CHAPTER

9

White-bellied pangolin *Phataginus tricuspis* (Rafinesque, 1820)

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Pangolins
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Taxonomy

Previously included in the genus *Manis* (Meester, 1972; Schlitter, 2005), the species is here included in *Phataginus* based on both morphological (Gaudin et al., 2009) and genetic (du Toit et al., 2017; Gaubert et al., 2018) evidence. Hatt (1934) reported that the species exhibits slight morphological variation across its range, including in scale pigmentation and hair length (e.g., on the ventrum). Allen and Loveridge (1942) and Meester (1972) proposed two distinct subspecies based on morphological analyses, *P. tricuspis tricuspis* (range except Uganda) and *P. t. mabirae* (Uganda). These subspecies are not considered valid here following Kingdon and Hoffmann (2013).

The species is included in the subfamily Phatagininae to designate small African pangolins based on mitogenomic distances between the genera *Manis*, *Smutsia*, and *Phataginus*, and morphological traits unique to *Phataginus* (see Chapter 2; Gaubert et al., 2018). Gaubert et al. (2016) identified six geographic lineages within the white-bellied pangolin that were identified as Evolutionarily Significant Units (ESUs) and may warrant species or subspecies status; this requires further research. These lineages were partitioned into Central Africa, Gabon, Dahomey Gap, Ghana, western Africa, and western Central Africa (see Chapter 2). Hassanin et al. (2015) discovered a high genetic nucleotide divergence between a white-bellied pangolin from Gabon and specimens from Cameroon, Ghana and Nigeria, and the potential for a new taxon in Gabon requires further research.

The type locality is given as "Guinée", West Africa (Rafinesque, 1820). Chromosome number is not known. Synonyms: *Manis multiscutata* (Gray, 1843), *Manis tridentata* (Focillon, 1850), *P. t. mabirae* (Allen and Loveridge, 1942).

Etymology: *Phataginus* (see Chapter 8); the species name refers to the three (*tri-*) points or cusps (*-cuspis*) on the scales (Gotch, 1979).

Description

The white-bellied pangolin (*Phataginus tricuspis*) is a small, semi-arboreal African pangolin with a body weight of 1–3 kg and a total length of about 100 cm (Table 9.1). It is the lightest pangolin species, marginally lighter than the broadly sympatric black-bellied pangolin (*P. tetradactyla*). The species is not sexually dimorphic but males are reported to be slightly longer and heavier than females (Pagès, 1968). Up to 60% of the total body length comprises the long, prehensile tail (35–60 cm); head-body length ranges between 25 and 38 cm, potentially longer (Table 9.1). The tail is flat ventrally and rounded dorsally, and has a naked cutaneous pad at the tip (which is truncated) on the ventral side that replaces two median and two lateral scales (Pocock, 1924). The sensory tail pad contains many mechanoreceptor nerve endings that aid sensitivity in terms of touch and grip (Doran and Allbrook, 1973), and the tail functions as a fifth limb when the species is climbing (see *Behavior*). There are 41 caudal vertebrae (Table 9.1).

The body is covered in small, overlapping scales that grow from the epidermis in a lattice-like arrangement and are tricuspid (Jentink, 1882; Rahm, 1956). The scales cover the dorsal and lateral surfaces of the body, the fore- (except the upper portions) and hindlimbs, the tail (dorsally and ventrally), and the neck and head, but are absent from the anterior of the face, the ventral body surface and inner-side of the limbs. On the upper portion of the forelimbs (elbow to wrist) dense (sometimes long) brown hair replaces the scales (Pocock, 1924). There are 18–22

TABLE 9.1 White-bellied pangolin morphometrics.

	Measurement		Country	Source(s)
Weight	Weight (♂)[a]	1.67 (1.2–2.3) kg, n = 8	Southwest Nigeria	FMNH[b]
		2.36 (1.74–2.86) kg, n = 4	Southeast Nigeria	Kingdon and Hoffmann, 2013
	Weight (♀)	1.71 (1.2–2.2) kg, n = 8	Southwest Nigeria	FMNH[a]
		2.6 (1.94–2.88) kg, n = 11	Southeast Nigeria	Kingdon and Hoffmann, 2013
Body	Total length (♂)	793.2 (617–1027) mm, n = 25	Democratic Republic of the Congo	Hatt, 1934
	Total length (♀)	768.4 (630–920) mm, n = 25	Democratic Republic of the Congo	Hatt, 1934
	Head-body length (♂)	350 (330–380) mm, n = 7	Côte d'Ivoire, Democratic Republic the of Congo, Liberia	FMNH[b]
		319 (254–375) mm, n = 17	Southeast Nigeria	Kingdon and Hoffmann, 2013
	Head-body length (♀)	333 (308–367) mm, n = 8	Côte d'Ivoire, Democratic Republic of the Congo, Ghana, Liberia	FMNH[b]
		310 (265–351) mm, n = 14	Southeast Nigeria	Kingdon and Hoffmann, 2013
	Tail length (♂)	469.6 (360–607) mm, n = 25	Democratic Republic of the Congo	Hatt, 1934
	Tail length (♀)	460.4 (350–590) mm, n = 25	Democratic Republic of the Congo	Hatt, 1934
Vertebrae	Total number of vertebrae	69		Frechkop, 1931; Jentink, 1882
	Cervical	7		Jentink, 1882; Mohr, 1961
	Thoracic	13		Jentink, 1882; Mohr, 1961
	Lumbar	6		Jentink, 1882; Mohr, 1961
	Sacral	2		Jentink, 1882; Mohr, 1961
	Caudal	41		Jentink, 1882; Mohr, 1961
Skull	Length (♂)	72.8 (63.8–80.8) mm, n = 22	Democratic Republic of the Congo	Hatt, 1934
	Length (♀)	68.7 (58.5–79.2) mm, n = 20	Democratic Republic of the Congo	Hatt, 1934

(*Continued*)

TABLE 9.1 (Continued)

	Measurement		Country	Source(s)
	Breadth across zygomatic processes (♂)	27.3 (22.7–32) mm, n = 22	Democratic Republic of the Congo	Hatt, 1934
	Breadth across zygomatic processes (♀)	25.4 (20.2–29.3) mm, n = 20	Democratic Republic of the Congo	Hatt, 1934
Scales	Total number of scales	935 (794–1141), n = 25	Cameroon, Nigeria, Sierra Leone, Uganda, unknown	Ullmann et al., 2019; D. Soewu, unpubl. data
	No. of scale rows (transversal, body)	18–22	Democratic Republic of the Congo	Frechkop, 1931; Hatt, 1934
	No. of scale rows (longitudinal, body)	19–25	Democratic Republic of the Congo	Frechkop, 1931; Hatt, 1934; Jentink, 1882
	No. of scales on outer margins of tail	35–40	Democratic Republic of the Congo	Frechkop, 1931; Hatt, 1934; Jentink, 1882
	No. of scales on median row of tail	30–33	Democratic Republic of the Congo	Frechkop, 1931; Hatt, 1934
	Scales (wet) as proportion of body weight	0.15–0.20		African Wildlife Foundation, unpubl. data
	Scales (dry) as proportion of body weight	No data		

[a]*Males are reported to be slightly heavier than females; these data are based on a small sample size.*
[b]*FMNH=Florida Museum of Natural History.*

transversal and 19–25 longitudinal scale rows on the body, and 35–40 rows of scales on the outer margins of the tail that are kite-shaped (Frechkop, 1931; Hatt, 1934; Jentink, 1882). The medio-dorsal row of scales on the tail is interrupted towards the tail tip and is replaced by two rows of 3–6 scales (Jentink, 1882). Total scales number between ~790 and 1140 (Table 9.1). The largest scales are on the dorsal surface and measure up to 47 × 26 mm; single scales weigh up to 0.66 g (O. Sodeinde, unpubl. data). The scales are uniform in color but vary substantially from brownish-gray to reddish- or yellowish-brown, and the distal edge may color faint yellow, especially in older individuals (Figs. 9.1–9.3; Rahm, 1956; R. Jansen, pers. obs.). The scales grow in length more rapidly than in width: scales from the mid-dorsal region grow from being approximately as long as wide, to four times length versus width. The scales are laterally striated (Fig. 9.2) and keeled on the flanks and limbs, and are less robust (i.e., are flimsy) compared to scales on the black-bellied pangolin and other pangolin species. The striations and cusps wear over time, sometimes completely, and the cusps may break off with age (Hatt, 1934; R. Jansen, pers. obs.). Unlike Asian pangolins, hairs do not project between the scales.

The skull demonstrates morphological features related to adaption to a myrmecophagous diet (Chapter 1; see Hatt, 1934; Heath, 2013).

FIGURE 9.1 White-bellied pangolin foraging for prey in Central African Republic. The cusps on the scales can clearly be seen on this individual. *Photo credit: Alex Ley.*

As in the black-bellied pangolin, the lacrimal bone is present – it is absent in other pangolin species (Emry, 1970). The head is conical-shaped and the muzzle is broader than that of the black-bellied pangolin (Hatt, 1934). The scales extend to the forehead but are absent from the face, which is covered in sparse hairs (Fig. 9.3). The skin around the snout and eyes is pinkish brown, with a black patch beneath the eyes; the lips are pinkish (Hatt, 1934). The irises are dark and the eyes large and bulbous with thick, swollen lids (Hatt, 1934). The rhinarium is well defined, naked and moist (Pocock, 1924). The ear pinnae are totally suppressed (Fig. 9.3), but the auditory orifice can be partially closed by a bordering small flange (Pocock, 1924). The belly is pale grayish-white and is covered with white hair up to 20 mm in length, which can be dense (Hatt, 1934).

The anatomy is highly adapted to a myrmecophagous diet. The tongue is 30 cm in length and, as in other pangolin species, is attached to the caudal end of the xiphoid process (xiphisternum) in the abdomen (Doran and Allbrook, 1973). In this species, the proximal region of the tongue is "U-shaped" and extends caudally to the right iliac fossa before turning cranially, terminating under the right side of the diaphragm (Chan, 1995; Heath, 2013). From the abdomen, the tongue passes through the thorax and neck to the oral cavity which is small (Doran and Allbrook, 1973). Large salivary glands located in the pharyngeal and cervical regions produce an alkaline mucus (pH 9–10; Fang, 1981) which is secreted into the sheath housing the tongue and onto the tongue itself (Doran and Allbrook, 1973; Heath, 2013). During feeding, the tongue is repeatedly extended and retracted and the anterior portion has a high density of fascicles, suggesting a sensory (i.e., prey location) rather than gustatory function; the tongue also lacks papillae

FIGURE 9.2 Scales of the white- (left) and black-bellied pangolin (right). White-bellied pangolin: top left – dorsal, post-scapular; top right – dorsal, scapular; bottom left – dorsal, tail; bottom right – marginal, tail. Black-bellied pangolin: top left – dorsal, marginal; top right – dorsal, post-scapular; bottom left – dorsal, tail; bottom right – marginal, tail. *Photo credit: Matthew H. Shirley.*

FIGURE 9.3 Aged white-bellied pangolin showing worn scales. *Photo credit: Frank Kohn.*

indicative of its transport function (Ofusori et al., 2008). The hyoid bone serves to scrape prey from the tongue and direct it down the esophagus to the stomach where it is masticated (Doran and Allbrook, 1973). The gizzard-like stomach is lined by keratinized stratified squamous epithelium and dense collagen fibers, which offer protection against ulceration by the hard chitinous parts of ants and termites (Ofusori et al., 2008).

The forelimbs are slightly shorter than the hindlimbs (Sodeinde et al., 2002); both terminate in five digits. On the forefeet, the first digit is vestigial; the second, third and fourth digits have long claws, the third being the longest and most extended (Fig. 9.3; Pocock, 1924; Rahm, 1956). The fifth digit is longer than the first and stems from the base of the fourth digit (Pocock, 1924). The claws on the forefeet are slightly

longer than on the hindfeet. As in the black-bellied pangolin, the hindfeet have four long, well-developed claws of approximately equal length, and the innermost claw is vestigial (Pocock, 1924). Both fore- and hindfeet are placed palm downwards and have well developed skin pads, extending from the level of the first digit to the heel in the hindfeet (Pocock, 1924).

Large anal glands are situated to the side of the anus, which produce a white secretion and foul-smelling odor and are important to the species' ecology (see *Ecology*; Pagès, 1968; Pocock, 1924). The perineum is short and in the female the vulva is anterior to the anus; the female has one pair of pectoral mammae. Male testes descend to the inguinal area.

Body temperature is regulated at 27–34 °C, potentially higher (see Heath and Hammel, 1986), and fluctuates with activity, being higher when individuals are active; resting metabolic rate has been estimated at 202.2 ml O_2/kg/h (Hildwein, 1974; Jones, 1973).

The white-bellied pangolin may be confused with its congener the black-bellied pangolin. Distinguishing features include the absence of very large post-scapular scales in the former, in addition to skin color, scale size and coloration (Fig. 9.2), and scale number (see Table 9.1). Other differences include the broader muzzle in the white-bellied, and proportionally longer tail in the black-bellied pangolin (Chapter 8). The species is distinguishable from the two larger African pangolins by its smaller size, longer tail, and scale coloration and morphology: dorsal scales on the white-bellied pangolin are typically longer than they are wide.

Distribution

A widely distributed species in West and Central Africa (Fig. 9.4). Recorded from Guinea-Bissau (Cantanhez National Park; Bout and Ghiurghi, 2013) and Guinea in West Africa (Ziegler et al., 2002) through Sierra Leone (Boakye et al., 2016a; Grubb et al., 1998), Liberia (Allen and Coolidge, 1948; Verschuren, 1982), Côte d'Ivoire (Rahm, 1956) and Ghana (Boakye et al., 2016b; Grubb et al., 1998; Ofori et al., 2012). There are no confirmed records in Senegal or The Gambia (Grubb et al., 1998). There are fewer records eastward in Togo and Benin, but the species has been recorded in southern Togo (Amori et al., 2016). Apparently infrequently recorded in Benin, there are records from the Monts Kouffé protected forest in 1978, in bushmeat markets in central Benin in the late 1970s (Sayer and Green, 1984), and from an ecological study undertaken in Lama Forest Reserve in the south in the mid-2000s (Akpona et al., 2008). There are unverified reports from northern Benin (H. Akpona, pers. comm.).

The species occurs in southern Nigeria (Angelici et al., 1999a; Sodeinde and Adedipe, 1994), and Cameroon (Allen and Loveridge, 1942; Jeannin, 1936), Equatorial Guinea (Kümpel, 2006), including Bioko island (Albrechtsen et al., 2007), Gabon (Pagès, 1965, 1975) and Republic of Congo, though published records are dated (Hatt, 1934; Swiacká, 2018; R. Jansen, pers. obs.). There are no records from Chad, but the species occurs across southern Central African Republic and in suitable habitat in Democratic Republic of the Congo (DRC; e.g., Garamba National Park; Monroe et al., 2015; van Vliet et al., 2015). There are records from Burundi and Rwanda (Verschuren, 1987) and Uganda, including in Semuliki National Park (Kityo, 2009; Treves et al., 2010; S. Nixon, pers. comm.). In Tanzania, the species is known from only two locations: the Minziro Forest Reserve on the northwestern border with Uganda, and close to Bukoba (Foley et al., 2014). The extreme eastern distribution comprises southwestern Kenya, including in the Kakamega Forest Reserve (Roth and Cords, 2015). Northern Mozambique has previously been suggested as the species' eastern limit (Smithers and Lobão Tello, 1976), but this has been rejected (Ansell, 1982; Kingdon and Hoffmann, 2013).

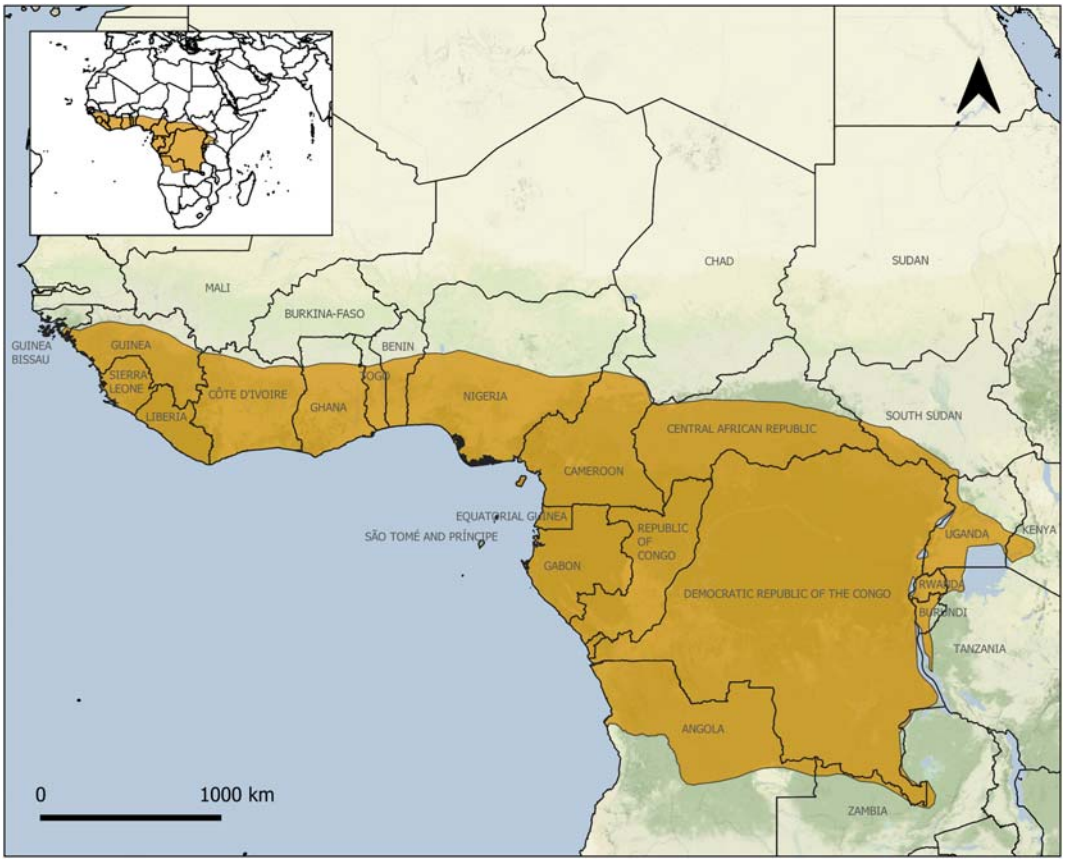

FIGURE 9.4 White-bellied pangolin distribution. *Source: Pietersen et al., 2019.*

To the south, the species occurs in northern Angola, including Cabinda, and there are recent records from Cangandala National Park (Beja et al., 2019; Hill and Carter, 1941). The southern distributional limit has previously been considered Mwinilunga District in northwestern Zambia (Cotterill, 2002) and there have been doubts about the species' occurrence in far south DRC (Schouteden, 1948). However, there are confirmed records from northwestern Zambia (near Solwezi) and central Zambia (Serenje) close to the DRC border from 2016 to 2018 indicating that the species occurs further south than previously recorded (Fig. 9.4; D. Pietersen, unpubl. data).

Habitat

The white-bellied pangolin predominantly inhabits moist tropical lowland forests and secondary forests (Angelici et al., 1999b; Happold, 1987; Kingdon, 1971), but also savanna-forest mosaics, dense woodland (including miombo woodland [*Brachystegia-Julbernardia*]), and riparian forests (Kingdon, 1997). The species also occurs in modified habitats including commercial plantations (e.g., teak [*Tectona grandis*], oil palm), in particular those that are little-used or abandoned, fallows, and farmland (e.g., areas of former lowland rainforest; Angelici et al., 1999b; Sodeinde and Adedipe, 1994). In Benin, Akpona et al. (2008) found no

statistically significant difference in observations of the species between natural forest and plantations, though most individuals (70%) were observed in the former. This study suggested that the species prefers closed forest habitats, and based on the distribution of observed individuals, may be more sensitive to forest age rather than composition (Akpona et al., 2008). In contrast, a study investigating camera trap records across multiple study sites within the species' distribution (Khwaja et al., 2019), estimated a higher probability of occupancy outside of protected areas. Although using a coarse measure of protected status, this supports the notion that the species is adaptable to modified and degraded habitats. Odemuni and Ogunsina (2018) note that particular woody plants such as *Vitex doniana* may influence white-bellied pangolin distribution (e.g., in plantations), as the fruit they bear attracts large quantities of ants.

The occurrence of the species in modified, artificial and degraded landscapes suggests a level of adaptability to these habitats, providing basic needs such as an adequate prey base, suitable den sites, and tolerable levels of exploitation are met. However, use of these habitats, including the ability of the species to persist long-term, and reproduce, has not been well documented. Use of modified habitats, together with associated impacts on distribution and densities, is thus an avenue for future research.

The species is broadly sympatric with the black-bellied pangolin. There is some habitat overlap, but the latter is reported to show a preference for swamp forest (Angelici et al., 2001; Kingdon, 1997), and for arboreal ants, as opposed to termite prey (Chapter 8). Ecological differences between the two species have not been fully elucidated.

Ecology

Elizabeth Pagès pioneered ecological research on tropical African pangolins in the late 1960s and 1970s and much existing knowledge of white-bellied pangolin ecology (and behavior) stems from this research. Pagès (1975) used radio-telemetry and determined that the species occupies home ranges that vary in size and by sex, and may change temporally. Males generally occupy a larger home range (20–30 ha) than females (3–4 ha) and male home ranges, which are mutually exclusive, overlap with those of several (up to 10) females, which may intersect, suggesting a polygynous social structure. Evidence indicates that males are territorial (Pagès, 1975). Females explore only a small portion of their home range each night, in contrast to males that traverse larger sections of their range, including that of several females. Females spend less time foraging than males and cover a smaller area in doing so; Pagès (1975) estimated that females travel a mean of 400 m per night compared to 700 m in males, and males may travel up to 1.8 km a night. Activity is dependent on conditions (e.g., season and weather) and individuals may be active for up to 10.5 hours a night (Pagès, 1975). In Gabon, in the dry season (May–June), females forage, on average, for 5 hours a night, dropping to 2.45 hours in the wet season (January–April); males forage for 6.45 hours a night in the dry season, reducing to 3.45 in the rainy season (Pagès, 1975). This variation is reportedly because prey are more abundant in the wet season (Pagès, 1975). The species appears to follow regular arboreal routes through home ranges and will actively scent-mark using secretions from the anal glands and/or urine (Pagès, 1968).

In Gabon, Pagès (1975) identified two types of burrows used by white-bellied pangolins. The first, used only occasionally, is a burrow of 20–40 cm dug into the soil substrate or frequently into a termite mound, where the animal may feed before resting. The second is a resting place in a tree, such as a tree hollow (e.g., the hollow trunk of a dead tree), which is usually 10–15 m above the ground, in the fork of tree

branches, or curled up amongst epiphytes. In Benin, Akpona et al. (2008) found that most refuges used were in trees and observed a preference for two tree species in particular, velvet tamarin (*Dialium guineneesis*) and kapok (*Ceiba pentandra*) in closed forest. While females will use resting places for extended periods (e.g., weeks at a time), males will use a new site nearly every night (Pagès, 1975).

The species is macrosmatic and uses olfaction to search for arboreal and terrestrial ant nests and termitaria (Pagès, 1975). The nests and termitaria are not destroyed and thereby provide a continuous source of prey. The species will also attack a column of ants traversing a tree trunk or branch and search for prey in dead branches and rotten tree trunks. Due to greater availability, it is likely that terrestrial ants and termites comprise the bulk of the diet (Pagès, 1975). Prey species include army ants (*Dorylus* and *Myrmicaria*), other ant genera including *Camponotus*, *Cataulacus*, *Oecophylla* and *Crematogaster* spp. (Pagès, 1970), and adults and nymphs of the termite genera *Nasutitermes* and *Microcerotermes* (Kingdon, 1971; Pagès, 1975). Leaf-processing mushroom termites (Macrotermitinae) are also preyed upon (Pagès, 1975).

There are numerous predators. White-bellied pangolin remains have been found in leopard (*Panthera pardus*) scat at various sites in Gabon (Henschel et al., 2005, 2011; Pagès, 1970) and other likely predators include African golden cat (*Profelis aurata*), African rock python (*Python sebae*), jackals (*Canis* spp.), ratels (*Mellivora capensis*), chimpanzees (*Pan troglodytes*), large owls, and possibly eagles (Kingdon and Hoffmann, 2013; Pagès, 1970). Ausden and Wood (1990) reported a marsh mongoose (*Atilax paludinosus*) eating the remains of a white-bellied pangolin in Sierra Leone, presumably a random scavenging event on a carcass.

White-bellied pangolins host internal and external parasites. Ticks from the genus *Amblyomma* are associated with the species (Allen and Loveridge, 1942; Ntiamoa-Baidu et al., 2005; Orhierhor et al., 2017) and Sodeinde and Soewu (2016) extracted acanthocephalans belonging to two genera, *Macracanthorhyncus* and *Oncicola*, from the gastrointestinal tract of individuals in Nigeria (see also Chapter 29).

Behavior

Primarily nocturnal, the species is semi-arboreal, spending time on the ground and in the trees (Pagès, 1975) and is less arboreal than the black-bellied pangolin (see Chapter 8). Although solitary, females are observed with young (Fig. 9.5), and Pagès (1965) often found pairs curled up together in tree hollows high off the ground. In Gabon, the species was recorded foraging mostly on the ground (Pagès, 1975), in contrast to Benin, where Akpona et al. (2008) observed the opposite – the species foraging largely in trees in a semi-deciduous forest. The same variation is apparent in DRC. In Lomami National Park, the species was detected most frequently on the ground at the edge of regenerating garden plots in forest adjacent to villages in the buffer zone, but were detected more often in the canopy in forest within the park's interior (D. Alempijevic, unpubl. data).

White-bellied pangolins spend most of the day sheltering in tree hollows, in the forked branch of a tree, or curled up amongst epiphytes. They are active nocturnally, devoting most of their active time to foraging for prey. However, they have been observed active diurnally (Jones, 1973). Pagès (1975) found that females and juveniles were active between 1900 and 2130, with males active over a wider interval, up until 0400 on occasion (Pagès, 1975). Camera trap studies in the Dja Biosphere Reserve, Cameroon found the species was active between 2000 and 0400 over 100 camera trap nights (ZSL, unpubl. data). In Lomami National Park, the species was recorded by video and was active between 1800 and 0500, with peak activity at 0300 (D.

FIGURE 9.5 White-bellied pangolin juvenile being "taxied" around on its mother's tail in Cameroon. *Photo credit: Jiri Prochazka/Shutterstock.com.*

Alempijevic, unpubl. data). Conspecifics were never recorded together, with the exception of a female carrying its offspring (D. Alempijevic, unpubl. data).

Generally quadrupedal, the species uses all four limbs for locomotion on the ground and in trees, and is an excellent climber. When walking most weight is taken on the hind legs, but all four feet are placed palm downwards (Kingdon, 1971). This contrasts with the giant and Asian pangolins where weight is taken on the margins of the forefeet. Hatt (1934) reports that the species' articulation and movement is fast for a pangolin; Pagès (1970) reports that white-bellied pangolins move at speeds of 1–1.5 km/h. When climbing, the fore- and hindlimbs move as pairs and the prehensile tail, with its sensitive distal pad, acts as a fifth limb, searching for and wrapping around branches – this movement resembles that of a caterpillar (Hatt, 1934; Pagès, 1970). There is enormous strength in the tail, which can serve as a counterweight, and can support the species' body weight enabling foraging to take place on the underside of tree branches and is generally used for support when climbing (Hatt, 1934; Pagès, 1965, 1970; D. Alempijevic, pers. obs.). When climbing large trees, the body is pressed against the tree trunk and the flat, ventral surface of the tail and the pointed scales along the tail margins take the animal's weight. Pagès (1965) reports that the species "spirals" down

large tree trunks, taking the weight on the tail as it goes. Grubb et al. (1998) suggest that white-bellied pangolins may roll into a ball when in trees before dropping to the ground, potentially as a means of evading a threat.

The white-bellied pangolin has poor vision (except in close proximity) but excellent olfactory senses; on locating an ant nest or termitaria the clawed forefeet are proficient at tearing them apart, and the long tongue, which is coated in a very sticky mucous-like saliva, is used in a rapid "protrude and withdraw" motion to ingest prey (Heath, 2013; Kingdon, 1971). Pagès (1975) noted that the species consumes prey in small successive quantities invariably without digging. Kingdon (1971) reports that the species will shiver the scales in order to loosen ants or termites clambering over the body, and erect and depress the scales to dislodge prey, both actions facilitating subsequent consumption of said prey.

Scent-orientated, the species displays scent-marking behavior, using a combination of urine and secretions from the anal glands (Pagès, 1968). In Lomami National Park, DRC, scent-marking was recorded in 26% of observations in the mid-high canopy (>9 m height) but never in the understory or on the ground during a multi-strata camera trap study (D. Alempijevic, unpubl. data). This behavior entailed individuals walking along a branch, then stooping to place the rear-end of the body directly on the branch, the hind legs dangling down either side, and then scooting along for the length of 3–4 paces, presumably while releasing urine or scent from the anal glands; alternatively individuals would place their entire ventral surface on a branch and slide along; in both cases the behavior is presumably to smear the scent further (D. Alempijevic, unpubl. data). In captivity in Gabon both males and females scent-marked at the base of trees and at numerous points on the tree trunk, on branches, and at the fork of branches (Pagès, 1968).

The species is sensitive to sounds and vibration and when threatened either climbs a nearby tree or curls up into a tight ball. Although protected by the armor of scales, white-bellied pangolin scales are not as thick and robust as in other species of pangolin and are insufficient against some predators (e.g., leopard). The species' preference for dense vegetation likely offers some protection from detection by larger predators (Kingdon and Hoffmann, 2013); if detected they likely respond by releasing repulsive secretions from the anal glands and potentially defecating and urinating (Kingdon, 1971). The species is an able swimmer, adopting a "doggy-style" paddling approach and using body undulations to move through the water; the tail is not used but hits the water regularly (Pagès, 1970).

Ontogeny and reproduction

Breeding is continuous. In Gabon, adult females found were seldom not pregnant (Pagès, 1965, 1972a, 1975). Tahiri-Zagret (1968) estimated a mean estrus cycle at 9 days but this was highly variant (range: 3–29 days). Males will seek out females using scent trails, and sexual behavior is reportedly elaborate. Males and females simulate aggression, including standing chest to chest, before the female submits, and prior to mating, the pair move to a tree; during copulation the male and female's tail are intertwined (Pagès, 1972b). The species usually gives birth to one young at parturition; twins are thought to be rare. The gestation period has been estimated at 140–150 days (Pagès, 1972a). However, observations of captive white-bellied pangolins at Brookfield Zoo in the United States suggest a gestation period of around eight months (~209 days; Kersey et al., 2018). This suggests the possibility of delayed embryo implantation or embryonic diapause, where the embryo is implanted into the uterus only under favorable conditions

(e.g., when prey is abundant). Considerable variation in gestation period has been observed in other species of pangolin (e.g., Chinese pangolin [*Manis pentadactyla*]) and requires further research. Post-partum estrus occurs 9–16 days after parturition (Pagès, 1972a).

At birth, neonates weigh ~100 g (Menzies, 1967) and are ~290 mm in length (Hatt, 1934), and well developed (Kingdon, 1971). The skin is pink and young individuals are hairless, except a ring around the eyes; the hair starts to become visible three weeks after birth (Rahm, 1956). As with other pangolins, the mother will sleep curled around the young, which aids in nursing, but at night will leave for short periods in order to forage for prey (Kingdon, 1971). In the first week after birth females, in estrus, leave the young and mate again and are pregnant for nearly the entire period of maternal care (Pagès, 1972a). The offspring will accompany the mother to forage as it grows and will be "taxied" around on the base of the mother's tail (Fig. 9.5). The age at which young white-bellied pangolins start predating on ants and termites is not known, but in captivity one young animal displayed interest in solid food at five weeks old (Menzies, 1967). Young are likely to become independent at 3–5 months old (upper limit 6 months), which may coincide with the next parturition. Sub-adults are errant and wander over large areas until a home range is established; they reach adult size by ~18 months old (Pagès, 1972a). Longevity in the wild is not known. In captivity, an individual at San Diego Zoo lived to an estimated 10 years of age.

Population

The most frequently encountered African pangolin species but apparently uncommon across its range. There are few quantitative data on white-bellied pangolin abundance and no population estimates exist at the site, national or global level. In the Lama Forest Reserve, Benin, Akpona et al. (2008) estimated a density of 0.84 individuals/km^2 during the dry season in natural forest and monoculture plantation. A review of Afrotropical forest mammals suggested a density of 10.9 individuals/km^2 (Fa and Purvis, 1997), but this would seem to be an overestimate based on a small sample size and inferred density. Based on observations in secondary growth forest in Uganda, Kingdon and Hoffmann (2013) suggest the species occurs at relatively high densities in suitable habitat. In contrast, Laurance et al. (2006) found that pangolins increased in abundance outside of protected oil concessions in Gabon, possibly in response to greater forest disturbance within concessions. In a multistrata camera trap study in Lomami National Park, DRC, 74 records of the species were accumulated over 14 months (7499 camera trap nights) between 2016 and 2018, with the highest detection frequency on the ground in the buffer zone; in the forest interior the detection frequency was highest in the canopy (15–30 m; D. Alempijevic, unpubl. data).

Most other accounts suggest that the species is declining. In Ghana, hunters in villages in the Ashanti region of the Upper Guinea Forest Ecosystem reported in 2011 that white-bellied pangolins were rare (Alexander et al., 2015), though they were considered common by more than 70% of hunters ($n = 35$) in the Akposa Traditional Area in the Volta Region (Emieaboe et al., 2014). In southern Benin, hunters considered the species to be rare in 2007–2008 (Djagoun and Gaubert, 2009). Soewu and Adekanola (2011) reported that the majority of traditional medicine practitioners of the Awori people in Ogun State, Nigeria believe that populations are declining, and inferred a decline in the size of individuals caught. In southwestern Nigeria, hunters have reported that the species is increasingly rare (Sodeinde and Adedipe, 1994). In Uganda, the white-bellied pangolin is thought to be

declining rapidly (Kityo et al., 2016), and declines have been reported for Ghana and Guinea (Bräutigam et al., 1994).

Status

The white-bellied pangolin is categorized as Endangered on The IUCN Red List of Threatened Species (Pietersen et al., 2019). The species was assessed as Endangered in Uganda in 2016 using the IUCN Red List Categories and Criteria (Kityo et al., 2016). No other national or regional assessments have been undertaken. There is a recognized lack of data on populations at all levels (site, national and global) and addressing this is a research priority (see Chapter 34). The species is afforded protection through national legislation in most range states: in some range countries the species is fully protected which prohibits exploitation. In Gabon, Republic of Congo, and Sierra Leone, the species may be hunted and traded legally subject to specific conditions, including that a permit is acquired from the relevant authorities. The species is not afforded legislative protection in Burundi, Kenya or Liberia (Challender and Waterman, 2017). Like other pangolins, this species is included in CITES Appendix I.

Threats

The main threats to the white-bellied pangolin are anthropogenic and comprise habitat destruction and alteration, and overexploitation for local and international use, including international trafficking to Asia.

The destruction, transformation and degradation of natural tropical forest across West and Central Africa has likely been the biggest threat to the white-bellied pangolin historically, and remains present (Megevand, 2013; Ofori et al., 2012). In parts of the species' range (e.g., Côte d'Ivoire and Ghana) loss of natural forest cover has been extremely high (Achard et al., 2014; Megevand, 2013). This is a consequence of logging activities, the establishment of agricultural crops (including shifting agriculture) and monoculture plantations (e.g., oil palm and cocoa [*Theobroma cacao*]), and a rapidly growing human population and urban development, which increases proximity to natural areas, and access to pangolin habitat (Mayaux et al., 2013; Sodeinde and Adedipe, 1994). Although white-bellied pangolins appear able to adapt to some degree of habitat modification, this has not been fully elucidated and further research is needed, in particular comparative ecological studies between natural and modified habitats, and the ability of the species to persist in such habitats long-term (Akpona et al., 2008; Sodeinde and Adedipe, 1994).

Unsustainable and intensive exploitation for local use and international trafficking is a major threat. The species has been used throughout human history as bushmeat and is sold in high numbers at bushmeat markets and roadsides, and traded for medicinal use (see Chapter 15). Fa et al. (2006) reported white-bellied pangolins to be the fourth most abundant species in bushmeat markets in Cameroon between 2002 and 2003. Boakye et al. (2016b) recorded 341 pangolins illegally traded between September 2013 and January 2014 in five regions of Ghana, 82% of which were white-bellied pangolins. Ingram et al. (2018) estimated that in Central Africa alone between 0.42 and 2.71 million pangolins (most likely 0.42 million) were harvested annually between 1975 and 2014, primarily involving the white-bellied pangolin, and that exploitation appears to be increasing. As a proportion of overall hunting catch, pangolins increased significantly from 0.04% in 1972 to 1.83% in 2014, and annual pangolin catch increased by ~150% pre- (1975–1999) and post-2000 (2000–2014; Ingram et al., 2018). This corroborates earlier research, which estimated annual offtake in the region to involve ~425,000 pangolins annually, the majority of which likely

comprised white-bellied pangolins (Fa and Peres, 2001). This trade drives exploitation of the species. Fa et al. (2006) reported that white-bellied pangolins were the fourth most harvested species across 47 sites in Cameroon between 2002 and 2003. Kümpel (2006) found similar results in Equatorial Guinea. The retail price of smaller African pangolins in urban markets in parts of West and Central is reportedly increasing, and more than doubled between 1993 and 2014 (Mambeya et al., 2018), and may reflect increasing demand or increasing rarity (Ingram et al., 2018).

Various body parts of the white-bellied pangolin are used in traditional medicine, which drives harvest of the species (see Chapter 15). In Benin, Djagoun et al. (2012) found that 26.4% of medicinal traders surveyed sold white-bellied pangolin parts. Sodeinde and Adedipe (1994) reported that traditional medicines practitioners in southwestern Nigeria, when using pangolins, used this species exclusively (see Chapter 15).

There has been limited international trade in white-bellied pangolins reported to CITES historically, especially compared to the Asian species. However, trade dynamics changed in the 2010s and international trafficking is a major, contemporary threat. Prior to 2000, international trade largely comprised small numbers of live animals (Challender and Waterman, 2017). The 2010s saw the advent of international trade in commercial quantities of white-bellied pangolin scales (involving ~7000 animals between 2013 and 2016) that were mainly exported from DRC and Republic of Congo to China, and animals reportedly exported for commercial captive breeding purposes (Chapter 16). This decade also saw the emergence of intercontinental trafficking of African pangolin scales to Asia, in particular from the Gulf of Guinea (Ingram et al., 2019). Estimates suggest that between 2000 and July 2019, international trafficking involved scales from more than 500,000 African pangolins, mainly between 2015 and 2019, the majority of which were likely from white-bellied pangolins (see Chapter 16).

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