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Vera Rduch

The Puku Antelope

MILITZKE

Contents

3. From nose to tail – Morphology and anatomy

The puku (*Kobus vardonii*) is a medium-sized antelope with a slight sexual dimorphism, that means males and females look slightly different (Fig. 3.1.). The males are somewhat larger and heavier and only they carry horns.

Table 3.1: Overview on external body measurements of puku (*Kobus vardonii*) (based on information from Skinner & Chimimba 2005, Huffmann 2011)

Feature	Males	Females
head and body length	139.8 cm (129.5–146.0 cm)	131.1 cm (126.0–142.0 cm)
shoulder height	80.9 cm (80.0–81.5 cm)	77.8 cm (73.5–83.0 cm)
tail length	26.5–32.0 cm	
ear length	13.4–15.9 cm	
length of hind foot cum ungis	37.5–44.0 cm	
length of horns	40–54 cm	––
body weight	77 kg (67–91 kg)	66 kg (48–78 kg)

Measurements: The head and body length, measured from the tip of the nose to the base of the tail along the backbone (see for example Skinner & Chimimba 2005), averages 139.8 cm in males (with a range of 129.5–146.0 cm). In females it is slightly less with an average of 131.1 cm (126.0–142.0 cm). The shoulder height reaches 80.9 cm on average (80.0–81.5 cm) in males and 77.8 cm (73.5–83.3 cm) in females (Skinner & Chimimba 2005). Additional body measurements encompass the tail length, 26.5–32.0 cm, or the ear length that is given as 13.4–15.9 cm. The length of the hind foot cum ungis is 37.5–44.0 cm (Skinner & Chimimba 2005).

Body weight: Generally, the males are not only larger than the females, they are also heavier. They reach a mean body weight of 77 kg (67–91 kg), while females weight 66 kg (48–78 kg). At birth a puku weights about 5 kg (Jenkins 2013) – that is based on a known weight of 5.8 kg of a three-day-old young (Rosser 1987).

Fig. 3.1: Puku (*Kobus vardonii*): a male (a) and a female with a young (b) in Kasanka National Park, Zambia.

The horns of the males reach a length of 40–54 cm (Huffmann 2011). The longest horns are reported from the Luangwa Valley, where they reach up to 56.2 cm (Jenkins 2013). If not specified, the horn length is measured using a measuring tape from its lowest point on the forehead along the curves to the tip (Castelló 2016). The form of the horns is described as lyre-shaped (Skinner & Chimimba 2005), they are stout and strong. From the forehead they first run vertical before they curve backwards (Huffmann 2011). Their surface has so called ridges or rings on the lower three quarters (Huffmann 2011) of two thirds (Skinner & Chimimba 2005) of its length. The top quarter at the tip is smooth (Jenkins 2013, Fig. 3.1 a, 3.2 a). There are occasional reports of horned females (Ansell 1960c).

Fig. 3.2: A closer look at the pukus (*Kobus vardonii*): head (a) legs and hooves (b) and non-bushy tail (c) (Photos: a in Kafue National Park, b and c in Namwala GMA near Kafue National Park).

Pelage: The colour of the coat on the upperparts is golden-yellow (Huffmann 2011) or golden-buffy-yellow (Groves & Grubb 2011). This colours extents downwards along the outside of the limbs (Skinner & Chimimba 2005). The underparts and the inside of the limbs are white in colour. In general, the fedlooks are without markings, some individuals have a pale white band above the hooves (Fig 3.2 b). At the outside, that means on the backside, the ears are generally golden-brown while the black tops can cover the ear to up to one third (see also chapter 4.3). The inside of the ear is white. The upper lip as well as the area between the rhinarium and the mouth as well as the throat are white, too. Sometimes the forehead

is browner than the rest of the body (Skinner & Chimimba 2005). The tail that has the same colour than the body is not bushy except a small tuft at the tip (Skinner & Chimimba 2005, Jenkins 2013; Fig. 3.2 c). The pelage of the puku is generally described as shaggy (Jenkins 2013) as well as long and coarse (Huffmann 2011). However, this changes throughout the year. During the cool dry season, when temperatures can be around 0 °C in the morning and mist rises, the pukus are indeed rather shaggy. During the rainy season the pelage of the puku is rather smooth (own observations). Individual hair is about 32 mm in length, the cross section is rectangular. The pattern of the cuticula, the outer scale cover of the hair, is irregular wave-shaped along the entire length of the hair (Skinner & Chimimba 2005, Fig. 3.3, see also Box 10).

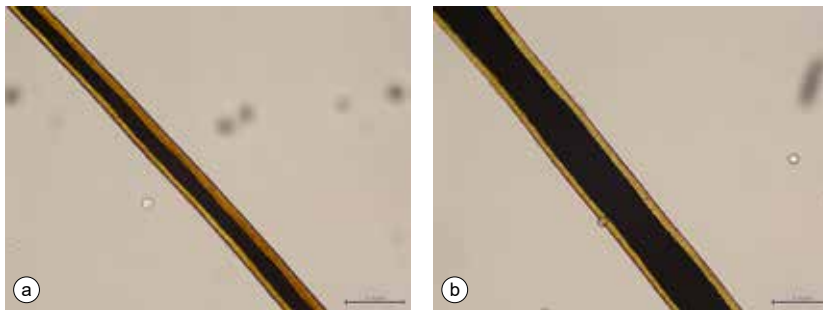

Fig. 3.3: Microscopic view of the puku (*Kobus vardonii*) hair: medulla and cuticula at the distal end (a) and at the base (b) of the hair. The scale gives 100 μm.

Specific features: Territorial males develop a powerful neck where there is a so called neckpatch extending on the neck and parts of the shoulder (Fig. 3.4). It underlines optically and perhaps olfactorically the muscles of the neck – and thus the ability to fight (Rosser 1990). Here the hair is provided with an oily secretion that gives them a darker colour. That secretion comes from the preorbital glands that is transmitted by running the head along the neck. The neckpatch is not developed to the same extent in every area, in all individuals or during any given part of the season. Sometimes it is only visible at a second glance. Inversely, dust can further increase the dark appearance of the neck-patch (own observation).

The preorbital glad itself is a small area of thicker, glandular skin. From the outside it is a small dark tuft of hair. From the inside and at a closer look, it is almost round (around 10-15 mm in diameter) and the hair follicles are visible. The secretion is slightly sticky with a sweet, not unpleasant smell (Ansell 1960b).

Fig. 3.4: Male puku (*Kobus vardonii*) with a well-developed neckpatch at a waterhole in the Mumbwa GMA during the cold dry season (a) and a male with strong neck musculature in Kasanka National Park at the beginning of the rainy season (b). Here you can also see the smooth coat at this time of the year.

Inguinal glands are present in several antelope species. It is assumed that they have a function in relation to mating or that they produce a smell allowing female and young to recognize each other. Additionally, there is the hypothesis that these glands produce a so called "alarm smell" in some species. It is reported from reedbucks that, if alarmed, they make a sudden noise that emerges when the glands are contracted and by this emit the secretion (Spinage 1986). Pukus have well developed inguinal pouches, one on each side, in which the inguinal glands are located. The inguinal pouches are 40–80 mm deep, their openings are larger in females reaching 20–25 mm compared to the males' reaching only 9–11 mm. These openings are nestled between the two teats of the udder in females and at the level or behind the rudimentary developed teats in males. In both sexes, the pouches run backwards and almost converge (Ansell 1960b). The secretion of the inguinal glands is waxy, light-yellow and has a strong, unpleasant smell (Ansell 1960b). The name of the genus *Adenota* (those that have glands), to which grouping the pukus were placed in for a while, seems to refer to this feature.

Between the hind-legs of female pukus is an udder with two pairs of mammae (Ansell 1960c).

Limbs: Above the hooves of the puku there is a vestigial duct of a foot gland. It is a tiny opening in the gap between the toes (Ansell 1960a). The cloven hoof is the characteristic feature of artiodactyls, the even-toed ungulates, and so also of the pukus. It enables antelopes to move under different environmental conditions from loose sand to swampy ground. In antelopes the bones of the hand and feet are extremely elongated, and their number is reduced (Spinage 1986; Fig. 3.5.). What we consider as their knee is actually their

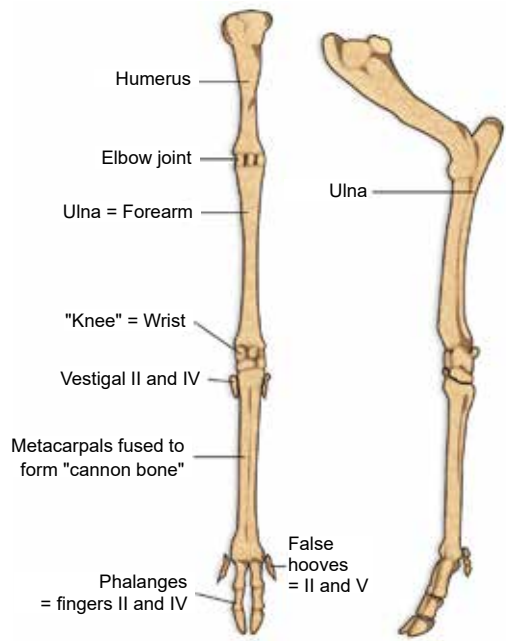

Fig. 3.5: The forlimb of the antelopes (Figure modified after Spinage 1986). Graphics: Daniela Veit.

ankle. Further down there is the cannon bone, a fusion of third and fourth metacarpals. The second and the fifths metacarpal remain as rudiments at the upper end of the cannon bone. The limb ends with the phalanges. The toes number two and five are much reduced and – as the so-called dewclaws or false hooves – they mostly do not reach the ground. At the end of the toes number three and four there are the two hooves. They are spreadable, by thus allowing stability according to terrain and activity, and they are different in shape regarding the different antelope species (Spinage 1986).

Head: The eyes of antelopes are situated at the sides of the head. This positioning, in combination with horizontal pupils, allows them a panoramic view. Compared to how we see colours, antelopes are colourblind, but in contrast they have a better night vision (Spinage 1986).

Pukus are said to have a poor sense of smell (De Vos & Dowsett 1964).

There is a total number of 32 teeth in the mouth of the pukus (Huffmann 2011, Fig. 3.6). In the lower jaw, they posess a total of six incisor teeth, 3 per half of the jaw. Next to these, is one incisor-like canine tooth per half of the jaw. As in all bovids (Bovidae) the upper incisor and canine teeth are missing (Storch & Welsch 2004). In puku – like in all grazing antelopes – the lower incisor and canine teeth are broad and spatulate in form (Spinage 1986). They bite against a horny pad. This is constantly renewed, though relatively soft so that the teeth wear out less. The diastema, a gap in the dentition, inserts between the canines and the back teeth (Spinage 1986). The puku has the following back teeth: three premolars and three molars per half of the jaw (Huffmann 2011); they are selenodont, which means that they are moon-shaped crests. This is a shared feature of all antelopes, they back teeth all look similar (Spinage 1986).

Ruminant stomach: Being a member of the family of the Bovidae, the puku belongs to the ruminants (see Box 1). They are characterized by – what the layman calls – four stomachs. In fact, this is only one stomach that is subdivided into four chambers: rumen, reticulum (or honeycomb), omasum (or prayer book), and abomasum (or true stomach). Sometimes rumen and reticulum are referred to as one organ, the reticulorumen. Large parts of fermentation and absorption of nutrients take place in rumen and reticulum. The rumen is divided into pockets by pillars and folds on, as well as in, the wall. Especially in the ventral area of the rumen there are papillae which carry out the actual nutrient absorption (Van Soest 1994). A large rumen allows for the fermentation of high-fiber food for a long period of time (Sinclair 1983).

Stafford & Stafford (1990) provide a detailed description of the four stomachs of the puku. The rumen is the largest of the chambers having a volume of six litres, followed by the abomasum, reticulum and omasum. The size of the omasum is about two third of the size of the reticulum; the length of the reticulum is 24 cm along the greater curvature, the kidney-shaped omasum is 15 cm long along the greater curvature. The abomasum has a total length of 30 cm, while a distinct pyloric part (the stomach opening) accounts for a length of 14 cm. The reticulorumen (rumen and reticulum) is large and subdivided by pillars and folds, without clearly distinctive papillae. The papillae in the rumen are unevenly distributed and are concentrated at mid level, and in the sacs and niches. The reticulum, that is medium-sized in comparison to other antelopes, shows irregular

Fig. 3.6: Total view of a skull of a dead puku *(Kobus vardonii)* (a), top view of view of mandible and the teeth of a puku (b) and a detailed view of the selenodont back teeth (c). (a and c: Luambe National Park, b: Kasanka National Park, Zambia).

honeycomb structures with four- to six-sided cells. In the omasum, that is relatively large, there are 70 so called leaves that can be attributed to five classes according to their size and position. The leaves are covered with conical papillae 2 mm in length – similar to those in the reticulum. The abomasum hat 14 mucosal folds. The combination of all characters allows the conclusion that the puku is a roughage feeder, thus a grazer (see also Chapter 8). There are similarities in the stomach of kob antelope and waterbuck.

1 Box 1: Ruminants

The group of ruminants (Ruminatia) is composed of the families of chevrotains or mouse deers (Tragulidae), musk-deers (Moschidae), deers (Cervidae), giraffes (Giraffidae), pronghorns (Antilocapridae) and hollow-horned ruminants (Bovidae). They are characterized by a four-chamber stomach that encompasses rumen, reticulum, omasum and abomasum (also known as rumen, honeycomb, prayer book and true stomach). However, chevrotains have numerous primary features – among them, they do not posess an omasum (Storch & Welsch 2004).

The first two chambers, rumen and reticulum, contain anaerobe bacteria and ciliated protozoa (Wilson 2009). They ferment the structural carbohydrates of the plant food: starch, cellulose, hemicellulose and pectin which in turn get processed into three volatile fatty acids, acetic acids, propionic acids and butyric acids by the microbial activity (Groves 2013).

The inner surface of the rumen is enlarged by papillae that are comprised of a complex vascular system. Both are adaptations, in order to absorb the products of the microbes, to transport them to the liver, where they are further processed. Another advantage of the fermentation in these so-called foreguts is that toxic i.e., poisonous, plant substances can be metabolized by the microbes. The saliva provides additional support. Many ruminants feeding on browse produce viscous, protein-rich saliva, while grazers, such as pukus, have copious saliva rich in water. Another benefit, from ruminating, is that large ingested particles can be retained and processed bit by bit. By doing so, ruminants gain more energy from less food compared to non-ruminants. This is associated with specific adaptations in the oesophageal musculature, as ruminating is an active process. Additionally, the content of the forestomach must be sorted into the material to be chewed again and to pass on in the digestive tract. The sorting is done by reticulum and omasum. The food particles are conveyed from the three forestomach to the abomasum together with the microbes. Being the true stomach, only this chamber has glands producing digestive enzymes. Hydrochloric acid kills microbes that are also digested. They represent a source of highly digestible protein and contribute significantly to the diet of ruminants (Hofmann & Kingdon 2013). By the way: Camels (Tylopoda), too, are ruminants and have a multi-chamber stomach which, however, shows different features and was developed in convergent evolution (Franklin 2011).

the 1970s, but due to poaching, the populations had thus declined sharply. Pukus also occurred on the edge of the Bangweulu swamps (cf. Ansell 1978), where they were also extinct. In 2017, 150 pukus were translocated from Kasanka National Park to the Bangweulu GMA. Some of them have moved from there to the neighbouring Lavushi-Manda National Park, so that pukus can now be found in both areas again (Kasanka Trust Ltd. 2017, cf. chapter 12.2).

The north of Zambia also counts as one of the important areas for pukus in the country (Jeffery et al. 1989). They were considered "common" in Mweru Wantipa National Park and "abundant" in Nsumbu National Park. For the Tondwa and Kaputa GMAs, which are situated between these two national parks, 1,468 and 41 pukus are reported respectively (East 1996). The number of pukus in Lusenga Plain National Park is uncertain (East 1996), but they do occur there (Nyirenda et al. 2008). No pukus are reported from Isangano National Park though (Nyirenda et al. 2008).

4 Box 4: Protected areas in Zambia

The area of what is today considered Kafue National Park was declared Zambia's first protected area on 20 April 1950 and was declared a national park on 25 February 1972 (Küpper & Küpper 2001). The Kafue National Park covering 22,400 km² (Nyirenda et al. 2008) is one of the largest national parks in the world. In general, concerning the area covered by national parks Zambia ranks high in comparison with other countries: Zambia has 20 national parks, which together cover about 64,000 km² (Lindsey et al. 2014), which corresponds to about 8 % of the country's area (Hupe & Vachal 2020). Additionally, there are 36 Game Management Areas (GMAs), which cover more than 167,000 km². In recent years, two more protected areas have been added: the Lusaka National Park with about 50 km² and the Mukungule GMA with 5,104 km². In addition, there are three game reserve and bird reserves, which occupy 33.5 km² (Lindsey et al. 2014). In total about 31 % of Zambia's land area is protected (DNPW 2020).

The establishing of protected areas was relatively easy: due to the tsetse flies (*Glossina* sp.), many areas are unsuitable for livestock farming, the soils are not productive, the climate is dry and there are hardly any mineral resources. In addition, these areas were generally only sparsely populated (Küpper & Küpper 2001). Unfortunately, the important role the tsetse flies play in nature conservation is demonstrated by the success of the anti-tsetse fly campaigns. Areas formerly infested by them are now being populated by people, villages and fields are established. This, in turn, almost inevitably leads to forests being cut down and to the decline of wildlife populations in these areas (Hupe & Vachal 2020).

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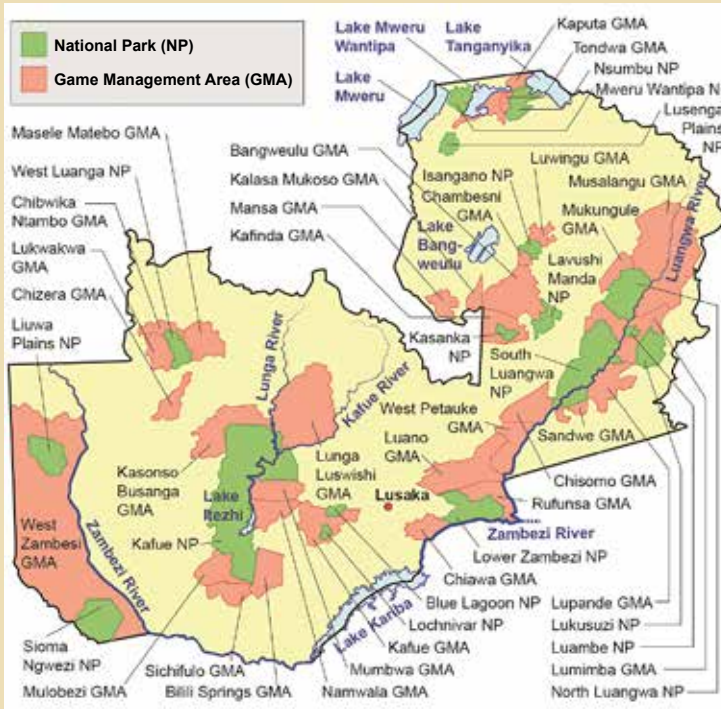

Fig. 6.5: Zambia with its National Parks and Game Management Areas (after Nyirenda et al. 2008). Graphics: Daniela Veit.

Fig. 6.6: The gate of Kasanka National Park, Zambia. It is rather a symbol as there is no fence around the national park. Here a wildlife police officer welcomes and registers the visitors while the latter pay the park entry fees.

11.4 Whistles

Pukus whistle for two different reasons: as an alarm signal and as a signal of territoriality. The whistles are produced by air being forced through the nostrils under pressure (DE VOS & DOWSETT 1964). As an alarm signal, they are emitted by all pukus. Here a single whistle is the rule. Especially in the presence of carnivores, pukus often whistle until the immediate danger has passed (DE VOS & DOWSETT 1964).

The territorial whistles consist of a series of 3-4 whistles in close succession (SKINNER & CHIMIMBA 2005). They are an important signal for males to emphasise their status as the owner of a territory (ROSSER 1990, see chapter 10.1). Especially the territorial whistles are a typical part of the sound inventory of the areas where pukus occur. ROSSER (1990) found that the rate of the whistles in different months is related to the presence of bachelor males. A rate of 0.5 whistles per hour per territorial male is given here. During the behavioural observations in Kasanka National Park and in Mumbwa GMA next to Kafue National Park, an influence of the time of day could also be noticed. There was a tendency that the frequency (whistles per hour) was high during twilight and especially at night (RDUCH 2014; Fig.11). Here, however, the whistles were not assigned to individual males or events.

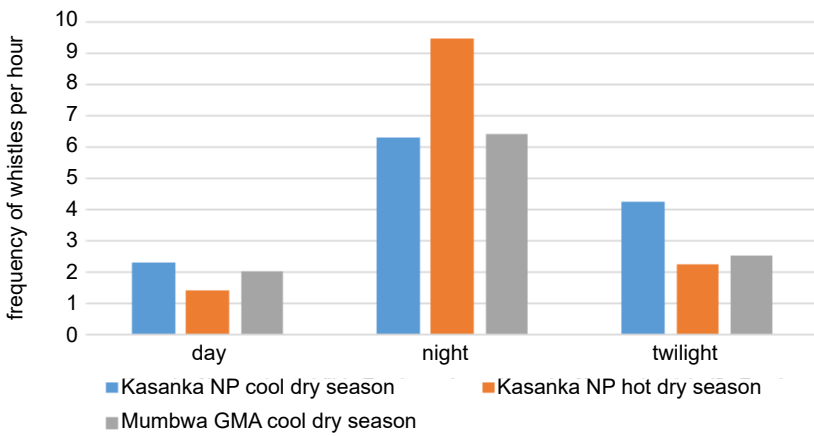

Fig. 11.11: Frequency of whistles of puku (*Kobus vardonii*), shown as territorial whistles per hour, in different study areas at different times of the year. A series of whistles was considered one unit. Day is 07:00 to 16:59, night is 19:00 to 04:59, twilight is 05:00 to 06:59 and 17:00 to 18:59 (modified after RDUCH 2014).

11.5 Different activity pattern in puku and impala

Impala have a considerable spatial overlap with puku in different areas of Zambia, including in and around the Kafue National Park (see Chapter 9.3; Rduch 2016a). The so-called "interference competition" (competition by disturbance) is influenced by differences or similarities in the activity patterns of bovids during the course of the day. This determines the extent to which herbivores have access to the same food plants (Belovsky & Slade 1986). Even though exploratory competition during the cool dry season is considered to be low in and around Kafue National Park (Rduch 2016a), disturbing competition may nevertheless occur (Rduch 2014).

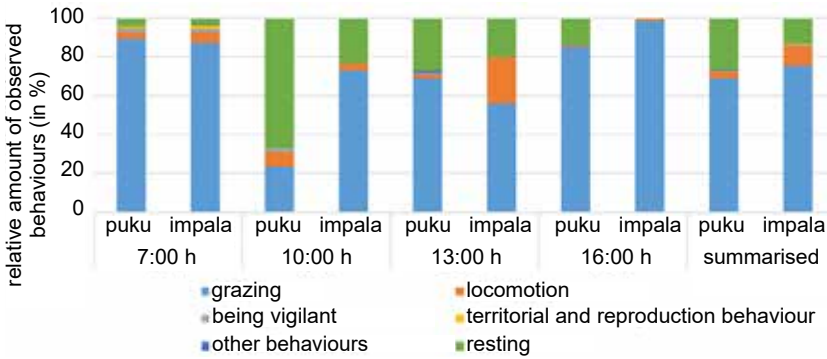

Fig. 11.12: Differences in the behaviour (activity budgets) in puku (*Kobus vardonii*) and impala (*Aepyceros melampus*) according to the observations along the line transects in and around Kafue National Park, Zambia (modified after Rduch 2014).

Interestingly, the impalas were hardly present in the observation area at the lodge in the Mumbwa GMA. If they came in the morning, they rested briefly and left the area again (Rduch 2014). For this reason, the behavioural data from the line transect sampling were used (Fig. 11.12). At first sight, the activity budgets are similar in general and at the different times of the day, but only the differences in the activity budgets in general are statistically significant. Impalas rest less and move more frequently (Rduch 2014). Impalas feed mainly during the day and only interrupt this activity to ruminate at midday (Jarman 2011). This is confirmed by observations from in and around Kafue National Park where this break falls in the (late) morning. A resting period between 10:00 and 10:59 is also known from impala in Luambe National Park (Simon 2008). In contrast to pukus, impalas are mainly diurnal and rest at night (Simon 2008; Jarman 2011). In general, impalas are said to have an energy-demanding lifestyle (Klein & Fairall 1986; Figure 11.13). Impalas – in contrast to pukus – are the

Fig. 11.13: Impalas (*Aepyceros melampus*), like these in South Luangwa National Park, Zambia, are almost constantly on the move and do not stay in any place for long.

preferred prey of many terrestrial predators (cf. e. g. Hayward et al. 2006a, 2006b, 2006c). This possibly speaks against staying in the same place for too long. In addition, impala show a different resting behaviour than the pukus. While the latter usually lay down and sometimes even lower their heads to the ground, impala usually remain standing (Rduch 2014). Also, in contrast to the pukus, the impalas seek shade for their breaks (Jarman 2011). They are sensitive to high temperatures (Klein & Fairall 1986).