

Module # 4 – Component # 12



Impala

Aepyceros melampus

TRAITS

The perfect antelope, comparable in size and conformation to a kob or Grant's gazelle.

Height and weight: males 75 - 92 cm, 60 kg (53 - 76), females 70 – 85 cm, 45 kg (40 - 53).

Horns: males only: 45 - 91.7 cm, far larger in East than in southern Africa, S-curved, strongly ridged but comparatively thin, tips wide apart.

Colouration: two-tone brown, a red-brown saddle sharply divided from tan lower torso and limbs; white belly, throat, lips, line over eye, inside ears, and under-tail; black markings include vertical stripe down tail and both thighs, fetlocks, ear-tips, ± forehead patch and line from eye corners (most developed in the black-faced impala of southern Angola, *A. m. petersi*).

Scent glands: fetlock glands on rear feet beneath black hair tufts; sebaceous glands concentrated in forehead (and dispersed on torso) of dominant males.

Mammae: 4.

DISTRIBUTION

A Southern Savanna antelope, which achieves very high density in areas affording both grazing and a varied diet of browse within convenient distance of water.

ANCESTRY

Although efforts have been made to tidy up bovid classification by putting the impala in the same tribe as gazelles, kobs, and most recently hartebeests, the impala is so different from all other antelopes that it clearly belongs in a separate tribe. There is no evidence that more than 1 species existed at any time in the past.

ECOLOGY

The impala is an edge (ecotone) species, preferring light woodland with little undergrowth and grassland of low to medium height. Added to dependence on free water, soils with good drainage, firm footing, and no more than moderate slope, its special requirements produce an irregular and clumped distribution. Though rarely found more than a few kilometers from water in the dry season, impalas with access to green vegetation can go without drinking.

DIET

Intermediate feeder (grazer / browser)

The impala is predominantly a grazer while grasses are green and growing and a browser of foliage, forbs, shoots, and seedpods at other times. If necessary, it also eats fallen dry leaves. It not only changes its diet in a given area according to season, but can adapt to different habitats by being mainly a grazer in one area and a browser in another. The impala's ability to utilize both monocots and dicots gives it an unusually varied, abundant, and reliable food supply, enabling this antelope to lead a sedentary existence and reach densities of up to 214 / km² in wooded savanna of Rwanda's Akagera N.P. It can also thrive in areas where the natural vegetation has degenerated because of overgrazing or bush encroachment. Thus, in mopaneveld of Zimbabwe, where perennial grasses have been largely eliminated by burning and overstocking, impalas increase while pure grazers (tsessebe, hartebeest, wildebeest, zebra) disappear.

As in other sedentary antelopes, impala home ranges include a variety of vegetation types which are utilized at different seasons. In the *Acacia-Commiphora* woodland zone of Serengeti N.P., impalas move up and down the soil catena, staying during the main rainy seasons on the upper slopes, where visibility and forage quality are optimal, and concentrating in the drainage-line greenbelts during the dry season.

SOCIAL ORGANIZATION

Seasonally or perennially territorial, gregarious, sedentary.

The existence of a territorial organization in impalas has been doubted by some observers, affirmed by others, and finally proven by long-term observations of known individuals. There are several reasons for the uncertainty:

- 1) In Southern Africa most males are only territorial for a few weeks around the time of the annual rut, and in East Africa, despite an extended breeding season, males lose territorial vigour in the dry season, when benefits in terms of mating opportunities are outweighed by the costs of herding females and excluding rival males. Consequently, bachelor males are typically found in proximity to or actually mixed with herds of females during the dry season.
- 2) Even vigorously territorial males may tolerate and indeed associate with bachelors when no females are present, as long as the landowner's dominance is unquestioned.
- 3) Although the roaring of territorial males makes the impala one of the noisiest of all bovids, and its other territorial advertising displays are conspicuous, the same displays are performed by high-ranking bachelor males (though generally at much lower frequency) and have often been interpreted as simply expressions of "activated dominance".
- 4) Mature males alternate between bachelor and territorial status and rarely hold a territory for more than a few months at a time; the turnover of males may also have contributed to the uncertainty about whether impalas are in fact territorial.

Paradoxically, the very features of impala social organization that raise doubts as to whether it is territorial are actually the result of unusually rigorous territorial and reproductive competition. Because of its clumped distribution and locally high population density, males that win positions in the most preferred habitat during the main mating season can achieve very high reproductive success (see under Territorial Males).

Female Clans

Groupings of females and young vary greatly in size, and composition rarely remains constant from day to day. Herds of half a dozen to 15 or 20 represent a minimal average and herds of 50 – 100 are quite common. In Nairobi N.P. groups of 16 - 25 females and young were counted in a heavily wooded area compared to over 35 in a more open area. The average size of female herds in Akagera N.P. was 36, with groups of over 100 in the custody of a single male not unusual on the large plains.

Only after 443 impalas were caught and marked in a 12 km² study area in the Sengwa Research Area of Zimbabwe was it finally established that females live in discrete clans within traditional home ranges. For the 3-year duration of the study, clans containing 30 - 120 impalas remained stable in composition and resident in home ranges of 80 – 180 ha. When the ranges of individual females were mapped, the centres were found to cluster within a radius of c.200 m in the case of clan members, whereas the distance between centres of impalas from different clans was 800 m. Yet clan ranges overlapped by as much as 31 % late in the dry season, and members of different clans sometimes mixed, though only temporarily. No more than 2% of the females per annum left their natal range and joined another clan. Most males, however, left their clan range by the age of 4 and moved an average of 1.2 km(0.4-3.2), just far enough to place them within the range of a different clan and avoid inbreeding.

Impala female herds are notable for their uniformity and lack of distinct peer or family subgroups. The maternal bond quickly dissolves after weaning. Juveniles often play together and may form temporary peer groups, and the Sengwa study also disclosed a tendency for young-adult females to associate. The only other division occurs during the calving season, when females with or without offspring tend to be segregated.

Apart from occasional episodes of *head-butting* and *reciprocal grooming* with partners apparently chosen at random, females do not come into physical contact, and there is no sign of a rank order or regular leadership. Yet female herds are very cohesive, with an average spacing of 1 m or less between individuals (author's estimate), and herd activities are closely synchronized.

Territorial Males

The degree of territorial Behaviour and enforced sexual segregation of impala herds is closely linked to the breeding season and climatic regime. In southern Africa, vigorous territorial behaviour is limited to a few months. The rest of the year males and females are free to associate in mixed herds, although a male preference for relatively dense habitats that females avoid (cf. eland and giraffe) results in a measure of separation. The extended breeding season in East Africa leads to the maintenance of territories and sexual segregation for most of the year. But most mating occurs during the rainy season, with a peak at the end of the rains. As the dry season progresses, territorial occupancy declines, and new or continuing occupants are less vigorous about expelling juvenile males, and about keeping females in and bachelor males out of their domains (see below).

Territory size varies with population density, location and habitat quality, individual prowess, and the seasons (table 8.2).

Table 8.2 Relation Between Population Density, Season, and Territory Size in the Impala

Location	Population density/km ²	Territory size (ha)		Season	Source
		Mean	Range		
Sengwa Research Area	50–68 49	10.8	8.5–13	Peak rut Dry season	19
Serengeti N.P.					7
Minimum average	32	17	13–>50	Peak occupancy	
Maximum average	32	58		Dry season	
	19	42	16–83	Peak occupancy	
Nairobi N.P.	15–18	51.5	20–90	Not compared	15
Mkuzi Game Reserve	80	66	50–80	Peak rut	24

Except for the surprisingly large size of impala territories in Mkuzi Reserve during the rut at high population density, the figures clearly show the tendency for territories to be small at high population density during the peak rutting season, and large under the opposite conditions. In the case of large properties, the distinction between territory and home range is often indistinct, especially during reproductive off-seasons.

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Those which are occupied for an extended period include both wet and dry-season forage; they expand during the dry season, and only the part in use is actively defended. In Sengwa, for instance, prime males tend to remain localized and often alone outside of the rut within ranges averaging 49 ha, where they assert dominance over other males. In other central and southern African populations, some 20% of the adult males are also found alone or as the only adult male with a herd of females

right through the dry season. At least some of them maintain dung middens (see under Territorial Behaviour). Even though territorial behaviour may be comparatively attenuated in such males, the very fact that they remain apart from other adult males within a fixed range where they display dominance clearly sets them apart from males in bachelor herds, and it is reasonable to consider them territorial.

Attachment to a particular place is characteristic of male impalas during their prime. After roaming widely in search of a favourable place to live and reproduce, Sengwa males pick their spot and settle there for good. Serengeti males become imprinted on the area where they first establish a territory and come back every time they are ready to try again (known also in the kob and wildebeest).

Among all the males that were observed starting a period of territoriality, an estimated 80 % had held territories before, most within the immediate vicinity.

Although only one third of the adult Serengeti males were territorial at any one time, nearly all those in the study area had territorial bouts during the 2-year study. In Sengwa, by contrast, there was evidence that some adult males reached old age without breeding. Only 12 of 69 males that were present in the range of 67 adult females during one rut were seen to do any mating. The same 4 prime (5 and a half - 7 and a half years old) males accounted for 52 (78%) and 47 (66%) of observed matings during 2 successive ruts, and 1 mated with over 30 females. But few if any males achieve the status of top breeders for more than 2 out of a possible 3 ruts during their prime years.

Actively territorial males invest up to 25% of their time in rounding up and attending the females that enter their grounds, time that would otherwise go into feeding and ruminating. The more females that come and the longer they stay, the more energetically costly it becomes for the male. When a herd enters his territory, a vigorous male herds them toward the center, chases any bachelor males that may be around, and even cuts out weaned juvenile males (whose horns give them away) (fig. 8.22), while moving through the herd in search of oestrous females.

To forestall their departure, he tries to keep the females tightly bunched and to turn back any that attempt to break free. Depending on how worked up he is, a male's herding behaviour varies from approaching at a walk to violent chasing while snorting and roaring. He redoubles his efforts when the herd comes near the border, blocking the way while performing dominance and threat displays. But if the females are determined to leave, all a male's efforts are in vain. Once the first few have crossed over, the rest inevitably follow.

The demands of being actively territorial are such that East African males are often in visibly poorer condition than their counterparts in bachelor herds, even when food is most abundant.

Maximum territorial tenure for 94% of the males in the Serengeti study was under 4 months, and the average tenure was 82.5 days. Far more intense competition during the peak rut in southern impalas is indicated by an average territorial tenure of only 8 days (\pm 4.4 days) in the Sengwa population.

Bachelor Males

Since females outnumber males by 1.5 or 2:1 in the adult population, and up to half the adult males may be on territories during the breeding season, bachelor herds are typically smaller than female herds. In Nairobi N.P., male herds rarely numbered over 10 in closed or 15 in open habitats; the mean number in Natal's Hluhluwe Game Reserve was 3.6 (2-25); and in Akagera, three quarters of bachelor herds numbered 10 or less, while the rest included 11 – 30 males.

In the Serengeti study area, male herds numbering from 5 to 35 impalas shared a range of about 6 km² in the wet and early dry seasons. Membership fluctuated as often as in female herds, and some bachelors left for several months in the dry season, travelling up to 10 km to reach a greenflush and returning with the onset of the rains. Males may be associated more often with female herds than in separate bachelor herds in southern populations, although a tendency for immature and old males to form peer subgroups is apparent, even in mixed herds. But males are not confined like females to a clan range. Sengwa males begin moving independently of females as yearlings, and gradually increase their ranges to a mean maximum of 90 ha at 3 – 4 years, as they disperse from their birthplaces and prospect for suitable places to settle during their reproductive years.

Bachelor males maintain individual distances of 2.5 –3 m, one indication of the greater antagonism that appears from an early age in male impalas. Nevertheless, *reciprocal grooming*, a social-bonding behaviour, appears to be about as frequent in bachelor as in female herds and involves individuals of the same and different classes, including adults.

Observations of aggressive interactions between known Serengeti bachelors revealed the existence of a largely linear rank hierarchy.

Males that had worked their way to the top of the hierarchy were fit to contend for positions in the territorial network, whereas those that rejoined the herd after being territorial for some months were worn out and low-ranking until their physical condition improved. Still, all currently territorial males that tolerated and interacted with bachelor males on their property always maintained dominance, even those in poor condition.

ACTIVITY

Impalas are primarily diurnal (active during the day), spending most of the night lying down, mainly ruminating, preferably in open terrain. By day they graze and usually stand while resting and ruminating, preferably in the shade. Feeding, standing, and lying accounted for 18.6 - 19.2 hours of a 24hour day in female Serengeti herds. The basic activity pattern was found to be quite regular and to be closely synchronized among herd members, though less so in large than in small herds.

The impalas rose from their lying places at dawn, and after relieving and grooming themselves, fed intensively until 10h00 or 11h00, ruminated until noon or later, then

began feeding again. Another well-defined rumination period often followed between 15h00 and 17h00, followed by another intensive feeding bout until dusk. Nearly all the impalas then lay down and ruminated. One feeding bout occurred at night, generally from 23h00 to 03h00 or 04h00, but like the mid-afternoon feeding period was often poorly synchronized.

Disturbance by a predator was often the trigger for the night feeding bout, which gave way to another lying and ruminating bout that continued until dawn. Sleeping individuals (lying with eyes closed for up to 10 minutes) were mostly seen at night.

Peaks of herd movement and of most social activity (social grooming, play, dominance interactions between bachelors) occur shortly after dawn and before dusk. From a third to a half less movement occurs at night. All kinds of social intercourse are minimal at night, except that mating activity continues at full swing by moonlight during the rut. Normal activity can be disrupted not only by predators but also by weather. Impalas all stop feeding when it rains, stand with their backs to the wind, bunch closely (females more than males), and begin ruminating. High winds often stimulate intense activity, including outbreaks of high-bounding, chasing, and roaring.

Activity cycles vary seasonally with the condition of the food supply. Impalas eat more, ruminate less, and move farther (up to 3 km daily vs. a minimum of 0.95 km in the wet season) within a larger home range in the dry season. The ratio of daylight feeding to ruminating time for female herds changed from 1.8 : 1 in April (peak rains) to 3.7 : 1 in July. Serengeti impalas go to water every second or third day, usually between 10h00 and 14h00, in the dry season only.

POSTURES AND LOCOMOTION

The impala is known for its spectacular leaps, up to 3 m high and 11m long, which are triggered by sudden disturbances especially when in dense vegetation. The sudden explosion of antelopes leaping in all directions is apparently an anti-predator tactic that increases the difficulty of selecting a quarry. The animals not only leap upward but to one side and then the other, and often pass or cut in front of one another. Impalas also engage in another form of leaping, equally spectacular, the motivation and function of which are unclear, which looks playful and is often infectious (fig. 8.23).

As an animal descends from a high jump, it kicks its hindlegs nearly to the vertical and lands on its forelegs, rebounds, and brings its hindquarters down before landing again. This gait is unique to the impala.

SOCIAL BEHAVIOUR: COMMUNICATION

The roaring of adult male impalas and their repertoire of visual displays are so colourful that the importance of olfactory communication in this species via their unique scent glands has received little notice. It has been established that a male's dominance status is signalled by strong-smelling secretions of the forehead skin (see Dominance/Threat Displays and Territorial Behaviour). But the function of the metatarsal glands remains indeterminate.

Their structure and equal development in the sexes suggest that the secretions of these glands diffuse through the air and serve some general social function, which could well be to maintain and restore contact between herd members, especially when vision is obscured.

TERRITORIAL BEHAVIOUR

Presumably because of the higher testosterone levels associated with territorial and reproductive activity, territorial males not only are more aggressive but also have thicker necks than bachelor males, and their skin is made greasy by copious amounts of smelly sebaceous secretions. Probably as a result of rubbing their forehead secretion on branches, dark bare skin around the eyes makes their eyes appear bigger than normal.

Advertising:

Erect posture (=proud posture), tail-raising, linked urination -defecation on dung middens, forehead-marking, roaring display, herding and/or chasing of females and trespassing males; prancing or goose-stepping and bipedal walking (during herding, both uncommon)

Territorial males commonly though not always urinate and defecate in sequence, in postures much like those of gazelles, and rarely excrete casually and at random as do other impalas.

The tail is typically raised to show the white side, a Behaviour also associated with dominance displays. Territorial males regularly use dung middens, located on bare ground such as paths or roads, and often in the 15 - 30 m neutral zone between adjacent territories. Other impalas and also other species often use the same latrines. Standing in the proud posture (fig. 8.21), with head high but hindquarters lowered, is a static-optic advertisement of territorial status that looks similar to and may derive from the urination posture (symbolic marking).

Forehead secretion is deposited both by rubbing the head up and down against objects and while *vegetation-horning*; both are performed by territorial males during all major social activities. However, horning is more closely associated with territorial defence against potential challengers, and *forehead-rubbing* is seen more often in interactions with females and inferior males. In addition to scent-marking while

moving and feeding, territorial males go on regular marking patrols, often in border zones, during which they walk steadily and directionally, in an upright, stately manner, stopping intermittently to urinate-defecate, *forehead-rub*, and so on.

Roaring is the most impressive and far-reaching (2 km) of the impala's displays. It is preceded by 1-3 explosive snorts with mouth closed, and followed by 2 – 10 deep, guttural grunts emitted with mouth open, chin lifted, and tail gradually raised to 45 degrees and spread (fig. 8.24).

Although adult bachelor males participate in a spectacular outbreak of calling and chasing during the mating season, territorial males were responsible for 86% of the roaring episodes observed during the Serengeti study. Uttered only when a male is highly excited, roaring is apparently addressed specifically to other males, which pay attention and frequently react to one another's roars, whereas females appear indifferent. During the height of the rut at Sengwa, 180 *roaring displays* were observed in 1 hour on a moonlit night.

AGONISTIC BEHAVIOUR

Dominance/Threat Displays: *erect or proud posture ± head-turned-away; tail-raising and spreading; yawning; tongue-flicking; high-, medial-, and low-horn presentation, head-tossing; head-dipping (exaggerated nodding), vegetation-horning; ground-horning (rare).*

Females: head-dipping; butting.

Defensive/Submissive Displays: *head-low posture, moving away in this attitude or while grazing, approaching and sniffing superior's forehead or under tail (uncommon).*

Fighting: *air-cushion fighting, front-pressing and twist-fighting.*

Impalas assert dominance by walking stiffly in the *erect posture* while displaying their neck and horn development to maximum effect (cf. Grant's gazelle dominance displays).

The ears are held back, the tail is clamped, and the performer usually faces his opponent but often with *head-turned-away*. Males appear very sensitive to even slight movements and changes of posture; for example, a barely noticeable head nod is enough to make a rank-inferior move aside. *High-horn presentation* invites an opponent to sniff the forehead skin during a rank-testing encounter. A subordinate responds by timidly approaching and *sniffing the forehead*; he then confirms the other's dominance by backing or walking away in the *head-low posture*.

An equal responds in kind to *high-horn presentation* and other assertions of dominance, such as raising and showing the underside of the tail, *yawning* (which intimidates inferiors), and *tongue-flicking*. The last, which is also an important

courtship display, often accompanies threat displays. Displacement grooming (scratching with a hindfoot, scraping a shoulder with incisors) is common during confrontations; sometimes a contestant erects and mouths his penis. Often dominance displays between territorial males end with one or both moving apart while grazing.

Only 2% of observed aggressive encounters between Serengeti bachelor males ended in combat and 7% of encounters between territorial males. Yet fights are a normal risk for territorial males, as indicated by horn scars on the neck of 14 of 19 territorial males examined, versus 6 of 20 adult bachelors. Males have a dermal shield of thickened skin which protects the neck and head against deep stab wounds. Sometimes while pushing and pulling with interlocked horns a male trips over his opponent's horns and breaks or dislocates a foreleg. But apart from one broken horn, none of the 70 marked Sengwa males suffered a serious injury during a year or more of observation.

REPRODUCTION

Females conceive first at 1 and a half years, whereas males, though fertile as yearlings, only begin reproducing as they mature and gain territories in their fourth year. Gestation is 194 – 200 days. Observations at Sengwa indicate that the 3-week peak rut among southern impalas is influenced by the lunar cycle (cf. wildebeest). The onset of the rut in May varied by up to 20 days in 5 years, with most mating between full moons. Males begin gearing up for the rut as early as March, when shorter days stimulate gonadal growth and hormone production, leading to increased aggressiveness and territorial behaviour.

SEXUAL BEHAVIOUR

Lowstretch; urine-testing; chasing; tongue-flicking; licking.

Female impalas do not urinate on demand when approached by a male, but males respond to the urinating female's crouched posture with white tail held out by approaching and *urine-testing*.

A male checks out females most energetically right after a herd comes onto his property, walking rapidly among the females in *lowstretch*, with nose and tail raised, nostrils flared, and mouth slightly open, occasionally *tongue-flicking*, turning his head to sniff at females' rumps.

Having located a female in oestrus, an excited male immediately begins an energetic courtship, of which the following is a generalized summary of what is in reality highly variable pre-copulatory behaviour. He runs at her *in lowstretch, snorting, wheezing, or roaring*, and the female runs away and circles back into the herd, pursued by the male. When he relocates her he continues his suit.

Presently the chase slows to a fast walk, the female keeping 3 – 5 m ahead of the male, which follows *flicking his tongue*, often emphasized by vigorous *nodding*.

Later she allows him to close the distance and he proceeds to lick all around her vulva as she walks slowly ahead, tail now held slightly from the body (but rarely raised in response to licking).

The *mating-march stage* leads into the *mounting stage*. The male runs or walks toward the female while rising to stand bipedally with body erect and head high. She usually walks forward and if he fails to penetrate he falls forward, clasping her with his forelegs and sometimes leaning his chest on her as he comes down. If his aim is true, the female usually holds still briefly. Mounting attempts are repeated at intervals of a few seconds to a minute or 2, averaging 4 and a half (1-14) attempts per successful copulation (fig. 8.25). In 9 of 14 observed copulations, the male roared and often ran around *chasing* bachelors and *herding* females for several minutes. But males rarely showed any further interest in females after the 1 copulation, even though females remained sexually attractive and were courted by other males (1 oestrous female was seen with 4 different males).

PARENT/OFFSPRING BEHAVIOUR

The female isolates in cover several hours before calving (usually in midday), though often only after strenuous attempts by a territorial male to prevent her leaving his herd. How long fawns remain concealed is unclear, but reportedly in as little as 1-2 days they follow their mothers back to the herd and there join a crèche of other small calves. Crèches containing a dozen or more fawns are characteristic of impalas, especially where there is a sharp annual calving season, and may be guarded by only a few females or even unguarded. Juveniles rest, move, play, and groom together, joining their mothers only to nurse, for herd movements, or when a predator is near.

Pushing contests between male calves begin before their horns emerge during the second month, although dominance interactions with accompanying displays appear only at 18 months and the full aggressive repertoire by 30 months. Impalas are weaned and able to survive without their mothers by 4 and a half months, which is just as well, because in East Africa juvenile males at that stage become subject to the aggression of the more active territorial males.

Chasing and harassment usually continue for some months before young males accept separation from female herds and join a bachelor herd, usually by 8 months or when their horns exceed ear length. In South Africa, thanks to the short calving season, young males gain a reprieve from the aggression of territorial males for a whole year, since territorial organization disintegrates before their horns develop.

ANTIPREDATOR BEHAVIOUR

Alert posture, alarm snorting, flight-intention movement, flight ± high-jumping.

Where numerous, impalas are staple prey of all the larger predators, and martial eagles are big enough to carry off fawns. Their habitat preferences make impalas more vulnerable to ambush than open-country antelopes. No wonder, then, that these animals are unusually alert and quick to take flight.

When walking through the undergrowth a suspicious impala will suddenly stop moving its head, while its eyes scan the landscape for movements and its ears rotate to pick up sounds. While staring at a suspicious object it cannot identify, an impala will move its head up and down and sideways, apparently to see it more "in the round." Or it begins to graze, then suddenly raises its head again and stares, a tactic well-adapted to detect a stalking lion or leopard. On the way to drink, the female that leads the file is extremely cautious, continually stops to look around with head high, and may stand motionless for minutes while her followers remain quite relaxed.

The *alarm snort* is powerful and the intention to flee is signalled by a sudden upward movement of the head with neck stretched forward, which may release flight in other impalas. The spectacular flight and dispersal of leaping impalas is described under Postures and Locomotion.

SOURCES

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