Module # 1 – Component # 1

Introduction to Carnivores

INTRODUCTION

<table>
<thead>
<tr>
<th>Families represented in Africa</th>
<th>Genera</th>
<th>Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Viverridae, genets, civets, mongooses</td>
<td>18</td>
<td>34</td>
</tr>
<tr>
<td>Hyaenidae, hyenas</td>
<td>3</td>
<td>4</td>
</tr>
<tr>
<td>Felidae, cats</td>
<td>3</td>
<td>10</td>
</tr>
<tr>
<td>Canidae, foxes, jackals, wolf, wild dog</td>
<td>4</td>
<td>10</td>
</tr>
<tr>
<td>Mustelidae, weasels, polecafs, skunks, badgers, otters</td>
<td>6</td>
<td>7</td>
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</table>

The most recent classifications of the Carnivora reduce the number of African genera and species recognized when the Guide was published from 34 and 65 to 30 genera and 58 species (e.g., Macdonald 2001).

ANCESTRY

Herbivores and carnivores both arose from insectivore ancestors soon after the Age of Dinosaurs ended some 65 million years ago. They have evolved and differentiated together from the beginning, inextricably joined by the predator’s nutritional dependence on its prey and the selection predation exerts in favour of the fittest prey.

The earliest carnivorous mammals were long-bodied, short-legged, and small-brained predators belonging to an archaic order, the Creodonta (“flesh-tooth”).

They differentiated and thrived as long as herbivores remained clumsy and slow-witted. But as speedier and brainier herbivores developed, only 1 family of creodonts was able to keep pace: the miacids, small, mongoose or weasel-like creatures with a proportionally larger, more advanced brain, which hunted game in dense undergrowth or in trees. All recent carnivores descend from the miacid line.

Between the late Eocene and the end of the Oligocene (40 - 24 million years ago), all but 2 of the existing families of carnivores arose, represented by species very like recent dogs, cats, weasels, and mongooses (fig. 18.1). The carnivore adaptive
radiation was paced by the rapid speciation of other mammals during the same period, notably the odd and even-toed ungulates and the rodents. The Carnivora divided very early into 2 separate lines, one of which culminated in dogs and the other in cats. Dogs, mustelids, bears, and raccoons are grouped in the superfamily Canoidea, whereas cats, civets, mongooses, and hyaenas are allied in the Feloidea. (Seals, walruses, etc., considered carnivores in some classifications, are generally treated as a separate order, the Pinnipedia, and are not included in this Guide.) Judged by similarity to the ancestral miacids, viverrids are the least-changed of modern carnivores.

CARNIVORE TRAITS

For all their diversity in size and life-style, carnivores share a number of physical and behavioural traits that show their common ancestry.

a) Their teeth are specialized for killing and eating other vertebrates: long, sharp canines for gripping prey, stabbing or slashing victims or enemies of other species, and attacking rivals of their own kind; cheek teeth reduced in number and modified for cutting meat and cracking bones, especially the carnassials (the fourth upper premolar and first lower molar), which function like shears to slice meat; and chisel-like incisors useful for gripping and stripping meat from bones. The jaws are correspondingly powerful and the skull is reinforced to anchor the jaw muscles.

b) The body is typically long and lithe, the limbs well-muscled and movable in all directions, with 4 or 5 toes, usually equipped with strong claws, which, however, only retract fully in cats and a few other species (including genets and palm civets).

c) Some carnivores walk on the whole foot (plantigrade), but most walk on their toes (digitigrade) with the heel well off the ground. Many are fast sprinters (cats), long-distance runners (dogs), or adept climbers.

d) Coloration and markings are cryptic, except for species with warning coloration and the African wild dog.

e) Carnivores tend to be intelligent, possessing the mental alertness and ability for coordinated action needed to outwit, capture, and kill other animals.

f) Predatory and fighting skills are rehearsed and developed in play, a major activity of most young carnivores.

g) The senses are well-developed, especially smell and hearing; also the sense of touch, aided by whiskers and other sensory hairs (vibrissae) on cheeks, head, ears, torso, legs, and tail. The cats, which hunt largely by sight, have exceptional binocular vision; they, and some mongooses may also have colour vision (see viverrid family introduction, ichneumon and suricate accounts).
h) Although *males* are generally somewhat **larger with bigger canines**, the only carnivore that is **highly sexually dimorphic** is the *lion*. Gender differences even in size are minimal among species that live in monogamous pairs: social mongooses, most canids, ratels (honey badgers), and some otters.

**ECOLOGY**

Of all carnivores, **85% weigh less than 11 kg** and range in size between a weasel and a fox. Hardly **2 dozen** of the 231 different species are **heavier than 20 kg** and only **11 are as big or bigger than an average man** (70 kg): the tiger, the lion, the jaguar, most bears, and the giant panda. Of the 66 African carnivores, half measure less than 50 cm long (head and body length) and 90% are under 1m. Weight ranges from the 300 g dwarf mongoose to the 172 kg lion.

**DIET**

Carnivores generally **select prey smaller** than themselves. The great majority depend on the host of **prolific small creatures** that are accessible to them out of the vast array of vertebrate and invertebrate organisms. **Few carnivores are strictly carnivorous**, as are cats and weasels. Most are **omnivorous** to some degree, supplementing their diet with a variety of plant foods, especially fruits. Some canids and mustelids, and many viverrids, **subsist largely on insects**. The presence of **molar teeth** adapted to grinding and crushing hard-shelled foods, instead of just slicing up meat, **reflects the omnivory** of many viverrids, mustelids, and canids.

Some carnivores are **quite specialized** or otherwise limited: otters for **aquatic existence**, aardwolf and bat-eared fox as **insectivores**, the wild dog as a **pack hunter** of medium-sized antelopes, the palm civet as a **frugivore**. Others take a **wide variety of prey**, from titbits the size of insects up to animals of their own size or even larger. The **more versatile** the predator, the **less dependent** it is on particular habitats, and the **wider its geographical range**. The leopard and lion, cheetah, caracal, wildcat, golden or Asiatic jackal, ratel, and striped hyaena are examples of carnivores that are or were widely distributed in Asia as well as Africa.

Surprisingly, there is **no niche for a pure mammalian scavenger** in African ecosystems. The supply of carrion is unpredictable and seldom adequate for more than a few scavengers. Vultures, with their network of aerial spotters, dominate the scavenging scene by day. Even **hyaenas and jackals are primarily hunters and only secondarily scavengers**. Many other carnivores will also scavenge food when the opportunity arises. The keys to carnivore success are **opportunism and conservation of energy**: the opportunist always takes the food that is obtainable with the least effort and risk.
The exceptional ability of jackals and hyaenas to capitalize on scavenging opportunities while remaining versatile and competent hunters explains why they often outnumber other associated predators.

**SOCIAL ORGANIZATION**

The main types of carnivore social organization are shown in table 18.1. The relatively few species that have become gregarious, notably the lion, wolf and wild dog, hyaenas, and some mongooses, have evolved societies that are among the most complex and cooperative to be found among mammals (see species’ accounts). As indicated in the table (reading from top to bottom), carnivore social groups consist primarily of related individuals; a pack is formed when offspring remain with the parents instead of dispersing. Generally daughters remain and sons disperse, making for matrilineal kinship units. But in the dog family, offspring of both sexes postpone emigration and breeding for a year or more and participate in rearing their younger siblings (see jackal accounts). The reverse is true of the African wild dog: sons remain in the natal pack and daughters disperse. When they have the same father and mother, helpers are as closely related to their younger siblings as they would be to their own offspring; such is the case in the Canidae and social mongooses, where monogamy is the rule. Even among species that live in sizeable clans containing several adults of both sexes, reproduction is usually monopolized by a dominant pair (but see lion, banded mongoose, and spotted hyaena accounts).

The great majority of carnivores are apparently unsociable. They range singly and probably in most species the sexes associate only long enough to mate. But to label all these animals "solitary" is misleading if it implies that their social organization is simple or primitive, unvarying, or the same from one species to the next. For whenever a solitary species is studied in depth, social organization is found to be variable and often complex (e.g., see palm civet, slender mongoose, and leopard accounts). Although the adult members of a population may be dispersed singly, it does not mean they are socially isolated. On the contrary, the residents of such a community in most cases know their neighbours individually and stay in communication even while avoiding meeting, through chemical and acoustic signals.

The commonest spacing arrangement is for females to defend territories large enough to meet the food requirements of themselves and their offspring, while males undertake to control a much larger area encompassing the ranges of several females. The biggest and fittest males in the population are the most polygynous. This pattern has been found in most of the unsocial carnivores studied up to now. But unexpected variability in a species social organization has also been found, under different ecological conditions. Where food is unusually abundant and concentrated, a normally "solitary" species may show sociable tendencies. For instance, feral housecats, belonging to a prototypical solitary species, live in kinship groups that have a social organization remarkably like the lion's (see cat family introduction).
### Table 18.1  The Main Types of Carnivore Social Organization

<table>
<thead>
<tr>
<th>Type (examples)</th>
<th>Dispersion pattern and mating system</th>
<th>Territorial behavior</th>
<th>Offspring</th>
<th>Care and feeding of young</th>
<th>Foraging</th>
</tr>
</thead>
<tbody>
<tr>
<td>Solitary (most carnivores: palm civet, slender mongoose, serval, leopard)</td>
<td>Male and female live singly, associate only for mating; male range typically includes up to several female ranges (polygyny)</td>
<td>Defense against outsiders of same sex</td>
<td>Disperse in adolescence; females may settle in mother's range</td>
<td>By mother only</td>
<td>Solitary</td>
</tr>
<tr>
<td>Monogamy (bat-eared fox, ratel)</td>
<td>Male and female live in pair territory</td>
<td>Joint marking, defense against outsiders of same sex</td>
<td>Both sexes usually disperse in adolescence</td>
<td>Male shares parental duties; provisions offspring and/or mate</td>
<td>In pairs or alone</td>
</tr>
<tr>
<td>Family (jackals)</td>
<td>Pair plus yearling offspring and young of year</td>
<td>Yearlings help parents defend against own sex</td>
<td>One/both sexes defer emigration and breeding</td>
<td>Offspring help care for and provision younger siblings</td>
<td>In pairs or alone, rarely in packs</td>
</tr>
<tr>
<td>Clan or pack</td>
<td>Group may include multiple adults of both sexes:</td>
<td>Scent-marking mainly by dominant pair</td>
<td>Some transfer to other packs</td>
<td>Communal care</td>
<td>Individual-foraging in packs; no food-sharing</td>
</tr>
<tr>
<td>(Dwarf mongoose)</td>
<td>A. Dominant pair monopolizes reproduction</td>
<td>Scent-marking mainly by dominant pair</td>
<td>Some transfer to other packs</td>
<td>Communal care</td>
<td>Individual-foraging in packs; no food-sharing</td>
</tr>
<tr>
<td>(Wild dog)</td>
<td>B. Dominant pair monopolizes reproduction; males related</td>
<td>Scent-marking mainly by dominant pair</td>
<td>Extra females emigrate</td>
<td>Communal care</td>
<td>Pack hunters; food-sharing</td>
</tr>
<tr>
<td>(Lion)</td>
<td>C. Several different females and males may breed; females with kinship ties</td>
<td>Individual and group defense against same sex; males form coalitions to win and hold female ranges</td>
<td>Males and some females emigrate</td>
<td>Communal care</td>
<td>Individual and group hunting; food-sharing</td>
</tr>
<tr>
<td>(Spotted hyena)</td>
<td>D. Small to large clans, females dominant over males; large clans include different matriline</td>
<td>Group and individual marking and defense</td>
<td>Males emigrate</td>
<td>No communal care, mothers rear own cubs unassisted</td>
<td>Individual and pack hunting; food-sharing</td>
</tr>
</tbody>
</table>
Other examples of supposedly solitary species that may become sociable at high density include the ichneumon, striped hyaena, and spotted-necked otter. There are also other species that were assumed to be solitary because they forage alone, but which turn out to den communally and be sociable: notably the brown hyaena and yellow mongoose. Conversely, there are normally social carnivores which, at low density, may live in a solitary mode: the lion, spotted hyaena, and wolf, for instance.

Even the accepted standard territorial arrangement of solitary carnivores is not fixed and immutable. Radio-tracking studies of males of known social status in several carnivore families (brown hyaena, Canadian lynx, marten), both during mating and non-mating seasons, show that male territorial networks can break down under certain conditions, namely when dominant males roam widely outside their normal range and compete with other males for mating opportunities. As postulated by the author of a paper on spacing in solitary carnivores, “Males may adopt one of two alternative ways to achieve matings; either they stay and try to monopolize a number of females, or they roam and compete over access to each single females that comes into heat” (Sandell 1996)

Home Range and Group Size.

Carnivore home ranges/territories tend to be larger than those of herbivores of comparable size, for obvious reasons: food plants are much more numerous and concentrated than animal prey. A pair of golden jackals weighing 10 kg apiece defend a range of at least 2 - 4 km², whereas a whole herd of 100 kg topi can subsist in an area of less than 1 km². Yet home ranges may vary enormously in size within the same species: from 10 to over 60 km² in the leopard, from 40 to 1000 km² in the cheetah, from 30 to 2000 km² in the spotted hyaena. Studies of various different carnivores indicate that home range size depends on the distribution pattern of prey and other food resources. Group size in sociable species, however, depends on the abundance of food. If there is only enough for an individual or pair for part of the year, offspring will have to disperse. If there is a surplus, even normally solitary species may become sociable.

Predatory Behavior

Carnivores are born hunter/killers, endowed with the instinct to hunt. Predatory behaviour can be readily stimulated even in a satiated predator. The normal hunting and killing techniques of the species appear spontaneously during development, but some practice is needed to acquire the necessary skill. The ability to discriminate between prey and non-prey species also has to be learned, in response to such factors as relative abundance, size, effort involved in capture, and parental example. Carnivores have only the innate tendency to flee from any aerial object or an approaching ground object above a certain size, to pursue any moving object below a certain size, and to hesitate to attack unfamiliar animals. An inhibition of predatory response, especially of the killing bite (see below), may be necessary to prevent mistakes with one’s own species during mating or while transporting young.
Techniques for locating and capturing prey vary with the type of prey and predator. As the species accounts make clear, few carnivores are limited to just 1 or 2 basic techniques and some, such as foxes, jackals, and leopards, are very versatile indeed. Yet most carnivores are specialized at least to the extent of being terrestrial or arboreal, diurnal or nocturnal (more under Ecology).

The most familiar predatory techniques are cursorial and ambush hunting, as typified by dogs and cats, respectively. These also happen to be the most specialized techniques.

The cursorial hunters have developed the speed and/or endurance to run down the fleetest prey, whereas the ambush hunters combine power and meat-hook claws with cunning, stealth, and quick reactions to capture and subdue animals that are faster and in some cases bigger than themselves. Big cats kill big game by strangling or suffocating it, whereas cursorial hunters, having run their quarry to exhaustion, have to "worry" it to death by biting and tearing at its vitals.

Predators tend to be more successful and can kill larger prey when hunting together than when hunting alone, an advantage of undoubted importance in the evolution of social carnivores. However, this would not apply to social mongooses, in which selection for increased security against a host of potential predators is the likely explanation.

The most primitive method of killing prey, seen in the handling of small animals, is to grab, bite, and toss or throw it. A precise killing bite to the head or neck, such as the felid neck bite and the canid death shake, are later, more refined developments. Similarly, grasping the prey with the paws is more specialized than grasping with the jaws.

SOCIAL BEHAVIOR: COMMUNICATION

Although carnivores have a rich repertoire of signals that utilizes all the senses, the development of scent glands and the prominence of scent-marking throughout the order would indicate that this is the most important channel of communication.

Olfactory Communication

The secretions of various skin glands, urine, and faeces are all employed in olfactory communication. It has already been demonstrated in a number of species (e.g., 2 mongooses, badger, red fox, wolf) that these secretions convey information about the sex, age, status, and identity of each individual (see viverrid introduction, Module # 2 Component # 1).

Scent-marking behaviour differs among species but is most common along the paths an animal regularly follows, on territorial boundaries, and around dens. Probably most species mark with greatest frequency during the mating season. Figure 18.2 shows the location and names of scent glands that are known to occur in
African carnivores. Invisible beneath the fur, many of these glands were discovered only because animals were observed rubbing the part against objects. The cat’s chin gland is an example. Very likely some of these glands will be found to occur in species not presently known to possess them; it is also possible that entirely new scent glands will be discovered.

The most specialized and important scent glands in carnivores are found near the anus and genitalia. Accordingly, sniffing the partner’s anal region features in meetings of most species. Nearly all carnivores possess anal sacs, though these structures are reduced in otters and relatively small in the dog and cat families.

The paired sacs lie beneath the skin and connect to the outside via a short canal on either side or just inside the anus (see fig. 19.1). Packed secretory cells, often of more than 1 type, drain into the sac or into the canals. In species that have developed an obnoxious, liquid secretion for self-defence, the whole structure is surrounded by a muscular coat which can squeeze the sac like a syringe bulb to squirt fluid up to several meters. But in most carnivores anal-sac secretions serve a scent-marking function.

In mongooses, hyaenas, and the ratel, the sacs and the anus are surrounded by a pouch (fig. 19.1b) which can be everted to bring the pouch lining, covered with secretion, into contact with the substrate or to waft the odour into the air (see figs. 19.4, 19.6, 20.2). In these and some other carnivores, the faeces and also the urine and vaginal secretions may be mixed with anal-gland secretions. In addition to the anal sacs, diffuse skin glands of uncertain function open directly onto the skin surrounding or just inside the anus. Civets and genets possess a unique perineal gland, the product of which is used as a perfume base (see viverrid introduction).

Vocal Communication

Having less to fear from predators than most other mammals, many carnivores can afford to be noisy. Howling, wailing, barking, yapping, roaring, screaming, and whistling make effective long-distance contact calls. The more sociable the species, the larger and more varied the vocal repertoire, and the more "conversational." Social mongooses, for instance, maintain contact and coordinate the movements of pack members through an almost continuous churring and murmuring. In contrast, adults of solitary species may require only 1 sound, with the opposite meaning of socially negative threat calls, to signify readiness for social contact when the time comes to mate.

Visual Communication Facial expressions

Carnivore facial expressions are basically alike. The similarity extends even to primates: a comparison of the repertoires of several canids with those of monkeys and apes indicates that all but 2 of the expressions and the situations evoking them are similar. In both orders, the importance of the canines as weapons makes the face the main focus of attention during social interactions; positions of the jaws, ears, and eyes which are associated with aggression, self-defence, and fear are virtually
the same across families and species. As these expressions and movements are automatically assumed by animals experiencing aggressive and fearful emotions, they also function as visual displays (see carnivore and primate family introductions).

However, the development of facial musculature and the degree of facial expression is far greater in cats and canids than in, say, mongooses, civets, and weasels, which have so little ability to alter their facial expressions that the difference between baring the teeth in anger and baring them in play may be imperceptible. Even in Canidae, the ability to show the canines by raising the upper lip is developed in only the most sociable species.

**Postures**

An alert and confident carnivore moves with an erect bearing and holds its ears cocked as it actively investigates its surroundings. An individual that is ill at ease or fearful has a tendency to crouch with ears back, to glance about nervously as though it wanted to make itself smaller or hide.

From these and other signs that show which individual is more confident, an observer can predict the probable winner of an aggressive interaction. Confidence spells the difference between offensive and defensive threat. Both types tend to be impressive in carnivores, because of their lethal capability. Threat displays follow 3 basic principles:

1. display your weapons
2. look as big as possible, and
3. attempt to startle and disconcert your opponent.

These objectives are accomplished by opening the jaws; by erecting the hair and standing broadside (lateral presentation), extending the legs for maximum height, humping the back (threat arch), and raising the tail; and by abrupt movements, including feigned attack, combined with short, explosive sounds such as spitting, barking, growling, and roaring.

One in 4 African carnivores has a dorsal crest or cape of longer hair that it erects to increase its apparent size (see figs. 19.8, 20.5). First prize goes to the aardwolf, whose cape enlarges its silhouette by up to 74%. Enlarging the silhouette is most developed among ground-dwelling carnivores of medium size which are either slow runners or poor climbers, or else live in places where trees are scarce and come into contact with a variety of somewhat bigger carnivores. In short, erectile capes and crests probably evolved for use against other species, specifically against competitors and potential predators, as an alternative to flight.

**Markings**

Markings serve to accentuate parts of the animal that are important for communication. A black gum line emphasizes open-mouthed threat in many
carnivores, through contrast with the white teeth and light adjacent hair. The black markings on the backs of a lion's ears and the white-tipped tail of the cheetah, wild dog, and side-striped jackal may function both as follow-me signals and as accentuations of ear and tail positions and movements.

The large ears of hyaenas and wild dogs, and the caracal's ear tufts, also increase ear visibility. The black mask of the bat-eared fox may function as a target for social grooming, and the white cheek ruff in some other canids and the black neck markings in civets may serve to direct bites to relatively well-protected areas during ritualised fights. In many species a white belly emphasizes the submissive attitude of lying on the back. Bold black and-white markings, visible even in the dark, are warning signals to potential predators that the bearer is obnoxious. Although skunks have the most effective chemical defence, a number of African mustelids and several viverrids can also emit nauseating chemicals, and they too display warning coloration.

REPRODUCTION

Since most carnivores are solitary, wide-ranging, and widely spaced, finding mates can take time. Even after a meeting, courtship between 2 dangerously armed individuals that normally avoid each other or interact aggressively takes time. The fact that females typically stay in heat for several days or longer provides the necessary leeway. Extended oestrus may, in turn, help to account for several other aspects of carnivore reproduction:

a) the possibility that most carnivores are induced ovulators,

b) the presence of a sizeable penile bone (a baculum occurs in all families but the hyaenas), and

c) protracted (up to 3 hours in some mustelids) or oft-repeated copulation. Having ovulation depend on the stimulus of copulation insures that eggs and sperm will meet while both are viable. Aspects b and c may help to provide sufficient stimulation to induce ovulation

PARENT/OFFSPRING BEHAVIOR

Carnivores produce multiple young (2 - 16) after a relatively short gestation period (3 - 16 weeks). With few exceptions (e.g., spotted hyaena), the young are born blind and deaf, and locomotion is limited to crawling on the front limbs. But unlike many rodents, newborn carnivores are not naked. The young require extended care, and many have to learn hunting techniques before they can become independent. The participation of the father, and in social species of siblings, has evolved in various families to meet the demands of rearing young predators.

ANTIPREDATOR BEHAVIOR
The saying, "eat or be eaten", hardly applicable to ungulates or other herbivores, could serve as the carnivore motto. Smaller carnivores are "fair game" for larger carnivores, and the young of even the largest species are vulnerable to adults of the smaller species. Consequently carnivores have evolved a rich repertoire of anti-predator stratagems, some of which are discussed under Communication (see also family and species accounts).

**SOURCES**