitors may have favored gregariousness among hyenas. There is relatively little potential for intensive direct intraspecific competition among aardwolves, striped or brown hyenas, as all rely on food resources that limit their populations to low densities. Termites and scavenged carrion, on which the other hyena species rely, are relatively scarce, and not readily replaced. By contrast, spotted hyenas prey on live ungulates, which represent an abundant and readily renewable food resource [13]. Thus their feeding ecology allows spotted hyenas to reach high population densities. Moreover, spotted hyenas often live and hunt in open habitat where competitors, such as lions and alien spotted hyenas, can easily detect kills, which are typically too large to be monopolized by a single individual. These circumstances should favor grouping by conspecifics in order to protect carcasses.

Gregariousness may also have been favored in spotted hyenas to facilitate defense of territories containing live prey animals as well as defense of individual carcasses. Because spotted hyenas feed on highly mobile ungulates that forage over large areas, cooperative defense of territories may be necessary to ensure an adequate and reliable food supply. Comparisons among spotted hyenas at different population densities and group sizes would be useful to test these alternative explanations for sociality.

What can we learn from comparisons among the hyenas?

Comparative studies of species in the hyena family promise to shed considerable light on factors favoring the evolution of female dominance. The female-dominated societies of spotted hyenas and various lemurs are among the very few exceptions to the typical mammalian 'rule' of male social dominance. For spotted hyenas, it has been suggested that intensive feeding competition combined with a prolonged period of juvenile development may have favored the evolution of large aggressive females better able to secure resources for dependent young. New studies comparing juvenile development, maternal behavior, and feeding competition among extant hyenas and other carnivores will be essential for testing this hypothesis.

Because they are mammalian carnivores that live in large, monkey-like social groups, spotted hyenas have recently emerged as a non-primate model for studying social cognition and testing hypotheses regarding the evolution of intelligence [14]. The demonstration of surprisingly complex cognitive abilities in spotted hyenas, such as the ability to recognize relationships among clan-mates, has generally supported the hypothesis that social complexity was a key force selecting for the evolution of intelligence. To test this hypothesis properly, however, it will be necessary to compare the cognitive abilities of spotted hyenas with those of other hyena species. If other, less gregarious species of hyenas are found to lack some of the cognitive abilities exhibited by spotted hyenas, this will offer strong support for the hypothesis that social complexity favors the evolution of intelligence. Because the four species in the hyena family exhibit such diverse societies and include social groups like those found in primates, the hyena family represents an excellent non-primate mammalian model system in which to address questions pertaining to the evolution of intelligence in general, and social cognition in particular.

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