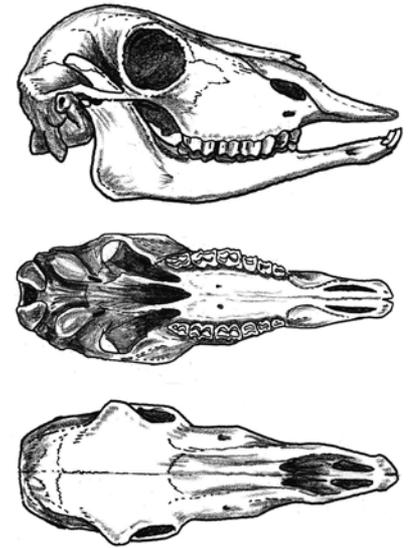
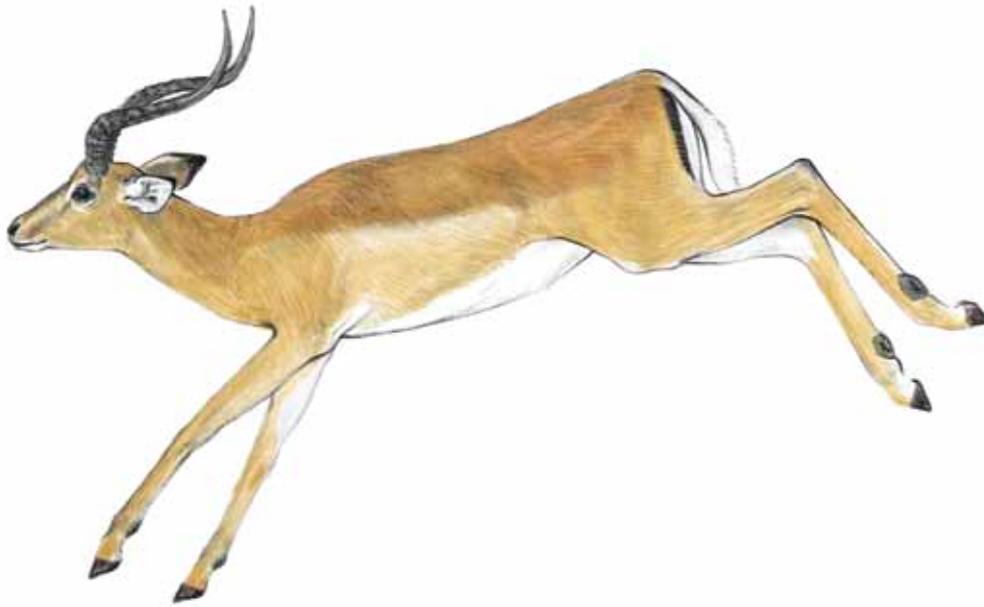


*Aepyceros melampus* IMPALA

Fr. Impala; Ger. Schwarzfersenantilope

*Aepyceros melampus* (Lichtenstein, 1812). Reisen Sudl. Africa 2, pl. 4 opp. p. 544. Khosis, Kuruman, South Africa.

ABOVE: Lateral, palatal and dorsal views of skull of Impala *Aepyceros melampus*.  
LEFT: Impala *Aepyceros melampus*.

**Taxonomy** Ansell (1972), largely following Haltenorth (1963), provisionally listed six subspecies, noting that the limits and intergradation between the subspecies are not well defined. Recent classifications, supported by molecular data (Nersting & Arctander 2001, Lorenzen, Arctander *et al.* 2006), recognize two subspecies: the nominate form, the Common Impala *A. m. melampus*, and the Black-faced Impala *A. m. petersi*. The Black-faced Impala has been considered a distinct species (Shortridge 1934, Oboussier 1965), and the two are highly genetically differentiated (Lorenzen & Siegmund 2004). Lorenzen, Arctander *et al.* (2006) also split the Common Impala subspecies into two genetically distinct groups, conforming with regional geographic affiliation to southern or East Africa, and also revealed the genetic distinctiveness of the Samburu population in Kenya, possibly indicative of a population bottleneck. More recently, Bastos-Silveira & Lister (2007) have examined morphometric data in more detail and have proposed four subspecies: *A. m. melampus* in South Africa; *A. m. petersi* in SW Angola and Namibia; *A. m. johnstoni* in Malawi and Zambia; and *A. m. suara* (including *rendilis*) in East Africa. Until these regional forms have been described in more detail and the exact boundaries of their ranges have been drawn we provisionally retain the conservative division into two subspecies. Synonyms: *holubi*, *johnstoni*, *katangae*, *pallah*, *petersi*, *rendilis*, *suara*. Chromosome number:  $2n = 58-60$ ; these differences are due to fusion metacentrics (Wallace & Fairall 1967b).

**Description** A medium-sized antelope with long, thin legs, slender body and clear sexual dimorphism. Easily identified by its marked two-tone, short-haired coat: back, nape and upper flanks are reddish-brown and have a distinct sheen – although in *A. m. petersi* upper parts

are duller, lacking distinct reddish-brown colour – while limbs and lower flanks are paler. Ventral pelage white. Hair is closely pressed to the body and averages 12 mm in length on the top of the shoulders, being slightly longer on the underparts (about 15 mm). Hairs are off-white at the base and broader and reddish-brown at the tip, though duller at the tip in *A. m. petersi*. Most of head is reddish-brown with white patches above eyes and around mouth. Chin and throat white. Crown, between the ears, is black. Ears large, inside white with tip black. On each buttock and upper thigh there is one vertical and distinct black band (surrounded by patches of pale brown hairs) running from the level of the tail to the upper hind leg. Paler patches occur on insides of legs, while on back of lower hindleg there are thick oval tufts of black hairs that cover metatarsal glands, unique to the Bovidae. Tuft of tail is black and continues in a thin black line that runs up to the rump. Underparts of the tail are white, and the white hairs are long (~100 mm). Preorbital, pedal and inguinal glands are absent. Females have two pairs of inguinal nipples. In adults, the cloven hooves have an average length of 47 mm (40–52 mm); there are no false hooves. Sexual dimorphism is distinct: ♂♂ are taller and heavier than ♀♀ in all age groups.

Only ♂♂ carry horns, which are deeply ridged for most of their length, but smooth towards the tips: in juveniles the horns are straight, vertical and short (<150 mm). They become curved like upright brackets (<250 mm long) when individuals are 12–18 months old. With age, the horns curve backwards in a lyrate shape, with an average length of 500 mm (365–820 mm) for adult ♂♂. The skull is characterized by the absence of preorbital fossae or ethmoid fissure and a premaxillo-maxillary vacuity is present, which is known otherwise only in Bates' Pygmy Antelope *Neotragus batesi* (albeit vestigially) and

the Suni *Nesotragus moschatus* (Ansell 1972). Tooth eruption has been used as a means of estimating age up to 2.5 years, after which age can only be estimated based on tooth wear (Lane *et al.* 1994).

### Geographic Variation

*A. m. melampus* (Common Impala): C Kenya to South Africa and west to SE Angola. Description mainly as above.

*A. m. petersi* (Black-faced Impala): NW Namibia and SW Angola. Larger and darker than Common Impala; a dark, nearly black band extends from the nostrils to between the eyes, and continues in a thinner band to the top of the head (these black facial markings are variable, and the thinner band is sometimes missing); black ear tip is larger and the tail almost 30% longer and much bushier than in the Common Impala.

There is a black colour variant of the Common Impala which is recessive to the common red colour of the pelage. Individuals are totally black and farmers in southern Africa have isolated individuals in large paddocks resulting in pure black populations (J. D. Skinner pers. comm.).

### Similar Species

*Litocranius walleri*. Sympatric only in East Africa. Of similar colouring, but with elongated legs and neck. Males with very robust horns that are shorter than in the Impala.

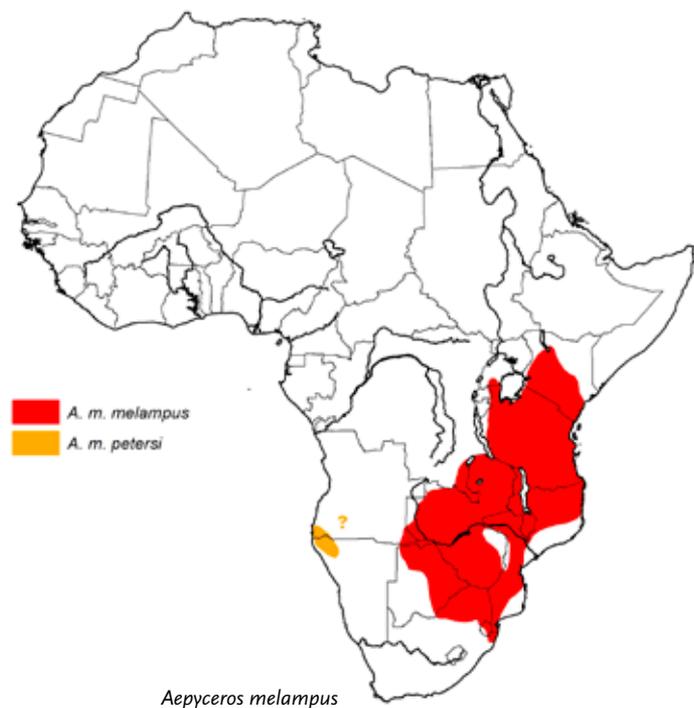
**Distribution** Endemic to Africa. Widespread in both the eastern and southern parts of the continent from Kenya to South Africa in savanna and woodland habitats close to water. The distribution range of Impalas remains largely unchanged from their historical range, although they have been eliminated from some parts through hunting and human settlement (East 1999). The northern extent of their range is the dry central and southern regions of Kenya, particularly in the Kajiado and Laikipia Districts. Their range includes SW Uganda,

mainly in Lake Mburo N. P., although they formerly also occurred in the north-east of the country. They still occur in Rwanda where they are confined to Akagera N. P., but they have been extirpated from Burundi. Their range extends southwards throughout Tanzania, Zambia (except parts of the country west of the Zambezi R.), and Malawi, where they are confined mainly to protected areas. They formerly occurred marginally in extreme SE DR Congo, but there is no recent information on their status (East 1999).

In Mozambique, they occurred throughout much of the country, except apparently much of the Nampula and Zambezia Provinces, but the civil war had a detrimental impact on their populations and they survive mainly in protected areas such as Gorongosa and Zinhave National Parks, Niassa G. R. and in W Gaza province; ongoing efforts to rehabilitate wildlife populations in this country will no doubt benefit this species. In Zimbabwe, they occur nearly throughout (although herds have been decimated by poachers since 2000), but are naturally absent from the Miombo *Brachystegia* woodland in the north-east. In Botswana, they are confined to the northern, north-eastern and eastern parts, particularly around the Okavango Delta (occasionally turning up in the eastern parts of the Kalahari), while the western part of their range extends to the extreme SE Angola and NE Namibia in the E Caprivi Strip. The southern natural limit of the range of the species includes the Limpopo, North West and Gauteng Provinces of South Africa, E Swaziland and N KwaZulu–Natal as far as the Mhlatuze R. (East 1999, Skinner & Chimimba 2005).

In the last four decades, Impalas have been introduced to numerous privately owned game ranches and small reserves throughout southern Africa, such as the Free State province and much of KwaZulu–Natal in South Africa, Namibia and Zimbabwe and widely in Namibia (East 1999). Today Impalas also occur in Gabon, central Africa, where they have been introduced into two protected areas, though they are now in decline (P. Chardonnet pers. comm.). It has been noted that Impalas easily colonize new areas, such as the south-eastern part of Hwange N. P. in Zimbabwe, providing that a regular supply of surface water is available (Matson 2003).

In NW Namibia, the Black-faced Impala is naturally confined to the Kaokoland and neighbouring SW Angola. Kaokoland was set aside as a protected area in 1928, when it formed part of Etosha N. P., Namibia, but lost its protection status in 1970. To guard against extinction, Black-faced Impalas were translocated to SW Etosha N. P. on the edge of the historic Black-faced Impala range (Green & Rothstein 1998). Today, this subspecies occurs between the Otjimborombonga area (ca 12°45' E) and Swartbooisdrift on the Cunene R., southward to the Kaoko Otavi area in the south-western part of the Etosha N. P., and the Kamanjab District just south of the Park (see also Conservation). There is no information on the current status of this subspecies in Angola, but they survive in Iona N. P. and may still occur in Bikuar and Mupa National Parks (East 1999, Crawford-Cabral & Verissimo 2005). Historically, the two subspecies were separated in Namibia by Ovamboland, an old geographical barrier stretching over a distance of more than 300 km, with *A. m. petersi* occupying the Cunene R. area and *A. m. melampus* the Okavango R. area (though see Crawford-Cabral & Verissimo 2005). Migration from the latter area would have been possible to Botswana and South Africa provided there was availability of suitable surface water (and see later) (Skinner & Chimimba 2005).



**Habitat** Throughout its range, the Impala is water dependent and a typical ecotone species, associated with light woodlands and savannas (see Estes 1991a, Skinner & Chimimba 2005 for reviews), selecting open *Acacia* savannas with nutrient-rich soils providing good-quality grass, and high-quality browse in the dry season (Pettifer & Stumpf 1981, Dunham 1982, Skinner *et al.* 1984, Fritz *et al.* 1996). In southern Africa, Impalas are sometimes found in association with mopane *Colophospermum mopane* woodlands (Jarman & Jarman 1974, Dunham 1982). Interestingly, both bachelor and breeding herds use the same habitat selection criteria, lightly wooded grassland and open woodlands, with ♂♂ tending to be more opportunistic in the dry season (Bourgarel 2004, H. Fritz & W. Crossmary unpubl.); these ecological criteria appear to be robust as they do not vary with changes in density (Gaidet 2005). Impalas often concentrate on areas of short grass, particularly close to lakes, or on post-fire flushes of grass (Monro 1978). In their semi-arid environment, Black-faced Impalas also select the interface between wooded savanna and open grassy vleis (Joubert 1971, Matson *et al.* 2005).

Impalas require canopy cover for shade and thermoregulation as they are not well adapted to dry heat (Klein & Fairall 1984, 1986; and see Matson *et al.* 2005 re. the Black-faced subspecies), but their most important requirement is surface water, perhaps associated with a physiological need to eliminate nitrogenous waste imposed by a high crude protein intake (Fairall & Klein 1984). They were rarely found further than 5 km from water in Tsavo N. P. (Kenya) during the dry season (Ayeni 1975), and less than 8 km from water in Kruger N. P. (Young 1972) or 2 km from the Chobe R. in Botswana (Omphile 1997). Impalas are thus rarely recorded in arid regions, except where they can use artificial man-made supplies such as spillage from wells and boreholes, as in Botswana. In Hwange N. P., the range expansion of the Impala population was probably favoured by the introduction of permanent waterholes, and in Etosha N. P. Impalas are restricted to areas close to waterholes, being found on average within 3.5 km around waterholes (Matson *et al.* 2006). Impalas have been noted to go for 2–3 days without drinking water in Serengeti N. P., Tanzania, provided there is sufficient succulent food available (Jarman & Jarman 1973b), while in the Zambezi valley marked individuals drank at 3–4 day intervals in the dry season (Gaidet 2005). This water-dependency, coupled with fairly strong territorial behaviour, often leads to clumped distributions. Impalas are absent from montane ecosystems, recorded to about 1700 m on the slopes of Mt Kilimanjaro (Grimshaw *et al.* 1995).

**Abundance** East (1999) details population estimates for most of the Impala's current range states, giving a total population of around 1,600,000 Common Impalas, with more than half in South Africa, and 2200 Black-faced Impalas. However, East (1999) cautions that the former does not account for undercounting in aerial surveys or areas for which population estimates are lacking. The latter estimate for Black-faced Impalas is slightly lower than that estimated by Green & Rothstein (1998), who estimated the population in Etosha N. P. at around 1500 individuals, with an additional 1200 on private land; the total population in Kaokoland was estimated at around 500. The number of Black-faced Impalas is currently estimated at more than 3200 individuals in Etosha, with a further 50–100 on communal conservancies and perhaps 1000 individuals in the north-west (J. Jackson pers. comm.). Correcting for undercounting biases, East (1999) provides

a crude estimate of nearly 2,000,000 Impalas, of which about half are on private land and one-quarter in protected areas.

The recorded densities of Impalas vary greatly, from less than 1/km<sup>2</sup> (Mkomazi N. P., Tanzania) to as many as 135/km<sup>2</sup> on the shores of L. Kariba, Zimbabwe (Bourgarel 1998) and 214/km<sup>2</sup> in the wooded savanna of Akagera N. P. in Rwanda (Monfort 1972), although total numbers in the latter area declined dramatically by about 75–80% between 1990 and 1998 (Williams & Ntayombya 1999). The average density in Kruger N. P., where they are a dominant ungulate, is around 7/km<sup>2</sup> (calculated from Owen-Smith & Ogutu 2003). In Lake Mburo N. P. and adjacent ranches in SW Uganda, highest population densities of 53.1/km<sup>2</sup> were found inside the park, while outside the protected area densities varied between 20.7 and 24.6/km<sup>2</sup> (Averbeck 2002). Such variation also exists within sites and between seasons, reflecting the heterogeneity of habitats and the availability of surface water (Dunham 1994, Jarman 1972b). These differences may also reflect difference in census techniques (and see East 1999).

**Adaptations** The 'metatarsal glands' on the hind legs are covered by tufts of black hair. Kingdon (1982) noted that these glands give the appearance of expanding at precisely the moment in which jumping Impalas make their characteristic 'empty kicks'. In behaviour that is unique to Impalas, they kick their hindlegs almost vertically while landing on their forelegs, rebound, and bring their hindlegs down before landing again. This action probably emits trails of scent that Kingdon supposes assist animals to regroup after frequent dispersals. The chemical constituents of the metatarsal glands have been analysed by Wood (1997a).

The Impala appears to be the only ungulate to perform, in addition to self-grooming, 'allo-grooming', i.e. reciprocal grooming to get rid of ticks and other ectoparasites on the head or neck (McKenzie 1990, L.A. Hart & B.L. Hart 1988, 1992, Mooring & Hart 1992, 1993). Like many small- and medium-sized antelopes, the Impala has a set of lateral incisor teeth that have been morphologically modified to form grooming tools. The second and third incisors, and the incisiform canine, are thin and needle-like, and arranged in the form of a comb on both sides of the lower jaw. These teeth are loose to facilitate see-saw action and are spaced to assist in the removal of parasites (McKenzie & Weber 1993) (see also Social and Reproductive Behaviour).

**Foraging and Food** Impalas are mixed feeders, consuming both grass and woody plants. The proportion of these food types in their diet varies greatly with season and location. A recent synthesis and attempt to classify the diet of African bovids has classified the Impala as a 'mixed-feeder, browser-grazer intermediate', with an average diet composition of 45% dicotyledon, 45% monocotyledon and 10% fruit (Gagnon & Chew 2000). This classification is in agreement with dietary classifications based on stomach morphology (Hofmann 1973), dental mesowear (Franz-Odenaal & Kaiser 2003), and stable carbon isotopes (Cerling *et al.* 2003, Sponheimer, Lee-Thorp *et al.* 2003). Even their digestive physiology, such as the rate of fermentation, seems to be adapted to their principal food (Giesecke & van Gylswyk 1975, Hoppe *et al.* 1977, Gordon & Illius 1994).

When succulent palatable green grass is available, Impalas graze: just after the first major rains, the proportion of grass in the diet peaked around Jan at 75% in Sengwa, Zimbabwe, while it decreased to less than 10% in the dry season (Jun/Jul) (Dunham 1980). Similarly,

in Serengeti N. P. the proportion of browse in the diet increased as the dry season progressed (Jarman & Sinclair 1979), and these patterns are mirrored in other studies (e.g., Van Rooyen 1992, Meissner *et al.* 1996). In the Midlands of Zimbabwe, dominated by miombo and mopane dry woodlands where primary productivity of grasses was poor, Impalas mostly browsed, even during the wet season (Fritz *et al.* 1996). The peak of browsing is often in the middle of the dry season, as some grass may be available at the end of the dry season, due to early sprouting as in *Cynodon dactylon*, or post-burn re-growth (Moe *et al.* 1990, Wisley 1996). In the open areas of Hwange N. P., around waterholes, the re-growth of grass (particularly *Cynodon dactylon*) in the middle of the dry season induces Impalas to graze. Similar observations were made in Lake Mburo N. P. where regular fires changed the foraging behaviour of Impalas from predominantly browsing to pronounced grazing in the dry season (Wronski 2003). The timing of fires and the possibility of early showers may occasionally allow Impalas to graze throughout the year (Underwood 1982). Impalas can also vary their habitat use to ensure the availability of green grass, as in Serengeti N. P. where they move up and down the catena, switching from the upper slopes in the wet season to drainage-line greenbelts during the dry season (Jarman 1979). A wide variety of grass species is eaten by Impalas, 13 in Hwange N. P. (Wilson 1975) and 23 in Nylsvlei, South Africa (Monro 1979). Preferred species include *Cynodon dactylon*, *Themeda triandra*, *Digitaria eriantha*, *Sporobolus* spp., *Panicum maximum*, *Eragrostis* spp. and *Urochloa* spp. Impalas exhibit a strong selectivity for green parts, across all heights (from 0 to >21 cm; Arsenaault & Owen-Smith 2008). Short grasses are often used, but taller swards are also well utilized.

A wide variety of browse species is eaten, with *Acacia* leaves and twigs commonly found in the diet, along with *Combretum* spp., *Dichrostachys cinerea*, *Grewia* spp., *Boscia* spp., *Maytenus* spp. and *Commiphora* spp. Wilson (1975) listed 28 browse species eaten in Hwange N. P., and Monro (1979) 46 species eaten in Nylsvlei. Fallen leaves of mopane may contribute the bulk of their diet during the dry season in the woodlands of southern Africa. Impalas also eat fruit, particularly pods, with those of *Acacia tortilis* and *Acacia nilotica* being actively sought for their high protein content. These feeding observations explain why most feeding is at ground level (Dunham 1982, du Toit 1990a). The high browsing pressure on *Acacia* spp. by Impalas is thought to be responsible for the low regeneration rate of these trees in some ecosystems (Prins & Van der Jeugd 1993, Moe *et al.* 2009). Joubert (1971) listed 21 browse plants and 12 grasses utilized by Black-faced Impalas in N Namibia.

The ratio of dicotyledons to monocotyledons in the diet may also vary with sex and social status (Van Rooyen & Skinner 1989). Territorial ♂♂ eat less dicotyledons (31% of diet) than ♀♀ (48%) or bachelor ♂♂ (49%). This difference between the sexes was also noted at L. Mburo, Uganda (Wronski 1999, 2002) and in a study in Kruger N. P. using stable carbon isotopes (Sponheimer, Grant *et al.* 2003). It may reflect the fact that dominant ♂♂ monopolize habitat where the grass layer is of prime quality, but probably reflects the fact that the time devoted to holding a territory prevents a ♂ seeking the dispersed, high-quality dicotyledons, as suggested by the greater proportion of dicotyledons in the diet of ♀♀ that share the home-ranges of dominant ♂♂.

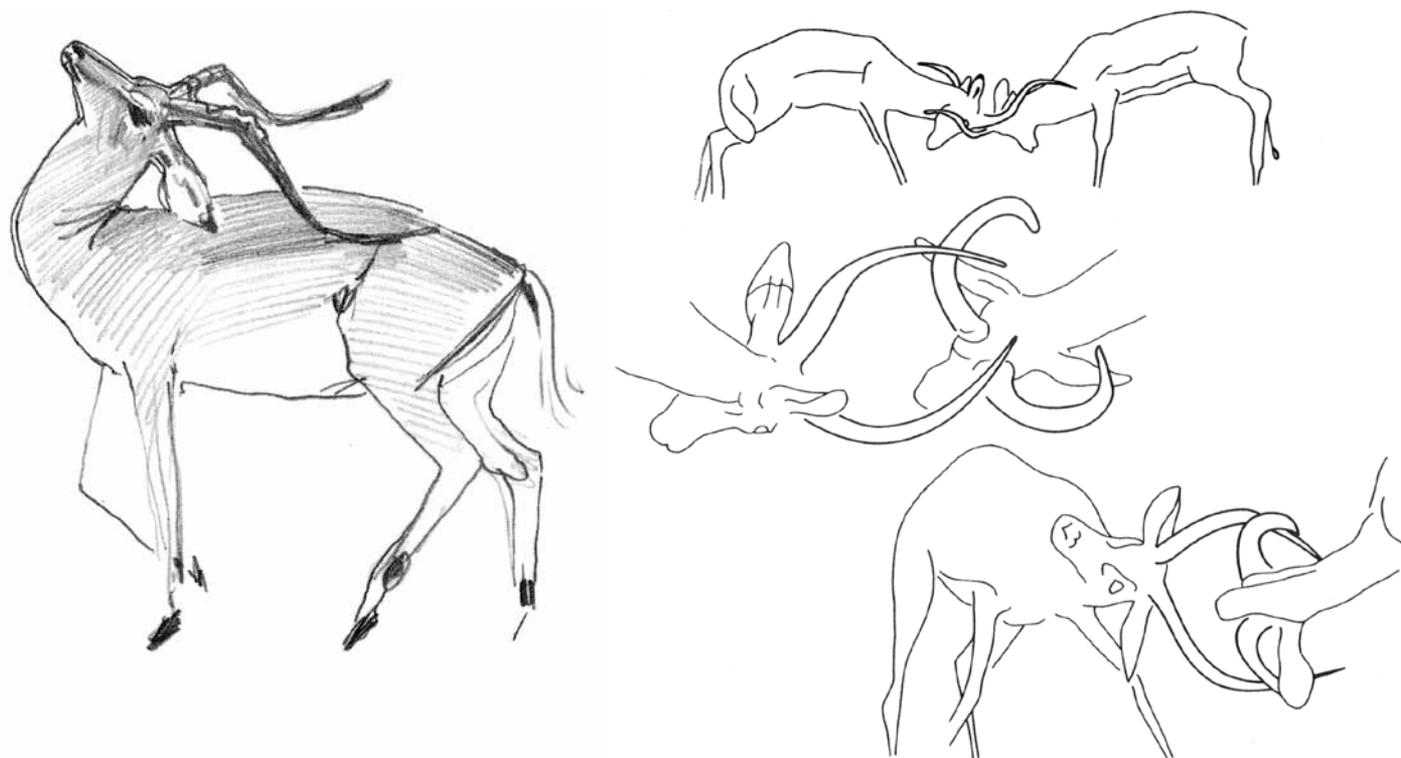
**Social and Reproductive Behaviour** Impalas are gregarious, forming herds of various sizes depending on the season and the

quality of habitat. In Hwange N. P., group size varies from 4 to 150 individuals with the largest herds found in open habitats (mean group size 15.4 in bush/grassland habitats, 12.2 in grassland and 7.3 in bushland; Bourgarel 2004). It is generally during the wet season, or the beginning of the dry season, that the biggest herds occur (Murray 1981). Black-faced Impala herds ranged from 3 to 15 individuals, occasionally up to about 20, with aggregations of larger herds formed during or after the birth season (Joubert 1971).

Impala social organization consists of territorial adult ♂♂ during the rut, bachelor groups and breeding herds. In the Sengwa area, ♀♀ seemed to be in separate, stable clans of 30–120 individuals, occupying discrete home-ranges of 80–180 ha depending on the season (Murray 1982a). Bachelor groups comprise juvenile, subadult and adult ♂♂ that are potentially territorial. An age-based hierarchy exists within bachelor groups. Highly mobile (in Hwange N. P., some marked subadults and adults moved 30 km from where they were born [M. Bourgarel pers. obs.]), bachelor groups tend to occur in lower-quality habitats where intra-specific competition and disturbance are less (especially during the rut). Cohesion within bachelor herds is poor, particularly when adult ♂♂ intending to become territorial become aggressive. After the rut, bachelor ♂♂ often mix with breeding herds. Breeding herds comprise adult, subadult and juvenile ♀♀, and subadult and juvenile ♂♂ that form cohesive herds (average spacing between individuals <1 m) without a true hierarchical structure (Jarman 1979). Except during the rut, breeding herds often include several adult and subadult ♂♂ (mixed herds). Studies of marked individuals in Hwange N. P. and the mid-Zambezi valley showed that daily changes in herd size and composition, and in individual association, are frequent throughout the year (Bourgarel 2004, Gaidet 2005). Big herds may split during the day into smaller groups, and individuals from neighbouring herds can join other herds for a few days. Temporary nursery herds have been frequently observed, especially during months following birth periods.

Herd activities are closely synchronized, especially within a breeding herd. Impalas are primarily diurnal (with some nocturnal activity), spending most of the night lying down generally in an open area, mostly ruminating. During the day, when they are not feeding or moving or disturbed, they rest, ruminate and groom themselves in the shade. Due to fairly tight group structure, local competition between individuals may also contribute to the strong group effect on foraging (Fritz & de Garine-Wichatitsky 1996, Blanchard *et al.* 2008).

Impalas display a frequent and highly reciprocal allo-grooming system between adults (♂♂ and ♀♀), but also between adults and young and between young individuals, regardless of sex, kinship or dominance status (Mooring & Hart 1992, 1993, 1997b). However, short self-grooming bouts occur more frequently than allo-grooming (Mooring 1995, Mooring & Hart 1995a). For many years, the Impala was the primary model organism for testing the predictions of the 'programmed grooming hypothesis', which postulates that tick-removal grooming by Impalas (and other ungulates, see comparative study by Mooring *et al.* 2004) is regulated by an internal timing mechanism that elicits a grooming action before the tick is able to engorge and cause cutaneous irritation. The programmed grooming model makes a number of predictions known as the vigilance, habitat, body size and tick challenge principles. These predict that breeding ♂♂ will groom more frequently than ♀♀ (vigilance principle), smaller individuals will groom at a higher rate than larger individuals



Impala *Aepyceros melampus*.

(body size principle), inhabitants of environments with a high density of ticks will groom more frequently (habitat principle), and seasonal increases in tick threat will result in more frequent grooming (tick challenge principle). All these predictions have been supported in studies on Impalas. The rate of grooming varies both seasonally and by region: Impalas increase their rate of grooming during the wet season when tick density is high (Mooring 1995), and populations in tick-dense habitat groom more frequently compared with those in habitats where ticks occur at lower densities (Hart *et al.* 1992, Mooring & Hart 1997a,b). Maternal allo-grooming occurs during nursing bouts, but its frequency declines rapidly after the first week. Young Impalas oral-groom more than adults, and consequently harbour a lower density of ticks than adults (Gallivan *et al.* 1995, Mooring & Hart 1997a,b). On the other hand, territorial ♂♂ groom themselves the least, probably related to the need for vigilance and territorial defence, and carry a higher density of ticks as a result (Mooring & Hart 1995a,b, Mooring *et al.* 1996) (see also Predators, Parasites and Diseases).

Just before the rut, adult members of bachelor herds become aggressive and sensitive to even slight movements and changes of posture in others. Dominant ♂♂ assert their position by walking stiffly in the arrogant posture, displaying their thicker neck and horn development (Jarman 1979). In addition, they occasionally fold the ears back and lift the tail, or face their challengers with head turned away, yawning or tongue flicking. Threat can also be expressed by high, medial or low horn presentation, head-tossing, head-dipping, vegetation-horning or (rarely) ground-horning and by mouthing their own penis. During confrontation, with the high horn presentation posture, the dominant ♂ invites his opponent to sniff his forehead. By sniffing and walking away with the low head attitude, the subordinate confirms his submissive position, which can

also be displayed by walking away while grazing, or by sniffing the under-tail of the dominant ♂ (uncommon).

With equal assertions of dominance between two rivals, the confrontation may end in combat. Whilst rare, a fight more often occurs between two territorial ♂♂ than between ♂♂ with different status. Fatal wounds are rare owing to the presence of a dermal shield of thickened skin that protects the neck and head, those parts of the body exposed during fights or pushing contests (Jarman 1972a). Dominant ♂♂ mark their territory with olfactory and auditory advertising. Sebaceous glands are concentrated on the forehead of dominant ♂♂ and the strong-smelling secretion is used to mark vegetation by frontal-rubbing, thereby contributing to scent-marking of territories. This is particularly common during the rut, and is not practised by ♀♀ (Jarman & Jarman 1974). Urine and faeces seem to have a smaller olfactory function even though urination and defecation are often performed in a ritualized fashion (Jarman 1979). Roaring is the most far-reaching display (up to 2 km) of dominant ♂♂, making rutting Impalas one of the noisiest ungulates. Roaring is used when intruders approach and it is occasionally followed by chasing. Roaring increases in intensity as the peak in the rut approaches.

The intensity of territorial behaviour depends on climatic conditions influencing the breeding season. In East Africa, nearer the Equator, an extended breeding season leads to a very long territorial period covering nearly the full year. However, mating generally occurs during the peak of territoriality at the end of the wet season (Jan–Feb in Serengeti N. P.; Jarman 1979). In southern Africa, the determining proximate factor initiating territorial behaviour and the onset of the oestrous cycle is shortening daylength (Skinner 1971, Skinner *et al.* 1974, Skinner & Van Jaarsveld 1987, Oliver *et al.* 2007). Murray (1982b) found that, during the rut, roaring by ♂♂ is also influenced by the lunar cycle; however, Moe *et al.* (2007)

found no consistent pattern to link conceptions with the lunar cycle in 17 years of data from South Africa and Botswana combined. The rut occurs only during a short period (a few weeks) (Fairall 1983) of the cold/dry season (Apr–Jun). Murray (1982b) found that in Zimbabwe the peak of the rut (centred in May) varied across a 20-day interval in five years.

The body condition and fat reserves of territorial ♂♂ decrease during the rut (Monro & Skinner 1979, Dunham & Murray 1982, Van Rooyen 1993) and so the number of territorial ♂♂, the duration of territorial period and territory size are a function of the seasons, population density, individual aptitude (age) and habitat quality. Generally, the number of territorial ♂♂ is greatest at the beginning of the rut and decreases progressively as food resources and intensity of territorial behaviour decline. At higher population densities, or at the beginning of the rut when competition between ♂♂ is greatest, territories are generally smaller. In Sengwa, where the density was 50–68 ind/km<sup>2</sup>, territory sizes were between 8.5 and 13 ha during the peak with an average annual home-range from 49 to 90 ha according to their age (Murray 1982a), but in Serengeti N. P., where the density was 32 ind/km<sup>2</sup>, mean territory size was 17 ha during maximum territorial activity and 58 ha during the dry season (Jarman 1979). Recently, in Limpopo Province, South Africa, Oliver *et al.* (2007) found mean territorial tenure was 67 days (range 23–99 days), with a mean territory size of 21 ± 11.3 ha compared with home-ranges of 34.1 ± 9 ha for territorial and 58.8 ± 33.4 ha for bachelor ♂♂ using the fixed kernel method; territorial boundaries remained constant, while around waterholes the area was neutral. Good-quality habitats increase mating opportunities by permitting long-lasting territorial periods and by allowing a territorial ♂ to keep more ♀♀ on his territory.

Compared with results of other studies, the home-ranges of Impalas in Lake Mburo N. P. were larger, and long-distance movements of young ♂♂ and ♀♀ occurred. Mean annual home-range size of female breeding herds was 168 ha, whereas home-ranges of up to 590 ha in young ♀♀ were observed (Averbeck 2002). Mean home-range size in adult ♂♂ varied between 70 and 110 ha, and exceeded values found by Murray (1982a) considerably. In NW Namibia, the home-ranges reported for female Black-faced Impalas (using minimum convex polygon) are the largest recorded for Impalas anywhere, at 33.3 ± 3.2 km<sup>2</sup>, perhaps a reflection of the considerable distances that Black-faced Impala ♀♀ must travel between patches of suitable foraging habitat compared with Common Impalas, which inhabit less arid environments (Matson *et al.* 2007).

The home-range of breeding herds (mean area 297 ha in Serengeti N. P. and 80–180 ha in Sengwa; Jarman 1979, Murray 1982a) is bigger than male territories, and so can overlap several territories. As soon as a territorial ♂ has acquired a breeding herd, he checks intermittently to detect ♀♀ in oestrus by genital smelling and licking, or by smelling their urine on the ground. This act is generally followed by display of flehmen. Pre-mating behaviour is variable (Jarman 1979). Generally, the ♂ approaches and follows oestrous ♀♀ with head lowered and nose held forward. With receptive ♀♀ copulation often occurs after perineal licking. Mounting lasts up to 10 sec, and many consecutive mountings will follow at variable intervals (few seconds to one or two minutes). After successful copulation, ♂♂ frequently snort, roar, or chase bachelors and herd ♀♀. After successful copulation, a ♂ does not display any further interest in that ♀ even if she remains sexually receptive.

The Impala ewe and neonate exhibit behaviour that is between the pure 'hider' and pure 'follower' (Jarman 1976): several hours before parturition the pregnant ♀ isolates and conceals herself (in tall grass or thick bush). The mother eats the afterbirth (Jarman 1976). How long the young stay hidden is uncertain, but after a day or two, they follow their mothers back to the herds during the day. At night, neonates (less than a week old) stay concealed in cover far from the adults. Often several young stay hidden in the same area. When disturbed, these 2–3-day-old young try to make themselves less conspicuous by laying with their head on the ground, but seven-day-olds are vigilant and run away if a potential threat comes too close (M. Bourgairel pers. obs.). After a week, young are no longer isolated from the herd and display anti-predator behaviour, including the formation of nursery groups, especially where there is a marked annual birth season. The weakness of mother–young bonds is illustrated by the rapid decline of the proximity between mother and young and the formation of groups of juveniles (Mooring & Rubin 1991). At 4–6 months of age, offspring preferentially associate with age-mates, forming crèche groups which are characteristic for Impala young (Jarman 1979, Estes 1991a). Females remain in the breeding herd for life, while weaned ♂♂ are subjected to aggressive behaviour by dominant ♂♂ and are eventually driven out of the breeding herds. Dispersal distances appear to be fairly low (less than 10 km), although male subadults have been recorded dispersing up to 40 km in Hwange N. P. (M. Bourgairel pers. obs.).

**Reproduction and Population Structure** Females become sexually mature at age 18 months, whereas ♂♂ are fertile as yearlings, but mate only when they become behaviourally mature and territorial in their fourth year (Kerr 1965). In southern Africa, the ♀ has a maximum of two cycles during the reproductive period, but normally conceives during her first oestrus. The fecundity rate is normally 95% in fully mature ♀♀ (>2 years old) but lower in two-year-olds (Fairall 1983). There is no sign of reproductive senility in animals up to 14–15 years old (Skinner 1969).

The relatively short parturition season takes place at the beginning of the wet season (Nov–Jan) in southern Africa (Skinner & Chimimba 2005); in Chobe N. P. Impala parturition is highly synchronized, with 90% of young born within two weeks in mid-Nov, shortly after the first rains (Moe *et al.* 2007). However, in eastern Africa there is no marked reproductive seasonality, as a consequence of little change of daylength near the Equator and the bimodal rainfall pattern (Jarman 1979). Moe *et al.* (2007) posited that Impalas synchronize births in areas with a highly seasonal food supply, and temporally space births in less seasonal (equatorial) areas to reduce predation risks.

Gestation lasts 27–28 weeks (Fairall 1972), and a single young is born (although twins have been recorded; Kayanja 1969, Joubert 1971). At birth, the lamb has an average mass of about 5 kg, but smaller lambs (3.5 kg) have been captured in Hwange N. P. (Bourgairel 2004). Young grow quickly and weaning occurs between 17 and 25 weeks of age. The asymptotic mass is achieved at 4–5 years, but 75% of mature mass is reached by two years of age (Howells & Hanks 1975, Hanks *et al.* 1976, Brooks 1978, Fairall 1983).

At birth and during the first year, the sex ratio is equal, but at adulthood it is biased towards ♀♀ (65% of adults were ♀♀ in Kruger and Hwange National Parks). In breeding herds in Hwange N. P., ♀♀ can reach 88% of the total adults. Overall, the age composition is 23% juveniles and this figure increases during the birth season to over

30% (M. Bourgarel pers. obs.). Recruitment appears highly variable, and the juvenile to female ratio seems to change strongly (0.47–0.81) with variations in density-dependent competition for resources (Gaidet 2005). Averbeck (2002) observed an average ♂ : ♀ sex ratio of 1 : 1.5 in Lake Mburo N. P., while the percentage of adult ♀♀ (38–45%) in the population was greater than of ♂♂ (21–27%). The proportion of juvenile and subadult Impalas remained almost unchanged throughout the study period, at a level of 5–10%. The ratio of sexually mature to sexually immature animals was 2 : 1, the ratio of adult ♀ to subadult ♀ was on average 1 : 1.1 (Averbeck 2002).

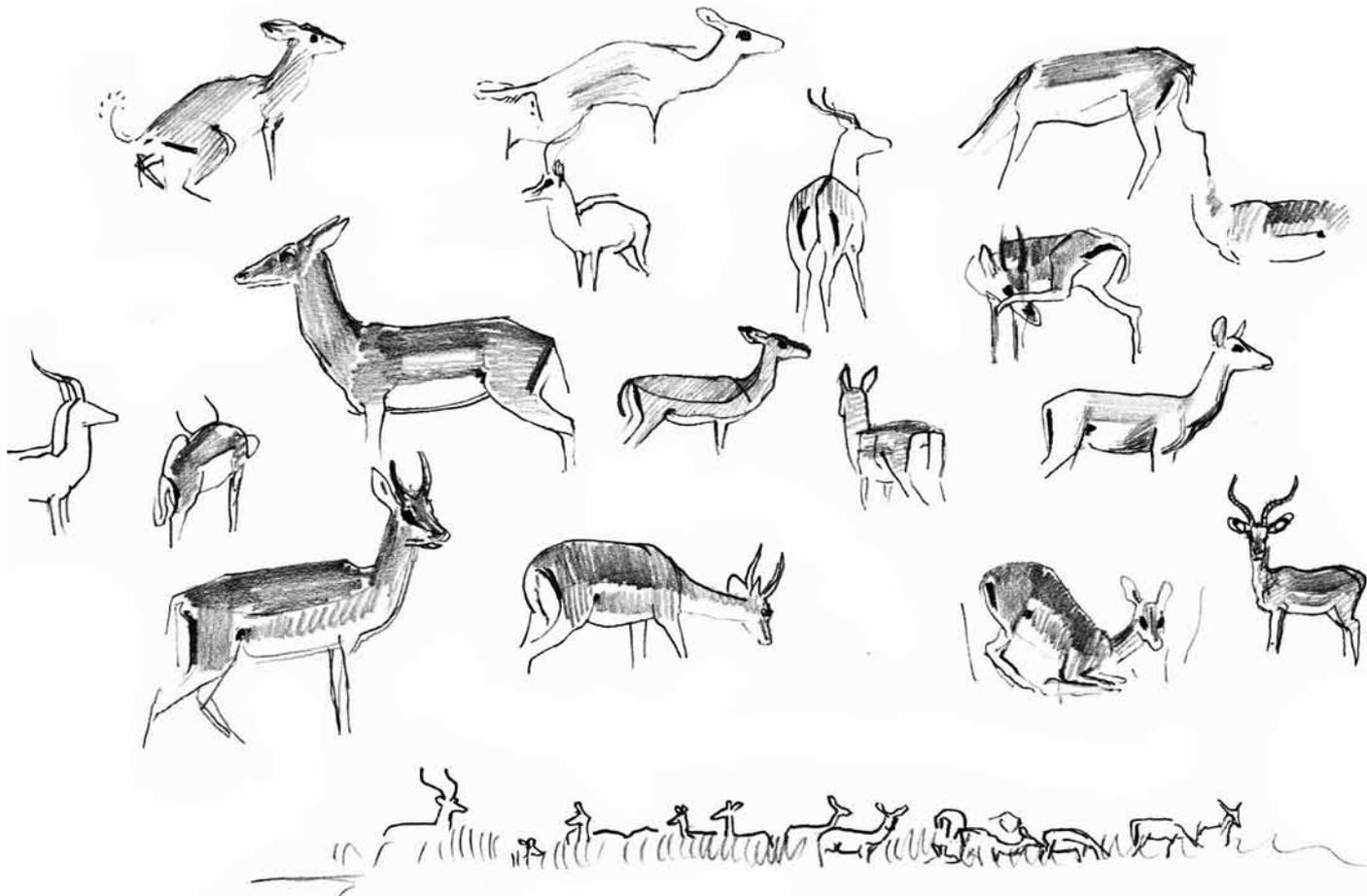
The survival rate depends on the environment, the sex and age (Ginsberg & Milner-Gulland 1994): the probability of survival is 0.6 during the first year for both sexes, but mortality occurs mainly during the first month of life (Bourgarel 2004) and reaches 0.95–0.97 at three years old. For ♀♀, the probability stays the same up to 8–9 years old, whereas for ♂♂ it starts to decrease after six years of age to reach zero at 9–10 years of age. Female longevity is 12–14 years in the wild, compared with ten years for ♂♂.

**Predators, Parasites and Diseases** Impalas are prey to all larger predators (including jackals *Canis* spp. and baboons *Papio* spp.), and are often considered as preferred prey for African Wild Dogs *Lycaon pictus*, Leopards *Panthera pardus* and Cheetahs *Acinonyx jubatus* (e.g., Pienaar 1969a, Pole *et al.* 2004, Hayward, Henschel *et al.* 2006, Hayward, Hofmeyr *et al.* 2006, Hayward, O'Brien *et al.* 2006). However, as the Impalas taken by predators are on average in poorer

condition than the average in the population (Pole *et al.* 2003), it is possible that the rank of the Impala in the prey list of large predators is density-dependent: when at high density, the proportion of weaker individuals would increase and Impalas would then become the main prey of most large carnivores. As medium-sized predators such as large eagles also prey on young Impalas (see, for example, Mooring 1993), the mortality of newborn Impalas is high, ranging from 15–60% in a study population at Hwange N. P. (H. Fritz pers. obs.): one pack of seven African Wild Dogs ate 4–5 newborns daily for a week (M. Bourgarel pers. obs.). Cheetahs seem also to specialize on young Impalas in the large game ranches in Namibia (Matson 2003).

In woodland (their favourite habitat), Impalas are more vulnerable to predation and so they are extremely alert and prompt to flee. They tend to use more open habitats preferentially when predators such as Lions are in the vicinity (Valeix *et al.* 2009). When disturbed by an intruder that is beyond their flight distance, they snort and move off slowly, but if the intruder is within their flight distance, they often run and leap in all directions, bounding up to 12 m. It is at such times that they commonly kick their hindlegs up, rebounding before landing again (see Adaptations). Seasonal parturition and nursery groups reduce predation risk by diluting the risk among newborns and enhancing vigilance, although this strategy is only likely to be effective against specialist predators (Ims 1990, Moe *et al.* 2007). In general, grooming increases predation risk (Mooring & Hart 1995a).

Ecto-parasites of Impalas include ticks, which are also vectors of blood parasites, and lice. Durden & Horak (2004) list five species of



Impala *Aepyceros melampus*.

lice known to parasitize Impalas, including the recently described *Linognathus weisseri*, while numerous studies have investigated tick burdens in Impalas (e.g., Horak 1982, Horak, Fourie *et al.* 1995, Horak *et al.* 2003). The intensity of infestation by ticks depends on the season and Impala density, and varies between individuals: the infestation is greater in subadults and adults than in juveniles, and in adult ♂♂ than in adult ♀♀ (Gallivan *et al.* 1995). Males on their territories harboured six times more adult ticks than did ♀♀, showing the cost of decreased grooming activity (Mooring & Hart 1995a,b). Impalas frequently associate with oxpeckers, *Buphagus* spp., which concentrate their time foraging around the ears, head and neck of impala, which are the regions supporting the highest density of ticks (Mooring & Mundy 1996, Mooring *et al.* 1996). When oxpeckers are in attendance, Impalas noticeably reduce their own grooming efforts (Mooring & Mundy 1996).

Impalas also harbour numerous endo-parasites, and again numerous studies have investigated prevalence, host specificity and seasonal incidence in Impalas (e.g., Horak 1978a, 1981a). In Zimbabwe, 26 nematode, eight cestode and three trematode species have been recovered from Impalas (Jooste 1987). Some of these are definitive Impala parasites and others are occasional. In Zimbabwe, on 20 farms where causes of Impala mortality were studied, 34% of natural deaths were due to predation and 10% to disease (acute fascioliasis, verminous aneurysm/*E. coli* septicaemia or clostridial infection). Endo-parasites did not cause death among Impalas and losses associated with ticks and tick-borne diseases were rare (Knottenbelt 1990). Mortality due to anthrax has also been recorded (e.g., Prins & Weyerhaeuser 1987).

**Conservation** IUCN Category: Least Concern (*A. m. melampus* – Least Concern; *A. m. petersi* – Vulnerable D1). CITES: Not listed.

Although Impalas seem to have been eliminated from some parts of their range (such as Burundi), they are still relatively widespread and common and abundant in numerous protected areas across their range. Owing to its high rate of reproduction and great adaptability, the Impala has become of prime interest for meat production (e.g., Fairall 1983, Bothma 1989), not only on wildlife ranches but also in remote communal areas (e.g., Feron *et al.* 1998, Bourgarel *et al.* 2001, Averbeck 2001, 2002).

The main threat to Common Impala seems to be active poaching at the edge of, within, protected areas (with strong influence on densities as well as population structure) combined with agro-pastoral development (Setsaasa *et al.* 2007, Averbeck *et al.* 2009b, Ogutu *et al.* 2011). However, the type of hunting may skew sex and age ratios in the population very differently (Setsaasa *et al.* 2007, Averbeck *et al.* 2009b). Hunting risk is also likely to affect Impala behaviour, such as change in habitat selection or waterhole attendance (Crosmary *et al.* in press).

Poaching, livestock development and severe drought are considered the main factors for the decline of *A. m. petersi* (Green & Rothstein 1998, East 1999). The introduction of 180 individuals of *A. m. petersi* from Kaokoland to the west of the Etosha N. P. between 1968 and 1971 helped promote the conservation of the subspecies, and a few were translocated from Etosha N. P. to private game farms in Namibia. Matson *et al.* (2004) analysed 21 translocations of Black-faced Impalas to 20 Namibian game farms that occurred between 1970 and 2001, with the aim of identifying characteristics of the translocated populations and the release sites that significantly correlated with the success of the

translocations (determined by whether the population had a positive growth rate). Initial population size was paramount to the success of translocations, and populations of over 15 individuals were more successful, while the presence of Cheetahs also influenced the success of translocated populations; in the presence of this predator, smaller translocated populations of Black-faced Impalas were less likely to be viable than larger populations.

The introduction of *A. m. melampus* to ranches and conservancies neighbouring Etosha N. P. may contribute a threat to *A. m. petersi* through hybridization. Green & Rothstein (1998) estimated that about one-quarter of all privately owned Black-faced Impalas occur in mixed herds with Common Impalas. In a recent study, Lorenzen & Siegismund (2004) analysed 127 Black-faced Impala individuals from five subpopulations in Etosha N. P. to determine whether any hybridization had taken place within the park, but could not find any evidence for hybridization between the two subspecies.

## Measurements

### *Aepyceros melampus*

#### *A. m. melampus*

HB (♂♂): 1402 (1271–1504) mm, n = 5

HB (♀♀): 1352 (1173–1506) mm, n = 55

T (♂♂): 280 (220–340) mm, n = 33

T (♀♀): 258 (205–300) mm, n = 23

HF c.u. (♂♂): 855 (820–905) mm, n = 5

HF c.u. (♀♀): 767 (672–860) mm, n = 55

E (♂♂): 145 (130–157) mm, n = 33

E (♀♀): 140 (130–155) mm, n = 23

WT (♂♂): 45.7 (31.3–61.5) kg, n = 32

WT (♀♀): 38.5 (23.2–60.5) kg, n = 81

Zambezi Valley and Hwange N. P., Zimbabwe (H. Fritz & M. Bourgarel pers. obs.; V. Wilson pers. comm.)

Sh. ht (♂♂): 873 (785–925) mm, n = 28

Sh. ht (♀♀): 800 (790–810) mm, n = 12

WT (♂♂): 56.9 (46.0–64.4) kg, n = 28

WT (♀♀): 42.1 (38.93–45.69) kg, n = 12

Serengeti N. P., Tanzania (Sachs 1967, with slightly different body measurements)

Maximum recorded horn length is 91.7 cm for a pair of horns from the Masai Reserve, Kenya (Rowland Ward).

#### *A. m. petersi*

HB (♂♂): 1350 (1240–1450) mm, n = 7

WT (♂♂): 63.0 kg, n = 10\*

WT (♀♀): 50.4 kg, n = 9\*

N Namibia (Joubert 1971)

\*Range not available

Maximum recorded horn length is 68.0 cm for a pair of horns from Grootfontein, Namibia (Rowland Ward).

**Key References** Averbeck 2002; Bourgarel 2004; Dunham 1980; Gaidet 2005; Jarman 1979; Jarman & Jarman 1974; Matson 2003; Murray 1981, 1982a,b.

**Hervé Fritz & Mathieu Bourgarel**