Home range, habitat selection and activity patterns of an arid-zone population of Temminck's ground pangolins, *Smutsia temminckii*

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All previous behavioural studies of Temminck's ground pangolins (*Smutsia temminckii*) have focused on populations in mesic regions. We examined home range size, activity periods, habitat selectivity and refuge site selection of 13 individuals over three years in the Kalahari Desert of South Africa, near the western edge of the species' range. Kernel home ranges of adults averaged 6.5 ± 5.9 km², while juveniles had average home ranges of 6.1 ± 4.0 km². Reliable prediction of 95% of the Kernel home range required 88 ± 67.7 tracking days. No significant habitat selectivity was observed. Earthen burrows were the most frequently used refuge type. The time at which activity commenced varied seasonally as well as among individuals, with an increase in diurnal activity during winter. Young pangolins also displayed more diurnal activity compared to adults. Individuals spent 5.7 ± 2.0 hours per 24-hour cycle outside of refuges, with no significant seasonal variation. Juvenile dispersal peaked during mid-summer, with individuals travelling up to 49 km from their natal areas. We estimate a breeding density of 0.16 individuals/km² and a total density of 0.31 individuals/km² for our study area. Our data suggest that activity patterns, movements and refuge selection is similar across the species' southern African range, but that densities may be higher in the Kalahari compared to populations in more mesic eastern areas.

Key words: *Smutsia temminckii*, *Manis temminckii*, home range, habitat selection, densities.

INTRODUCTION

Pangolins (Pholidota: Manidae) are unique mammals with bodies covered in hard, keratinous scales rather than hair (Heath & Coulson 1997a; Richer *et al.* 1997). There are eight species worldwide, four of which occur in Africa whereas the remaining four species are restricted to the Indomalayan region (Gaudin *et al.* 2009). Only Temminck's ground pangolin, *Smutsia temminckii*, occurs in southern Africa, the remaining three Afrotropical species being restricted to forests and forest-savanna mosaics in Central and West Africa (Heath 1992; Gaudin *et al.* 2009).

Temminck's ground pangolin (hereafter, pangolin) is a seldom-seen, predominantly solitary species (Sweeney 1956) that occurs at low population densities (Sweeney 1956; Heath 1992; Heath & Coulson 1997a) and is considered rare and threatened (Challender 2011; Challender & Hywood 2012; Pietersen *et al.* 2014a). It is widely distributed in savannas and woodlands in southern and East Africa, at latitudes from 29°S in South Africa (excluding the central Highveld) northwards to Chad and southern Sudan (Heath 1992; African Pangolin Working Group, unpubl. data). The species is predominantly nocturnal (Wilson 1994; Gaubert 2011) or crepuscular (van Aarde *et al.* 1990; Jacobsen *et al.* 1991) although some authors have reported limited diurnal activity (Smithers 1971; Smithers & Wilson 1979; Coulson 1989; Jacobsen *et al.* 1991; Swart 1996; Heath & Coulson 1997a; Richer *et al.* 1997). Pangolins are entirely myrmecophagous and selective in terms of prey species (Jacobsen *et al.* 1991; Swart 1996; Richer *et al.* 1997; Swart *et al.* 1999; Pietersen 2013) and their distribution is thought to closely mirror that of their ant and termite prey (Swart *et al.* 1999; Pietersen 2013).

Patterns of circadian activity and home range size vary among studies. Some authors (van Aarde *et al.* 1990; Jacobsen *et al.* 1991) report a crepuscular

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peak in activity, while Swart (1996) attributes this apparent peak to observer bias rather than a real increase in activity. Home range size also varies considerably between Zimbabwe (0.2–23.4 km^2; Heath & Coulson 1997a) and South Africa (1.3–7.9 km^2; van Aarde *et al.* 1990). There also appears to be variation between sexes, with males having larger home ranges (Heath & Coulson 1997a).

When inactive, pangolins shelter in abandoned animal burrows, in caves, between rocks or in piles of debris (Jacobsen *et al.* 1991; Heath 1992; Heath & Coulson 1997a). Refuges are used predominantly for protection and during parturition (Jacobsen 1991; Swart 1996) although a recent study suggests that burrows may also provide thermally-buffered microclimates facilitating energy savings through reduced costs of thermoregulation (Pietersen 2013).

Temminck's ground pangolin is listed as *Vulnerable* by the IUCN (Pietersen *et al.* 2014a) and in light of the growing number of threats facing this species (Pietersen *et al.* 2014b) it is vitally important to understand its ecological requirements in order to develop a comprehensive conservation management plan. All previous studies of Temminck's ground pangolin have focussed on populations inhabiting mesic savannas in eastern South Africa (van Aarde *et al.* 1990; Jacobsen *et al.* 1991; Swart 1996; Swart *et al.* 1999) and Zimbabwe (Coulson 1989; Heath & Coulson 1997a,b, 1998; Richer *et al.* 1997), and data for populations in arid environments are currently lacking.

The aims of this study were to (1) quantify age- and sex-specific variation in pangolin home ranges; (2) determine habitat preference or selectivity; (3) quantify daily and seasonal patterns of activity; (4) determine refuge site preferences; and (5) estimate dispersal ability.

METHODS

Study site

Kalahari Oryx Private Game Farm is a 52 000 ha farm situated in the Kalahari biome of the Northern Cape Province in South Africa, between latitudes 28°21′S–28°42′S and longitudes 21°55′E–22°15′E (Fig. 1). The study site is at the arid western edge of the pangolin's distribution in South Africa (Heath 1992; Pietersen *et al.* 2014a; Fig. 1).

Study animals and telemetry fitting

Thirteen pangolins were monitored between October 2009 and October 2012, after being located by following fresh tracks or through chance encounters. Once located, a very high frequency (VHF) transmitter (Africa Wildlife Tracking, Pretoria, South Africa) was attached to a single median dorsal scale at the level of the pelvis and secured with two 3-mm machinery bolts and Pratley® Quickset Epoxy. Holes were drilled in the non-vascularized portion of the scale and the bolts inserted from beneath to ensure a flush fit and avoid potential injuries to the animal (van Aarde *et al.* 1990; Jacobsen *et al.* 1991; Swart 1996). Animals were not anaesthetized during transmitter attachment as the procedure was of relatively short duration and the non-vascularized portion of the scale lacks nerve endings. The exposed nuts and any gaps between the transmitter and scale were sealed with Pratley® Quickset Putty to prevent vegetation snagging or pangolin mites (*Manitherionyssus heterotarsus* Vitzthum) sheltering under the transmitter. All pangolins were released at their sites of capture. The VHF transmitters, including the Pratley® Quickset Putty, weighed 100–120 g, representing ≤4% of body mass.

Spatial data

Study individuals were located daily or once every three days, and their location recorded with a handheld Global Positioning System (GPS) receiver (GPS V, Garmin, Kansas, U.S.A.) with a stated accuracy of 4–7 m. Focal individuals were followed from the time that they were located until they retired to their refuge for the night to determine diet (Pietersen *et al.*, in prep.). Spatial data were downloaded using DNR Garmin 5.04 software (Minnesota Department of Natural Resources, Minnesota, U.S.A.) and plotted in Arc-View GIS 3.2 (Environmental Systems Research Institute, Redlands, California, U.S.A.). Four pangolins were fitted with custom-designed GPS loggers (Ecotone, Poland) to determine fine-scale movements after an initial VHF tracking period of one month suggested that they were resident and unlikely to disperse beyond the study area. The GPS loggers weighed 200 g each and were only used on individuals weighing more than 6 kg. The GPS loggers were programmed to record locations every hour, taking six locality readings in rapid succession to improve accuracy. GPS logger accuracy was assessed by comparing the logger-recorded localities to coordinates of known locations, which indicated that loggers were accurate to within 20 m, and often to within ≤10 m. GPS logger data were downloaded in
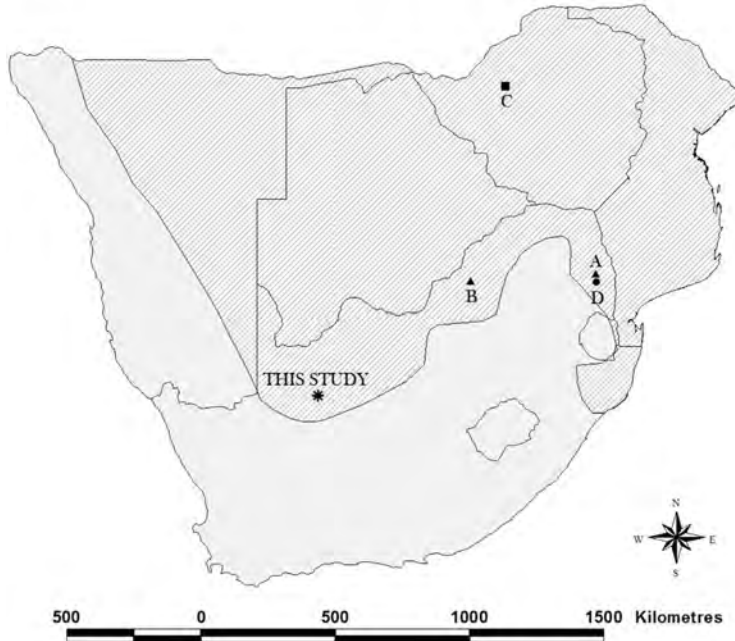
Fig. 1. Location of the present study in relation to previous pangolin research and the distribution of pangolins in southern Africa (shaded region). (**A**) Hans Hoheison Wildlife Research Station and (**B**) Thabazimbi: van Aarde *et al.* (1990), Jacobsen *et al.* (1991); (**C**) Sengwa Wildlife Research Station: Heath & Coulson (1997a,b, 1998), Richer *et al.* (1997); and (**D**) Sabi Sand Game Reserve: Swart (1996), Swart *et al.* (1999).

the field with an Ecotone Remote Download Base Station and transferred to a personal computer.

Home ranges

GPS logger spatial data were visualized in Google™ Earth prior to being converted to Arc-View format using DNR Garmin 5.04. Outlying records were visually identified and removed prior to analysis and duplicate coordinates removed, so that only one of the six coordinates recorded each hour were retained in order to ensure that no artificial weighting of localities occurred. Spatial data recorded with the handheld GPS did not require editing. Co-ordinates were converted to Universal Transverse Mercator prior to analyses, using the software program Ranges 7 v. 2.9 (Anatrack Ltd., Wareham, U.K.). Three measures of home range were calculated for each individual: Minimum Convex Polygon (MCP), 95% Harmonic Mean (using default settings) and 95% Kernel (using default settings). Kernel home range calculations most likely reflect the true home range extent as MCP calculations include all data points, including outliers, and thus do not reflect the core regions most frequently used by the animals (Seaman & Powell 1996). Likewise,

Harmonic Mean home range estimates are highly sensitive to outlying data points and thus result in the inclusion of many additional grid points (i.e. area) that are not used by the animal (Seaman & Powell 1996). Hence, both MCP and Harmonic Mean analyses tend to overestimate home range size whereas Kernel analyses are well-defined and more precise and thus provide a better estimate of home range extent (Seaman & Powell 1996). However, as MCP is the most often used measure of home range size, both MCP and Kernel home range characteristics were investigated. All values are presented as mean ± S.D.

Incremental Area Analyses were performed on the Kernel home range data to determine the number of localities required to predict the 95% core home range, by sequentially adding spatial data to an individual's home range plot and recording the number of records required to predict the core home range. Seasonal differences in home range size were assessed by assigning spatial data for each individual to either the austral summer (November–February) or winter (May–August). Data were analysed using GraphPad InStat v 3.0 (GraphPad Software, San Diego, California, U.S.A.).

Table 1. Vegetation types present on Kalahari Oryx Private Game Farm, classified according to geology and physiognomy. The corresponding Mucina & Rutherford (2006) vegetation community is indicated.

Vegetation type	Physiognomy	Mucina & Rutherford community(ies)
Grassy Dwarf Shrubland	Flat, calcareous plains. Vegetation is of Karroid origin and <0.4 m in height. A moderate amount of bare ground, especially where over-utilized.	Kalahari Karroid Shrubland (NKb 5)
Dwarf Karroid Shrubland	Flat landscape with calcareous soils and Karroid vegetation that is <0.5 m in height. There is a preponderance of bare ground.	Gordonia Plains Shrubland (SVk 16) Olifantshoek Plains Thornveld (SVk 13)
Acacia mellifera–Rhigozum trichotomum veld	Flat areas on shallow red sands overlying calcrete. Moderate clay content resulting in this being a sweetveld, with concomitant high levels of overutilization and invasion by *Rhigozum trichotomum*. *Acacia mellifera* is the dominant tree.	Olifantshoek Plains Thornveld (SVk 13) Kalahari Karroid Shrubland (NKb 5)
Acacia erioloba veld	Sandy soils with higher clay content, typically at the base of mountains. Trees vary from 2–6 m in height, with medium to high grass cover. Dominated by *Acacia erioloba*.	Olifantshoek Plains Thornveld (SVk 13)
Acacia mellifera thickets	Dense to open *Acacia mellifera* savanna with moderate grass cover on sandy soils with intermediate clay content. Typically found between *Acacia erioloba* veld and mixed savanna.	Gordonia Duneveld (SVkd 1) Olifantshoek Plains Thornveld (SVk 13)
Acacia haematoxylon savanna	Undulating duneveld on sandy soils. Low tree density and high grass cover; trees usually 2–3 m in height. *Acacia haematoxylon* is normally the only tree in this landscape.	Gordonia Duneveld (SVkd 1) Olifantshoek Plains Thornveld (SVk 13)
Mixed savanna	Undulating duneveld with a high proportion of grass cover and moderate levels of tree and shrub cover. Various tree and shrub species dominate, including *Boscia albitrunca*, *Acacia mellifera*, *Acacia erioloba*, *Acacia haematoxylon*, *Grewia flava* and *Ziziphus mucronata*.	Gordonia Duneveld (SVkd 1) Olifantshoek Plains Thornveld (SVk 13)
Duneveld grassland	Flat to undulating duneveld on sandy soils, nearly devoid of trees and shrubs.	Gordonia Duneveld (SVkd 1)
Mountain Veld	The most diverse vegetation type, restricted to rocky ridges and mountains. Clay content is high. Rock cover is high (50–60%) and vegetation cover between rocks is nearly absolute.	Koranna-Langeberg Mountain Bushveld (SVk 15)

Habitat selectivity

Vegetation at the study site was categorized into nine types based on dominant plant species, structure and geology (Table 1). Habitat selectivity was quantified with a modified selectivity index *S* (McNaughton 1978):

$$S_j = \Sigma |P_{Hi} - P_{Li}|/2$$

where P_{Hi} is the proportional abundance of the *i*-th habitat in the study area and P_{Li} is the proportional abundance of locality records in the *i*-th habitat for pangolin *j*. An *S*-value of zero denotes no habitat

selectivity, whereas a value of 1.0 denotes maximum habitat selectivity. Seasonal differences in habitat selection were assessed by assigning an individual's spatial data to either the austral summer (November–February) or winter (May–August).

Duration of activity and emergence times

The times at which pangolins emerged from and returned to their refuges were determined for three individuals fitted with GPS loggers. The loggers were able to record geographic locations only when above ground, and thus the first recorded position for each day occurred within one hour of the study animal emerging. The loggers provided an unbiased record of emergence and return times as data were recorded in the same manner for all individuals and were not influenced by the presence of an observer. Because locations were recorded hourly, emergence times were likewise assigned to 1-hour bins based on the 24-hour clock (00:00 represents 00:00–00:59, 01:00 represents 01:00–01:59, etc.). When study animals rested in exposed sites continuous hourly data collection continued, these data being discernable as a cluster of successive points confined to a very small area. In these instances the earliest datum in the cluster was regarded as the return time of the previous day and the first datum outside of this cluster was considered the emergence time of the following day. Mean duration of activity (the time spent out of the refuge within each 24-hour cycle) was calculated from the time between emergence and return. Multiple regression analysis was performed on the emergence times using GraphPad InStat v 3.0 to determine whether emergence time was affected by ambient air temperature.

Refuge sites

Study animals were regularly located while inactive, or followed until they entered a refuge at the end of a foraging bout. The location and nature of each refuge was recorded using a handheld GPS unit. Refuges that were re-used by the same or different individual on subsequent occasions were recorded as such.

RESULTS

Home ranges

Home ranges were estimated for seven adult (≥6 kg) and six juvenile (<6 kg) pangolins, of which two and three individuals, respectively, had fewer than 50 locations each and were excluded from statistical analyses. Home range size varied depending on the length, and hence age, of individuals (Table 2). Mean MCP and Kernel home ranges for adults (males and females combined) were 10.0 ± 8.9 km^2 and 6.5 ± 5.9 km^2, respectively, whereas juveniles (both sexes combined) had smaller mean MCP and Kernel home ranges of 7.1 ± 1.1 km^2 and 6.1 ± 4.0 km^2, respectively. The degree of home range overlap could be determined for two adult pairs: the respective home ranges of STEM 22 and STEM 35 overlapped by 12.7%, while the home range of adult male STEM 38 was entirely encompassed by the home range of adult female STEM 5.

Only two adult individuals (STEM 5 and STEM 38) had sufficient locality data to compare seasonal differences in home range size. Seasonal trends in these two individuals were opposite in direction, with the female using a larger area in summer and the male using a larger area in winter (Fig. 2).

The incremental area analysis indicated that four adult and two juvenile pangolins had additive home range graphs that reached a plateau, suggesting that additional points were unlikely to significantly alter the estimated home range size. Analysis of these data indicated that 88 ± 67.7 locations (i.e. tracking days) were required to predict 95% of the Kernel home range at this study site.

Densities

The maximum kernel home range sizes of adult male and female pangolins at the study site were 11.91 km^2 and 13.76 km^2, respectively. Thus the average maximum home range size for a pair of pangolins was 12.8 km^2, suggesting a density of 0.16 reproductively active adult individuals/km^2. In addition to the breeding pair, each home range also supported the most recent offspring. Field observations also suggested that each home range regularly supported a transient individual, although the period that it remained within the home range varied considerably and could not always be reliably determined. Thus the overall density of pangolins at the study site was approximately 0.23 individuals/km^2 (including offspring) but may be as high as 0.31 individuals/km^2 if transient individuals are included.

Habitat selectivity

An analysis of five adult and six juvenile pangolins' home ranges indicated that there was no apparent habitat selectivity (Table 3). Only one

Table 2. Three measures of home range size for seven adult (≥6 kg) and six juvenile (<6 kg) pangolins. The number of observations corresponds to the number of geospatial locations used to calculate home range size. Animal IDs marked with asterisks indicate individuals for which a 95% Incremental Area Analysis indicated that stationarity had been reached and that the entire home range had thus likely been mapped. Duration of tracking is the total period over which an individual was monitored.

Animal ID	Age	Sex	Average mass (kg)	Number of observations	Minimum convex polygon (km²)	95% Harmonic mean (km²)	95% Kernel (km²)	Duration of tracking (days)
STEM 5*	Adult	Female	9.7	210	23.90	10.98	13.76	1111
STEM 20*	Adult	Female	7.7	43	3.40	0.33	2.45	182
STEM 22*	Adult	Female	7.1	82	3.95	0.85	2.67	362
STEM 39	Adult	Female	6.8	128	1.45	0.73	0.69	90
STEM 40	Adult	Female	6.2	18	1.92	0.03	2.60	148
STEM 35	Adult	Male	10.0	53	12.89	2.81	11.91	426
STEM 38*	Adult	Male	7.5	241	7.63	4.93	3.32	456
STEM 19*	Juvenile	Female	3.5	51	6.94	1.26	8.50	202
STEM 70	Juvenile	Female	2.8	18	1.99	0.08	2.49	82
STEM 18*	Juvenile	Male	4.4	98	8.34	1.70	8.37	579
STEM 21	Juvenile	Male	2.6	10	0.90	0.01	2.61	9
STEM 23	Juvenile	Male	3.8	90	1.29	0.69	1.11	225
STEM 46	Juvenile	Male	3.3	24	0.20	0.02	0.07	45

adult male (STEM 38) and one adult female (STEM 5) had sufficient locality data to investigate seasonal differences in habitat selectivity, with neither individual showing any seasonal preferences (Table 3).

Duration of activity

Emergence and return times from refuges (Fig. 3) varied among individuals and across seasons. There was a tendency for earlier emergence times in winter compared to summer, with a concomitant increase in the proportion of diurnal activity during winter. Juveniles were also observed to be more prone to diurnal activity than adults, whereas both age classes were more diurnal during cold weather. Emergence time was highly dependent on air temperature, with minimum temperature ($t = 2.701$, $P = 0.008$, d.f. = 175) a statistically stronger predictor than maximum temperature ($t = 2.121$, $P = 0.035$, d.f. = 175). Emergence times were unaffected by the lunar cycle (data not shown).
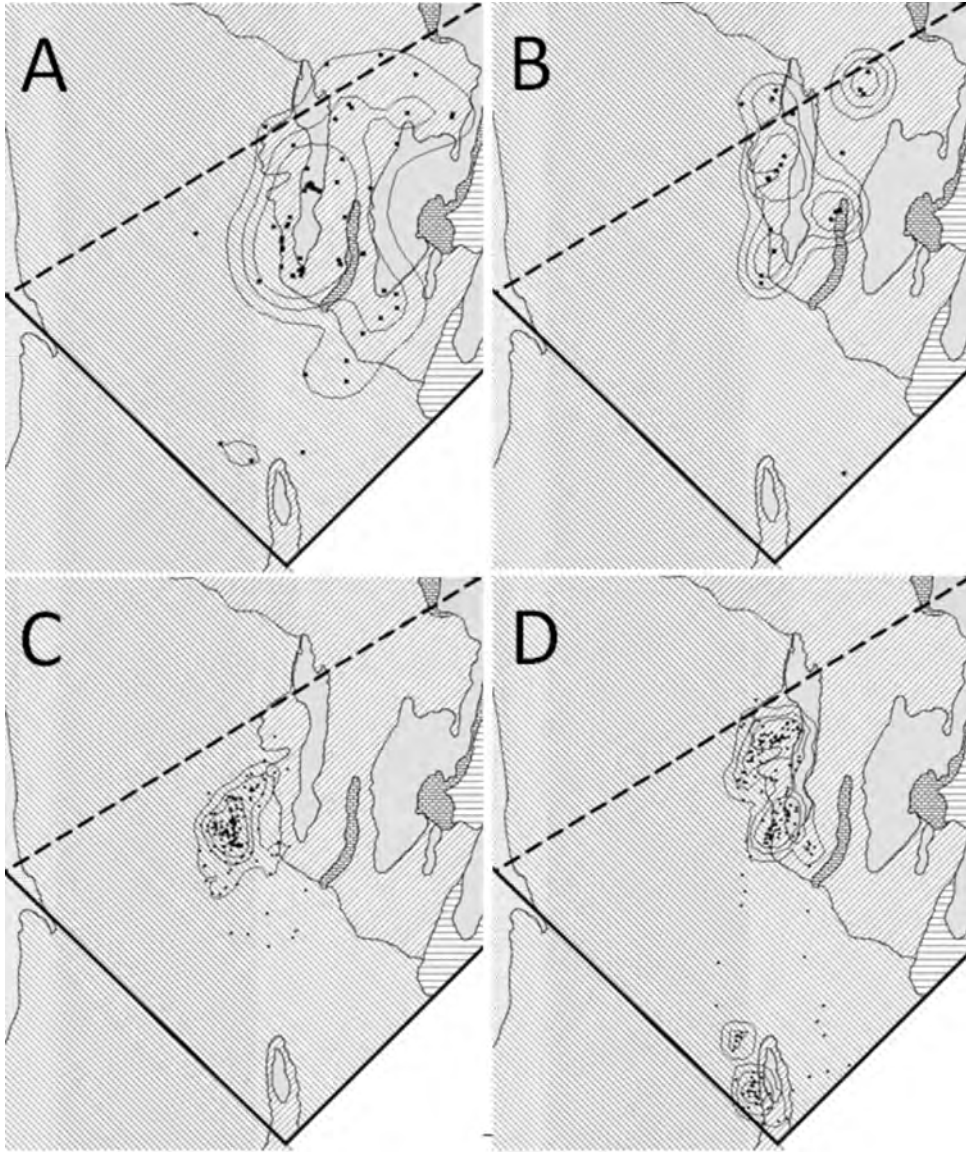
The mean daily duration of activity was 5.7 ± 2.0 hours, ranging from 1–12 hours. The total duration of activity did not differ between winter and summer, although individuals typically became active earlier in winter. Mean winter daily foraging periods were 5.6 ± 1.6 hours (range 2–10 hours) whereas mean summer foraging periods were 5.7 ± 2.2 hours (range 1–12 hours).
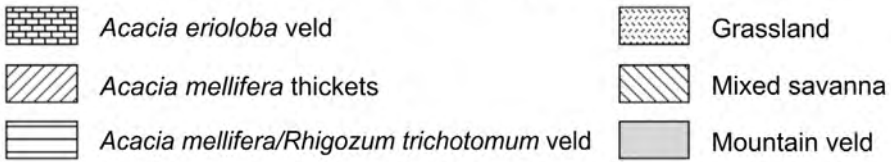
Refuge sites

Pangolins were recorded using refuges on 492 occasions during this study (Table 4). Burrows, especially those excavated by aardvark (*Orycteropus afer*), were the most favoured refuge type (89.8%, $n = 442$). Only juvenile pangolins used vegetation as cover and were also more likely to take refuge among rocks. Only one adult, a dispersing male (STEM 31), was observed excavating its own burrow, which was <1 m in depth. Refuge selection did not differ significantly between adults and juveniles (Student's t-test $t = 0.005$, $P = 1.0$, d.f. = 7).

Dispersal

Dispersal was defined as young animals leaving their natal home range without returning to it within the study period, or older individuals that were not resident in any particular area indicating that they had no fixed home range. Four individuals were observed dispersing during this study. A young female (STEM 19, 3.5 kg) that was tagged in

Vegetation types

Acacia erioloba veld		Grassland
Acacia mellifera thickets		Mixed savanna
Acacia mellifera/Rhigozum trichotomum veld		Mountain veld

Fig. 2. Summer (Nov–Feb) and winter (May–Aug) home ranges for an adult female (STEM 5) and adult male (STEM 38) pangolin on Kalahari Oryx Private Game Farm. **A**, STEM 5 summer home range (n = 61 observations); **B**, STEM 5 winter home range (n = 24 observations); **C**, STEM 38 summer home range (n = 154 observations); **D**, STEM 38 winter home range (n = 210 observations). The 50th, 75th and 95th percentile Kernel home ranges are displayed for each season. Solid dark lines show electrified game-proof fences; the dashed dark line indicates an electrified fence that was removed during this study.

Table 3. Habitat selectivity values for 12 pangolins on Kalahari Oryx Private Game Farm. A value of zero represents no habitat selectivity, whereas a value of one represents maximum habitat selectivity.

Animal ID	Overall selectivity	Summer	Winter
STEM 35	0.122	–	–
STEM 5*	0.182	0.164	0.247
STEM 20*	0.155	–	–
STEM 38*	0.075	0.067	0.142
STEM 22*	0.142	–	–
STEM 39	0.370	–	–
STEM 18*	0.322	–	–
STEM 23	0.068	–	–
STEM 19*	0.122	–	–
STEM 46	0.046	–	–
STEM 70	0.203	–	–
STEM 21	0.330	–	–
Overall	0.081		

her natal home range remained in this area for six months (28 June 2010 – 30 December 2010) before starting to disperse. She moved 36 km in 11 days before contact was lost, before being detected again nine months later 24.5 km northeast of her natal home range and 17.5 km southeast of her last known location, where anecdotal evidence suggests that she had been present since September 2011. In total she travelled a minimum distance of 48.5 km in eight months. A young male (STEM 23, 3.8 kg) was tracked for four months in his natal home range before he started dispersing during December 2010. He appeared to establish a small home range 5 km north of his natal home range before contact was lost, presumably due to him leaving the area. A young adult male (STEM 47, 6.7 kg) was located within the home range

of female STEM 5 and remained in this area for a month before starting to disperse on 6 October 2011, covering at least 32 km in 20 days. Another young adult male (STEM 31, 6.5 kg) was tracked for 18 days between 22 December 2010 and 11 January 2011 before contact was lost. During this time he moved 81 km in an area of 154 km^2 (MCP), but in no consistent direction.

DISCUSSION

A home range is broadly defined as the minimum area required by an individual to obtain adequate resources such as food, shelter and breeding opportunities, but excludes cases of vagrancy or exploratory sallies (Burt 1943; Fielden 1991). This study confirms that *S. temminckii* does indeed have a clearly defined home range and our find-
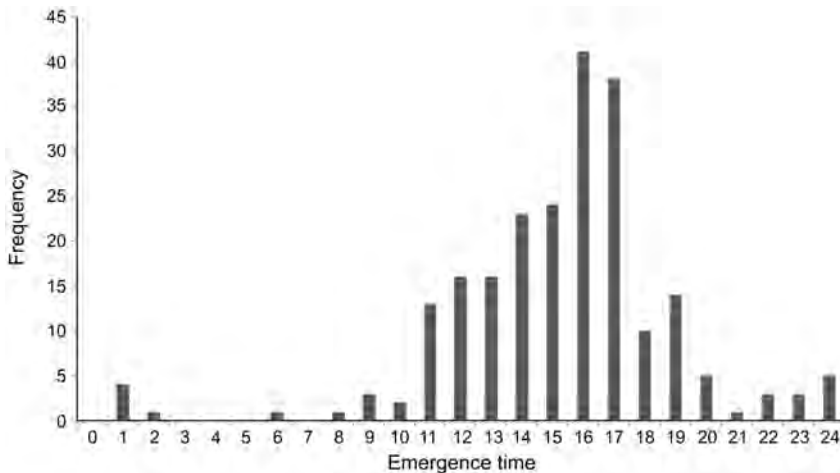
Fig. 3. Pooled emergence times of two adult males and a young adult female pangolin fitted with GPS loggers at Kalahari Oryx Private Game Farm. Emergence times are divided into 1-hour intervals according to the 24-hour clock.

Table 4. Nature and proportion of refuges used by 13 pangolins on Kalahari Oryx Private Game Farm between September 2009 and October 2012. *n* = number of times pangolins used each refuge type, % = proportional use of each refuge type.

Refuge type	Overall		Adults		Juveniles	
	n	%	*n*	%	*n*	%
Aardvark burrow	343	69.7	237	74.8	106	60.6
Springhare warren	68	13.8	48	15.1	20	11.4
Cave	32	6.5	15	4.7	17	9.7
Porcupine warren	30	6.1	13	4.1	17	9.7
Rocks	13	2.6	2	0.6	11	6.3
Vegetation	3	0.6	0	0	3	1.7
Termite mound	2	0.4	1	0.3	1	0.6
Self-excavated burrow	1	0.2	1	0.3	0	0
Total	492		317		175	

ings are similar to studies on the same species in Zimbabwe (Heath & Coulson 1997a) but are larger than the data published on individuals in northeastern South Africa (van Aarde *et al.* 1990). The latter study involved following five individuals over 52 monitoring nights, and the small home ranges recorded in that study can be attributed to the shorter duration of the study. Our estimate of 88 ± 67.7 tracking days being required to predict an individual's core home range is similar to the corresponding value of Heath & Coulson (1997a), although the large standard deviation of our mean value suggests that substantially more observations may sometimes be required. The large standard deviation could be as a result of the relatively small sample size, and this should be further investigated in future studies.

Habitat selection can be broadly defined as the process by which a species chooses between the available resources and this, in turn, can have implications on its behaviour (Johnson 1980). The lack of habitat selectivity at our study site contrasts with the high selectivity recorded by Swart (1996) in the eastern savanna of South Africa. One possible explanation concerns the uniform geology and climate at the Kalahari study site (Mucina & Rutherford 2006) presumably resulting in a fairly uniform ant community (Pietersen 2013; Pietersen *et al.*, in prep.). As prey availability is one of the major driving forces behind habitat selection (Langvatn & Hanley 1993; Storch 1993; Alcala-Galvan & Krausman 2013), this uniformity probably invalidates habitat selection as there would be no energetic gain in selecting specific habitats if all have similar prey communities (Langvatn & Hanley 1993; Edwards *et al.* 2002). This lack of selectivity may also be attributable to

the individual vegetation types in the Kalahari being more extensive than those in Swart's (1996) study (Mucina & Rutherford 2006), with individual home ranges thus incorporating fewer vegetation types. Our data also suggest that pangolins used their entire home range continuously, moving between successive refuges on an *ad hoc* basis, and that home ranges are stable across successive years. This pattern is similar to the findings of Heath & Coulson (1997a) but contrasts with those of van Aarde *et al.* (1990) who suspected that although pangolins have a home range of *c.* 20 km², they only use a small portion for periods of up to three months at a time before moving to a different, often adjoining, portion.

Animals in arid environments typically have larger home ranges than their conspecifics in higher rainfall areas (Mares *et al.* 1982; Attuquayefio *et al.* 1986; Fielden 1991; Alcala-Galvan & Krausman 2013), possibly due to lower primary productivity in xeric environments resulting in fewer available food resources (Fielden 1991; Alcala-Galvan & Krausman 2013). However, pangolins in the Kalahari are 25–30% smaller than individuals from northeastern South Africa and Zimbabwe (D.W. Pietersen, unpubl. data) and smaller individuals tend to have smaller home ranges than do larger individuals of the same species (Mohr 1947; McNab 1963). We speculate that the lack of variation in home range size across an aridity gradient reflects the interacting effects of variation in body size (i.e. smaller in the arid west, with an expectation of smaller home ranges) and primary productivity (lower in the arid west with an expectation of larger home ranges). According to this notion, the differences in body mass and primary productivity effectively cancel

each other, resulting in similar home range sizes across the species' southern African range.

The comparatively large difference between MCP and Kernel home range estimates for adults, and the relatively small difference between these estimates for juveniles, likely reflects differences in statistical approaches and the relatively small sample sizes. Adults appear to be more prone to exploratory wanderings than juveniles, occasionally wandering outside of the core home range for short periods, which results in more outlying data points. Juveniles, by comparison, tend to initially accompany an adult while foraging, thus obtaining knowledge of the core home range and later wandering within this core area (prior to dispersal). This apparent concentration on the core area by juveniles may be as a result of familiarity, particularly with regards to refuge locations and prey distribution. All juvenile pangolins fitted with telemetry during this study initially established home ranges within their natal home range before subsequently dispersing. These results concur with those of Heath & Coulson (1997a) who recorded a newly weaned pup initially establishing its home range within its natal home range and suspected that juvenile dispersal would occur at a later stage. Pangolins are probably able to disperse much further than the 49 km and 154 km^2 (MCP) recorded during this study as van Aarde *et al.* (1990) report a young male travelling 300 km in four months, suggesting extensive dispersal with consequent implications for recolonization and gene flow. Our data also suggest that male pangolins may disperse further than females and may also remain rovers (reproductively mature adults without a fixed home range) for longer.

Heath & Coulson (1997a) recorded a male pangolin's home range overlapping with those of a number of females, suggesting a polygynous mating system (see also Gaubert 2011). This is contrary to our findings, where home ranges of territorial adult males closely mirrored those of adult females, suggesting a single pair of sexually mature adults in each home range. Furthermore, no movements of males into adjoining females' home ranges were observed, except for roving males. These divergent results could conceivably arise from previous authors overlooking the presence of roving males whose presence within a given home range is transient. Further studies are required to assess whether roving males actively engage in reproduction (i.e. a polygynous mating system), or whether they are transient without any reproductive input (i.e. a monogamous mating system).

Swart (2013) estimated a breeding density of 0.12 individuals/km^2 and total density of 0.24 individuals/km^2 for *S. temminckii* in eastern South Africa. Both our breeding density and total density estimates exceed these estimates, suggesting a higher pangolin density in the Kalahari biome. This is supported by the higher sighting frequency in the Kalahari (D.W. Pietersen, unpubl. data). Heath & Coulson (1997a) did not calculate densities, but using their MCP home range values a total density of 0.11 individuals/km^2 is obtained, substantially lower than both South African density estimates and possibly reflects variation in study design rather than true density differences. Further research is required to verify this possibility. The aforementioned densities are below the average density of 1.0 ± 0.3 individuals/km^2 that has been calculated for thick-tailed pangolins (*Manis crassicaudata*) in Pakistan (Mahmood *et al.* 2014).

The average duration of activity we observed is comparable to previously reported values (Jacobsen *et al.* 1991; Swart 1996; Heath & Coulson 1997b), and our data support Swart's (1996) finding of no seasonal differences in the duration of activity, although the onset of activity varied seasonally as well as with the age class of the individual, while weather conditions also had an impact. Our data also support Swart's (1996) assertion that the apparent increase in crepuscular pangolin activity reflects an increase in observer effort rather than a true effect. Compared to the findings of Swart (1996) and Richer *et al.* (1997), we recorded a higher proportion of diurnal activity in all age classes. This increased diurnal activity in the Kalahari is likely due to the more extreme climate within this region. Pangolin scales provide little thermal insulation (McNab 1984; Heath & Hammel 1986; Weber *et al.* 1986) and body temperature is atypically variable (D.W. Pietersen, A.E. McKechnie and R. Jansen, unpubl. data) and it may be that behavioural avoidance of low environmental temperatures is an important component of thermoregulation in this species. Moreover, winter is a nutritionally stressful time as ant activity decreases and more energy is expended to maintain a constant body temperature (Swart 1996; Pietersen 2013). By becoming more diurnal during winter, pangolins are able to avoid nocturnal activity and the associated low air temperatures, thereby conserving energy. Conversely, by being nocturnal during summer indi-

viduals are able to avoid the extreme daytime temperatures, thus conserving water that would otherwise be required for evaporative cooling. As ant activity remains consistently low during winter regardless of the diel cycle (Pietersen 2013), pangolins probably do not take prey activity cycles into consideration during this time.

Aardvark burrows were the most frequently used refuges, although other burrows, caves and rock piles were also opportunistically used. Most records of individuals using exposed refuges were juveniles or dispersing individuals, possibly reflecting juveniles lacking an intimate knowledge of their home range, or individuals finding themselves in unfamiliar surroundings during dispersal. Van Aarde *et al.* (1990) reported individuals returning to the same burrow every 3–5 nights. During our study, the length of time that an individual occupied any particular burrow varied from one to *c.* 30 nights and new burrows were continuously added and old burrows abandoned as burrows collapsed and new ones created through the digging actions of other species.

Our results suggest that many of the ecological traits are similar between pangolin populations living in arid and mesic environments, although further studies within a variety of ecosystems are required to justify this. This study further suggests that pangolin densities may be higher in the Kalahari than they are in eastern South Africa and Zimbabwe, which may have conservation implications. The reasons for this purported higher density require further investigation, but may reflect a higher prey density. Our data also suggest that individuals of a species in arid environments do not necessarily have larger home ranges than do conspecifics in mesic regions, but that morphology may also play a role in determining home range size. The data suggest that most dispersal events occur over relatively short distances but that larger dispersal events, especially by young males, may occasionally occur. Despite being the largest study to date of Temminck's ground pangolin, our sample size remains small for some aspects and this limits extrapolation of some of the results to the broader pangolin population.

ACKNOWLEDGEMENTS

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