Diet and prey selectivity of an arid-zone population of the specialist myrmecophage, Temminck's ground pangolin (*Smutsia temminckii*)

Darren W. Pietersen[1,5,*], Craig T. Symes[2], Stephan Woodborne[1,3], Andrew E. McKechnie[1] and Raymond Jansen[4,5]

[1]Mammal Research Institute, Department of Zoology and Entomology, University of Pretoria, Private Bag X20, Hatfield, 0028, South Africa

[2]School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Private Bag 3, WITS, 2050, South Africa

[3]iThemba LABS, Private Bag 11, WITS, 2050, South Africa

[4]Department of Environmental, Water and Earth Sciences, Tshwane University of Technology, Private Bag X680, Pretoria, 0001, South Africa

[5]African Pangolin Working Group & IUCN Species Survival Commission Pangolin Specialist Group

*****Address for correspondence: pietersen.darren@gmail.com

Abstract

The diet of Temminck's ground pangolin *Smutsia temminckii* (hereafter, pangolin) has thus far been studied only in mesic savannahs. We provide arid-zone dietary data for this species based on direct observations, and compare these to available prey species assemblages. We also report stable carbon and nitrogen isotope enrichment values for liver and scales compared to the diet. Pangolins were recorded consuming four ant (*Anoplolepis steingroeveri*, *Camponotus fulvopilosus*, two *Crematogaster* spp.) and one termite (*Trinervitermes trinervoides*) species, which represent 7.5 and 25 % of the available ant and termite species, respectively.

The stable isotope data corroborate the direct observations and confirm that pangolins display a high degree of prey selectivity, however stable isotopes alone were not able to infer the diet of pangolins as a number of non-prey species had similar isotopic values to prey species. Direct observations suggest that these latter species are not preyed on, possibly because they have chemical or mechanical defences or gallery structures that make them unsuitable as prey. Liver was enriched by 3.8 ± 1.2 ‰ (mean ± SD) and 2.5 ± 1.4 ‰ for $\delta^{15}N$ and $\delta^{13}C$, respectively, relative to the mean $\delta^{15}N$ and $\delta^{13}C$ values of the prey species, and scales were enriched by 2.9 ± 1.0 ‰ and 5.3 ± 1.8 ‰, respectively. We observed no seasonal variation or age or sex-related differences in diet, either from direct observations or isotope data. These results support previous findings that pangolins have further specialised within an already unusual mammalian dietary niche.

Key Words

Smutsia temminckii, Kalahari, Forage ratio, Stable light isotopes

Introduction

Ants (Hymenoptera: Formicidae) and termites (Isoptera) have colonised nearly all terrestrial ecosystems (Schoeman & Foord 2012), and comprise a diverse and abundant component of biomass (Hölldobler & Wilson 1994). They are an important food resource for many vertebrate species (Redford 1986) and represent a potentially rewarding food type due to their generally clumped occurrence (Redford 1986; Abensperg-Traun & Steven 1997). More than 200 mammalian species are known to prey on ants, of which approximately 25 species are obligate myrmecophages (Redford 1987). Dietary specialisation often has a knock-on effect on biological and ecological traits, including social and population dynamics (Abba & Cassini 2010), and as Temminck’s ground pangolin (*Smutsia temminckii*) is one of the most widespread African myrmecophages it is an ideal model to explore the consequences of dietary specialisation on strict myrmecophagous mammals.

Pangolins (Pholidota: Manidae) are scarce, predominantly nocturnal mammals that are rarely observed (Sweeney 1956; Pietersen et al. 2014a) and are the only group of mammals with a dermal covering of scales rather than hair (Heath & Coulson 1997; Richer, Coulson & Heath 1997). Temminck’s ground pangolin is wholly myrmecophagous (Coulson 1989; Jacobsen et al. 1991; Swart 1996) and previous studies employing direct observations and/or stomach content analyses suggest that they select specific ant and termite species rather than foraging on the most abundant species (Coulson 1989; Jacobsen et al. 1991; Swart 1996). While these methods are valuable for providing information on the feeding biology of pangolins, they are often of relatively short duration and seldom capture seasonal or age-related dietary variation. Stable isotope analyses of tissue provide an alternative method with which to reconstruct animal diets and in particular understand assimilated, as opposed to ingested, nutrients (Ayliffe et al. 2004; West et al. 2006; Newsome et al. 2007; Boecklen et al. 2011). Different tissues provide information on temporal variation in diets, with tissues characterized by rapid turnover rates (e.g. blood and liver) providing information on recent diets while tissues with slow turnover rates (e.g. bone apatite and scales) provide dietary information integrated over longer time periods (months to years) (Tieszen et al. 1983; Tieszen & Fagre 1993; Hilderbrand et al. 1996). Inert tissues such as scales reflect the diet during the period the tissue was grown, and as keratin is produced continuously it facilitates diachronic indication of diet variability (Ayliffe et al. 2004; West et al. 2006; Newsome et al. 2007).

All previous studies investigating the diet of Temminck’s ground pangolin took place in mesic savannah environments (Coulson 1989; Jacobsen et al. 1991; Swart 1996). As ant and termite assemblages vary spatially and are closely linked to habitat complexity (Samways 1990; Andersen 1993; Swart 1996; Lindsey & Skinner 2001; Schoeman & Foord 2012), prey availability may differ substantially along aridity gradients. Indeed, overall prey diversity and abundance may be expected to be lower in arid environments due to the lower primary productivity (Kaspari, O’Donnell & Kercher 2000; Parr et al. 2004) and habitat complexity (Samways 1990; Andersen 1993; Swart 1996; Lindsey & Skinner 2001; Schoeman & Foord 2012). In view of the strong prey selectivity previously reported for pangolins, populations in arid environments may remain as selective as their conspecifics in mesic habitats due to evolutionary constraints. Alternatively, the lower primary productivity and decreased habitat complexity in arid environments may result in a depleted potential prey base, necessitating pangolins to become more generalist feeders. In light of previous studies, we predicted that pangolin diets in arid environments will not merely reflect the relative abundance of individual ant and termite species, but will instead show similar specialisation to mesic populations.

The objective of this study was to investigate the dietary preferences of pangolins near the most arid edge of the species’ range through direct observation, and to compare these data with stable isotope analyses of tissue from pangolins at the same site. In particular, we sought to establish whether there is a difference between the time-integrated (diachronic) diet reconstructed from stable light isotopes and the short-term (synchronic) observations that are indicative of temporal dietary variability. We also sought to determine whether pangolins in arid environments remain selective feeders, or whether the dietary niche breadth is relaxed due to lower prey availability.

Materials and Methods

Study Site

This study was conducted on Kalahari Oryx Game Farm, a 52,000 ha farm in the arid Kalahari bioregion in the Northern Cape Province of South Africa between latitudes 28°21’S – 28°42’S and longitudes 21°55’E – 22°15’E. Summer air temperatures may exceed 40°C, with an average maximum of 34°C and minimum of 17°C. Winter temperatures may drop as low as -14°C, and average a minimum of 3°C and maximum of 19°C (Mucina & Rutherford 2006; D. Pietersen unpubl. data). Rainfall is recorded in all months of the year with the majority falling between October and April, with a peak from December to March (Figure 1). The study site was divided into nine vegetation types based on dominant plant species, structure and geology (Pietersen et al. 2014a).

Invertebrate Sampling

Invertebrate sampling was conducted monthly from March 2011 to February 2012 in eight of the nine habitat types (Grassy Dwarf Shrubland was excluded due to logistical constraints). Invertebrate assemblages were sampled with non-lipped plastic pitfall traps (45 mm diameter, 64 mm depth), with each pitfall array consisting of a 3 x 4 grid of traps placed 10 m apart and sited near the centre of each habitat. Due to time and material constraints a single array was sited per habitat. This may have under-represented the total ant and termite diversity for that habitat, however considering the uniformity of the climate, geology and structure of each habitat (Pietersen et al. 2014a) and the fact that trapping was undertaken monthly for a full year, we believe that our sampling methods closely approximate the actual invertebrate species assemblages. Whenever possible, equal numbers of pitfalls were placed in sunny and shaded locations (Swart 1996) and each pitfall was filled to a depth of 20 – 35 mm with a 50 % propylene glycol solution as preservative. To overcome the ‘digging-in’ effect (Joosse 1965; Greenslade 1973) traps were buried two weeks prior to the onset of sampling. Traps were activated for 48 consecutive hours at monthly intervals and sampled at dawn and dusk daily (total of 2,304 trap nights), following the time recommended for a standard ant sampling protocol (Agosti & Alonso 2000). Traps were left *in situ* with lids fitted between successive sampling sessions.

Pangolins feed on surface-active ant and termite species while the latter are inactive in their galleries or mounds (Coulson 1989; Jacobsen et al. 1991; Swart 1996). As it was not feasible to sample inactive ants and termites, surface activity as established by pitfall trapping was deemed a suitable proxy to determine species abundance and diversity. As all ant and termite species that pangolins preyed on were captured in pitfall traps, we believe that our methods and efforts were both appropriate and adequate. Any species that may have been missed likely do not contribute, or only contribute negligibly, to the pangolin’s diet at this site.

Termite richness was additionally assessed using two subterranean bait varieties. Baits were placed 5 m apart in a 6 x 6 grid and consisted of alternating toilet paper rolls and pine stakes (300 mm x 35 mm x 35 mm) buried vertically and covered with 50 mm of soil. As a large proportion of the toilet rolls were dug up by bat-eared foxes *Otocyon megalotis*, and initial observations indicated that termites only form a small proportion of the pangolins’ diet at the study site, monitoring of termite baits was discontinued after the first month and excluded from all analyses.

Sampled ants and termites were sorted microscopically into morphospecies based on external morphological characteristics, the number of individuals of each morphospecies in each sample was recorded, and a reference collection established. Samples from each site were pooled according to the sampling period, resulting in two day and two night samples per site per month. Traps disturbed by animals were excluded from the analyses and a statistical correction made for the bias.

Certain ant species travel in armies, thus a single pitfall may trap disproportionately high numbers of these species. Likewise, if a pitfall is inadvertently placed near an active nest this particular trap may induce biases (Swart 1996). In order to ensure that the data are representative, in instances where more than 50 % of individuals from a morphospecies in a sample were collected in a single pitfall, this trap was excluded and statistically compensated for (provided that ≥ 10 individuals of that morphospecies were captured in the entire sample). A representative sample of each morphospecies was identified by ant taxonomists (Peter Hawkes & Jonathan Fisher, AfriBugs, Onderstepoort, Pretoria) to the lowest taxonomic level possible. If the species could not be determined, the specimen was assigned an AfriBugs morphospecies code (AFRC-za code) matched to the AfriBugs collection.

Pangolin feeding observations

We observed 146 feeding bouts (feeds from individual ant or termite nests) by 14 habituated pangolins spanning an observation period of 1,111 days, while monitoring other ecological aspects of wild pangolins. Observations were made from a distance of 1 – 5 metres at various times of the day and night. Feeding observations were made in approximately equal proportions in *Acacia erioloba* Veld, *Acacia haematoxylon* Savannah, *Acacia mellifera* Thickets, Duneveld Grassland, Mixed Savannah and Mountain Veld, mirroring the distribution of tracked pangolins (Pietersen 2013; Pietersen et al. 2014a). After a pangolin had fed a sample of the prey was collected and stored in absolute ethanol and microscopically compared to the reference collection, with a subset being sent to AfriBugs for verification.

To assess whether any particular prey species was preferentially selected, each ant and termite species was assigned a forage ratio (Manly, MacDonald & Thomas 1993):

$$\dot{w} = o_i / \pi_i$$

where o_i is the proportion of prey type *i* observed in the diets of pangolins and π_i is the proportion of prey type *i* available to pangolins as prey (i.e. the proportional abundance of that species in pitfall traps). These ratios were standardised by dividing the individual forage ratio for each species by the sum of all forage ratios. This results in a value between zero and one, with zero indicating that the species was not consumed and one indicating that the species was exclusively consumed or was consumed more frequently than predicted by its abundance.

Isotope sampling and analyses

Corresponding liver and scale samples were collected from pangolins found electrocuted on game fences, road mortalities, and gin trap mortalities (Pietersen et al. 2014b). Carcasses and samples were assigned unique corresponding field numbers (STEM prefix) and the carcasses subsequently deposited in national collections. Sample ages ranged from < 1 hour to ca. 8 hours and had not started putrefaction, and as sample age does not affect the isotope values the age of these samples will not affect our results. Morphological measurements followed the African Pangolin Working Group's standard protocol (APWG 2013). Liver samples were stored individually in absolute ethanol and scale clippings stored in paper envelopes prior to analysis. For analyses, a section of liver was dried to constant mass and homogenised using a mortar and pestle. Scales were scrubbed with a toothbrush and cleaned with ethanol:chloroform (2:1 mix) to remove external dirt and contaminants, and scrapings of the keratinous layer were collected from the proximal section (representative of a more recent contribution to diet than the distal end).

Two scales were sampled at regular intervals across their entire length to investigate temporal variation in the diet (see also Ayliffe et al. 2004; Zazzo et al. 2007; Hartman 2011). One scale (STEM 15) originated from a fence mortality predating 2010, while STEM 50 was killed by African lions *Panthera leo* during 2011. Both scales originated from adult individuals and based on the size and appearance of the scales each is believed to represent a growth period of > 5 years and possibly > 10 years (DWP unpubl. data). Pangolin scales grow continuously from the stem cells embedded in the epidermis, while the distal portion of the scale is continuously worn away through abrasion. Scales cannot be shed and thus represent a dietary time continuum. Each scale was discretely sampled (at 12 and seven locations, respectively) and therefore do not portray the averaged diet over protracted periods, but rather the near-instantaneous diet at intervals during the scale formation.

For isotopic analysis we included all five prey species and an additional nine ant and three termite species, which were of a similar size to the prey species and thus appeared to be candidate prey taxa. Depending on size and availability, 3–10 individuals of each species were dried to constant mass and homogenised using a mortar and pestle. Samples were weighed into tin cups (pre-cleaned in toluene) and combusted on-line in a Flash EA1112 series elemental analyser at 1,020°C coupled to a DeltaV stable light isotope ratio mass spectrometer using a Conflo IV device (all instrumentation supplied by ThermoFinnigan, Bremen, Germany). A calibrated laboratory standard and blank were run after every 12 unknown samples. The results are reported in per mille (‰) in standard delta notation relative to the international standards VPDB and AIR for $\delta^{13}C$ and $\delta^{15}N$, respectively. The precision of repeat analyses of the standards (excluding inhomogeneity effects in the tissues) was 0.11 ‰ for $\delta^{13}C$ and 0.10 ‰ for $\delta^{15}N$.

Statistical Analyses

The monthly total number of ants and termites captured at each site was used as a proxy for abundance, while the total number of individuals captured during either the day or night was used as a proxy for activity period. We used a one-way Analysis of Similarity (ANOSIM) with square root transformation to assess the similarity of the ant and termite communities between sites, as well as to assess the prey species communities between sites. A square root transformation allows species of intermediate abundance to also influence the similarity index, whereas if the data are not transformed only the most common species contribute to the index (Lindsey & Skinner 2001). A Spearman Rank correlation was used to determine whether ant and termite abundance was associated with monthly temperatures, and a Wilcoxon Matched-pairs Signed-rank test was used to investigate whether abundance varied seasonally and whether activity was correlated with day or night periods. A Chi-squared test was used to determine whether pangolins selected specific prey species or whether prey selection was random.

Correlations between isotope values and biological data were investigated using a two-tailed Spearman Rank Correlation test (corrected for ties), while potential age and sex-related differences in isotope values were investigated with unpaired two-tailed t-tests (with Welsh correction). A linear relationship has been recorded between the length and mass of pangolins (Heath & Coulson 1998; Pietersen 2013), although mass may vary seasonally (Pietersen 2013) and thus length is a better indicator of age. To examine whether diet changes with age we compared mean $\delta^{15}N$ and $\delta^{13}C$ tissue values with the length of the individual. Statistical analyses were performed with the software programs PRIMER 5 (PRIMER-E Ltd, Plymouth, UK) and GraphPad InStat v.3.0 (GraphPad Software, San Diego, California, USA).

Results

Ant and Termite Richness and Abundance

Fifty-three ant species and four termite species were recorded in pitfall traps (Table 1). The ant and termite communities differed significantly between sites (Global R = 0.489, P = 0.001), with most of the variation being attributable to Mountain Veld (Figure 2). The prey species assemblages showed a similar trend (R = 0.469, P = 0.001), with the Mountain Veld again contributing the most to variability.

Ant abundance showed pronounced seasonal variation, with significantly more species and individuals captured in summer (Nov – Feb) than winter (May – Aug) (P < 0.001, df = 36; Figures 1 & 2). There was a significant correlation between the total number of individuals caught and the average monthly minimum (r = 0.923, P <

0.001, df = 11) and maximum (r = 0.874, $P < 0.001$, df = 11) air temperatures. Significantly more species were active during the day (58.5 %, n = 31) than at night (17 %, n = 9; t = 1.803, P = 0.009, df = 39; Figure 1). The remaining 24.5 % (n = 13) could not be assigned to either period, either because the sample sizes were too small or because these species were crepuscular or genuinely active during both the day and night. When the five prey species were considered independently, there was no significant difference in diurnal and nocturnal activity (t = 0.079, P = 0.087, df = 4).

Feeding Observations

A total of 146 feeding bouts by 14 pangolins were observed, involving four ant and one termite species (Table 2). *Anoplolepis steingroeveri* was consumed most frequently, followed by *Crematogaster* AFRC-za08 and *Crematogaster* AFRC-za12. Pangolins fed on Termitidae sp. 1 and Termitidae sp. 2 on one occasion each, although on both occasions the time spent at the exposed subterranean nests suggested that they excavated the nests and moved on without consuming any termites, and thus these species are not considered prey species. If pangolins do feed on these species they form a negligible proportion of their diet.

Pangolins did not prey on the most abundant species but rather selected specific species (Chi-squared test $\chi^2 = 19.090$, $P < 0.001$, df = 1; Figure 3). *Trinervitermes trinervoides* formed an important component of the diet of those pangolins that had access to mountainous terrain, where epigeal termitaria were prevalent and where the majority showed signs of predation. Although termites were present in all habitats sampled (Table 1), termitaria not in Mountain Veld or Dwarf Karroid Shrubland were subterranean. *Crematogaster* AFRC-za12 was most prevalent in mountainous terrain (Table 1) and also frequently occurred in moribund termitaria. In contrast, *Crematogaster* AFRC-za08 occurred almost exclusively in the sandy dunes and plains, where it was particularly common at the base and on the stems of trees and logs. *Anoplolepis steingroeveri* and *Camponotus fulvopilosus* were almost exclusively encountered in sandy, flatter areas, where they were particularly common at the bases of grass clumps.

Stable Isotope Analyses

As the quantity of each prey species actually consumed is unknown, we could not calculate a weighted average and thus use the arithmetic mean of the pooled prey isotope values as the mean dietary value. The $\delta^{15}N$ and $\delta^{13}C$ values of liver samples (n = 12) were enriched by 3.8 ± 1.2 ‰ and 2.5 ± 1.4 ‰, respectively, compared to the mean $\delta^{15}N$ and $\delta^{13}C$ values of the observed prey species. The $\delta^{15}N$ and $\delta^{13}C$ of scales (n = 11), in comparison, were enriched by 2.9 ± 1.0 ‰ and 5.3 ± 1.8 ‰, respectively, compared to the prey (Figure 4). In contrast the $\delta^{15}N$ and $\delta^{13}C$ liver values were enriched by 1.7 ± 1.2 ‰ and 1.2 ± 1.4 ‰, respectively, compared to the mean values of the non-prey species and the scale $\delta^{15}N$ and $\delta^{13}C$ values were 0.8 ± 1.0 ‰ and 3.9 ± 1.8 ‰ enriched compared to the non-prey species. There was no seasonal variation in liver isotope values (One-way ANOVA: $P > 0.999$, df = 9). No significant difference was found between adult and juvenile $\delta^{15}N$ ($t = 1.007$, $P = 0.353$, df = 6) or $\delta^{13}C$ ($t = 0.059$, $P = 0.955$, df = 6) scale values, nor was there a difference in the $\delta^{15}N$ ($t = 0.400$, $P = 0.702$, df = 7) or $\delta^{13}C$ ($t = 0.345$, $P = 0.740$, df = 7) liver values between adults and juveniles. There were no significant differences between male and female scale ($\delta^{15}N$: $t = 0.042$, $P = 0.974$, df = 1; $\delta^{13}C$: $t = 0.514$, $P = 0.698$, df = 1) or liver ($\delta^{15}N$: $t = 0.504$, $P = 0.641$, df = 4; $\delta^{13}C$: $t = 1.533$, $P = 0.176$, df = 6) values.

We found a marginally significant correlation between body length and scale $\delta^{15}N$ values (r = 0.677, P = 0.050, df = 8), but no correlation between length and scale $\delta^{13}C$ values (r = -0.130, P = 0.744, df = 8). There was no correlation between liver $\delta^{15}N$ (r = 0.326, P = 0.297, df = 11) or $\delta^{13}C$ values (r = 0.182, P = 0.573, df = 11) and body length.

Sample series taken across two scales revealed an inverse relationship between $\delta^{15}N$ and $\delta^{13}C$, as well as temporal variation in these isotope ratios (Figure 5). Across each time series, $\delta^{15}N$ varied by 2.8 ‰ (range 6.6 to 9.4 ‰) for STEM 15 and 2.5 ‰ (range 6.7 to 9.2 ‰) for STEM 50. $\delta^{13}C$ showed similar intra-individual variation, with the scale series varying by 2.5 ‰ (range -14.3 to -11.9 ‰) for STEM 15 and 4.3 ‰ (range -15.6 to -11.3 ‰) for STEM 50. The variation between individuals was 2.6 ‰ (range 7.9 to 10.5 ‰) for $\delta^{15}N$ and 4.2 ‰ (range -17.8 to -13.6) for $\delta^{13}C$.

Discussion

Direct observations indicate that pangolins consume only four ant and one termite species, representing 7.5 % and 25 %, respectively, of total species richness. As the termite diversity was not specifically sampled it is probable that this diversity is higher, suggesting an even greater prey selectivity. Further observations may have revealed additional taxa being preyed on, however these additional species probably only contribute negligibly to the diet of pangolins at this site, as was also found during previous studies (Jacobsen et al. 1991; Swart, Richardson & Ferguson 1999). The presence of ant and termite prey taxa in all habitat types may explain the lack of habitat selection previously observed in this pangolin population (Pietersen et al. 2014a).

The liver $\delta^{15}N$ and $\delta^{13}C$ values corroborate the direct feeding observations but also suggest that additional ant and termite species may isotopically contribute to the pangolins' diet. That these species were not preyed on may suggest that their gallery structures are incompatible with the pangolins' foraging mode, or they may possess chemical or physical defences that make them unsuitable as prey. Additional observations may have revealed pangolins feeding on these species as well, but if they were predated they likely comprise a negligible fraction of the pangolins' diet. It is interesting to note that the four most likely candidate prey species, based on isotope signatures, are three species of termites (two of which were observed to have possibly been preyed upon by pangolins), and an ant species in the same genus as a known prey species. We observed no age- or sex-related prey selection in either the direct observations or isotope signatures of tissue. Stable isotope ratios did not show any temporal variation, suggesting that there is no (or at least very little) variation in the diet through an annual cycle.

Our diet-tissue isotopic discrimination value for $\delta^{13}C$ in scales ($\Delta^{13}C_{\text{Diet-Scales}}$ = 5.3 ± 1.8 ‰) is higher than the range of 1.1 to 3.2 ‰ previously recorded for other species (Tieszen et al. 1983; Tieszen & Fagre 1993; Roth & Hobson 2000; Lesage, Hammill & Kovacs 2002; Newsome et al. 2010). Our $\Delta^{15}N_{\text{Diet-Scale}}$ value (2.9 ± 1.0 ‰) is within the range of 2.4 to 4.3 ‰ recorded in previous studies (Roth & Hobson 2000; Lesage et al. 2002; Newsome et al. 2010) but is lower than the 4.8 ‰ enrichment recorded for other insectivores in xeric environments (Kelly 2000). Our diet-tissue discrimination values for liver ($\Delta^{13}C_{\text{Diet-Liver}}$ = 2.5 ± 1.4 ‰; $\Delta^{15}N_{\text{Diet-Liver}}$ = 3.8 ± 1.2 ‰) are within the range of 0 to 3.1 ‰ reported for $\delta^{13}C$ and 2 to 5 ‰ reported for $\delta^{15}N$ (Cerling & Harris 1999; Balter et al. 2006; Newsome et al. 2010). The preservation of blood and muscle in ethanol has been shown not to affect $\delta^{13}C$ and

$\delta^{15}N$ values (Hobson, Gibbs & Gloutney 1997) and we assume that this is the case with the liver and prey samples in this study.

The diachronic evidence for the pangolin diet revealed in the sequential isotopic analyses provides insight into subtle dietary change through time. An inverse relationship between $\delta^{13}C$ and $\delta^{15}N$ in this dataset is similar to that observed in the synchronic scale sample, and is indicative of a dietary mixing model. The results suggest that individual pangolins exploit slightly differing proportions of available prey species, although this may not be apparent from observational data as it is not possible to determine how many ants or termites are consumed in any feeding bout. Of interest is the subtle dietary shift that manifests as opposite trends in the isotope values: A decrease in $\delta^{15}N$ and simultaneous increase in $\delta^{13}C$ in STEM 15 through time is matched by an increase in $\delta^{15}N$ and simultaneous decrease in $\delta^{13}C$ in STEM 50. As these two scales likely represent different temporal periods, it is possible that this change is attributable to an environmentally driven baseline shift, such as that caused by seasonal variations in rainfall. We recorded as much intra-individual as inter-individual variation in the diachronic $\delta^{15}N$ and $\delta^{13}C$ values, suggesting that dietary specialisation is occurring at the species or population level rather than at the individual level.

Our results differ somewhat with those of Swart et al. (1999) who recorded pangolins feeding on 15 ant and five termite species (30 % and 100 % of species richness, respectively) in the Sabi Sand Game Reserve, a site in the mesic east of South Africa. However, five ant and one termite species constituted 97.7 % of pangolin diets at their site (Swart et al. 1999), which is similar to our findings. Similarly, Jacobsen et al. (1991) recorded pangolins consuming 13 ant and three termite species while Coulson (1989) recorded five ant and four termite species in pangolin stomachs also within mesic savannah habitats. These data suggest that pangolins selectively feed on a small subset of species, but that they may opportunistically or inadvertently include additional species in their diet.

That many potential prey species (including the most abundant ant species) are not consumed whereas less abundant species are, supports the notion that pangolins are selective in their prey choice (see also Swart 1996). This selectivity does not appear to be based on the size of the prey alone, as the four most commonly collected ant species (none of which were preyed on) all have average body lengths of 3.2 – 3.9 mm, as do *Crematogaster* spp., the latter being regularly preyed on by pangolins. Chemical and mechanical defences are likely to play a role in determining whether species are suitable as prey, as would gallery characteristics. If the nest chambers are deep underground they will be out of reach of pangolins, which typically only dig shallow excavations while foraging (see also Swart 1996; Swart et al. 1999). Ant and termite species with well-developed chemical and physical defences are also likely to be avoided (see for example Redford 1985), while species occurring at low densities may be encountered less often, or more energy would be required to find these species.

Detailed data on the diet of other obligate myrmecophagous mammals and marsupials is limited, but does allow for some comparisons. The Aardwolf *Proteles cristatus* is perhaps the most specialised African myrmecophage, with > 90 % of its diet consisting of *Trinervitermes* spp. termites (Richardson & Levitan 1994), although *Hodotermes mossambicus* increases in importance during winter when they are more active above ground (Kruuk & Sands 1972; Richardson 1987; Taylor & Skinner 2000). As the distributions of the respective *Trinervitermes* species are largely mutually exclusive, Aardwolf prey mainly on a single species in any geographical region (Kruuk & Sands 1972; Richardson 1987). Although specialised, Aardwolf are known to prey on 15 species of ant, termites and other invertebrates (Dean 1978; Matsebula et al. 2009). In contrast, ants are the most important component of the Aardvark's *Orycteropus afer* diet in South Africa, with four ant and two termite species comprising the bulk of the diet (Taylor, Lindsey & Skinner 2002). However this species is also known to feed on 15 ant and termite species (Willis, Skinner & Robertson 1992; Taylor et al. 2002). The banded ant-eater or numbat *Myrmecobius fasciatus* of Australia feeds on 27 termite and 29 ant species, with five termite and two ant species constituting the bulk of the diet (Calaby 1960). The numbat appears to prey on termite species in relation to their proportional abundance, while also depredating ants in smaller numbers (Calaby 1960). As the majority of ingested ants are carnivorous, it is believed that they are accidentally ingested when they swarm to prey on the exposed termites (Calaby 1960). Redford (1985) recorded the giant anteater *Myrmecophaga tridactyla* feeding on eight termite and six ant species, with four termite species forming the bulk of the diet. Elsewhere in its range the giant anteater feeds exclusively on ants (Montgomery 1979), and these geographical differences are believed to be the result of differences in prey availability (Fox & Morrow 1981). Lubin and Montgomery (1981) recorded northern tamandua *Tamandua mexicana* and southern tamandua *T. tetradactyla* preying on four termite and four ant species in central and South America. It therefore appears that most mammalian and marsupial myrmecophages select specific prey species, but will consume other species opportunistically or incidentally. Unlike the giant anteater which shows geographic variation in diet, Temminck's ground pangolin consistently consumes a greater quantity of ants across its range, and this may be in response to the defensive chemicals of Isoptera or possibly the lower diversity and prevalence of Isoptera in southern Africa compared to South America.

Our results support those of previous studies in that pangolins are wholly myrmecophagous and selective in their dietary habits, selecting specific ant and termite species rather than preying on the most abundant species. We found ants to comprise the bulk of the diet, but that termites remain an important food source as well. Contrary to what might be expected, pangolins in arid environments remain as selective as mesic populations with regards to prey species and only prey on a small subset of available ant and termite species. Importantly, this specialisation is consistent at the species level over time, regardless of individual size or sex.

Acknowledgements

The owner and managers of Kalahari Oryx Game Farm are thanked for allowing this research to be conducted on their property. Chené Barnard, ‘Tokman’, Dirk van Wyk and Michèle Pietersen are thanked for assisting with invertebrate sampling. Peter Hawkes and Jonathan Fisher are thanked for identifying ants and for their valuable discussions. This research was conducted under permits FAUNA 767/2009, 016/2010, 806/2010 and 082/2012, and transport permits FAUNA 653/2010, 032/2011 and 929/2011 issued by the Northern Cape Department of Environment and Nature Conservation. Ethical clearance was received from the University of Pretoria Animal Use and Care Committee (EC055-09). Financial support was received from the Mohamed bin Zayed Species Conservation Fund (project 0925713), the National Research Foundation (grant 71454), the Tshwane University of Technology and the University of Pretoria, for which we are grateful. Andrew

Taylor and an anonymous reviewer are thanked for their valuable comments on an earlier draft of this manuscript.

References

ABBA, A.M. & CASSINI, M.H. 2010. Ecological differences between two sympatric species of armadillos (Xenarthra, Mammalia) in a temperate region of Argentina. *Acta Theriologica* 55(1): 35–44.

ABENSPERG-TRAUN, M. & STEVEN, D. 1997. Ant- and termite-eating in Australian mammals and lizards: A comparison. *Australian Journal of Ecology* 22: 9–17.

AGOSTI, D. & ALONSO, L.E. 2000. The ALL protocol: A standard protocol for the collection of ground dwelling ants. *In*: AGOSTI, D., MAJER, J.D., ALONSO, L.E. & SCHULTZ, T.R. (eds), Ants. Standard methods for measuring and monitoring biodiversity. Smithsonian Institution Press, Washington DC. pp. 204–206.

ANDERSEN, A.N. 1993. Ant assemblages in the gulf region of Australia’s semi-arid tropics: Species composition, patterns of organisation, and biogeography. *Australian Journal of Zoology* 41: 399–414.

APWG – African Pangolin Working Group 2013. Ground Pangolin *Smutsia temminckii* DNA sampling protocol. Unpublished guidelines.

AYLIFFE, L.K., CERLING, T.E., ROBINSON, T., WEST, A.G., SPONHEIMER, M., PASSEY, B.H., HAMMER, J., ROEDER, B., DEARING, M.D. & EHLERINGER, J.R. 2004. Turnover of carbon isotopes in tail hair and breath CO_2 of horses fed an isotopically varied diet. *Oecologia* 139: 11–22.

BALTER, V., SIMON, L., FOUILLET, H. & LÉCUYER, C. 2006. Box-modeling of $^{15}N/^{14}N$ in mammals. *Oecologia* 147: 212–222.

BOECKLEN, W.J., YARNES, C.T., COOK, B.A. & JAMES, A.C. 2011. On the use of stable isotopes in trophic ecology. *Annual Review of Ecology, Evolution, and Systematics* 42: 411–440.

CALABY, J.H. 1960. Observations on the banded ant-eater *Myrmecobius f. fasciatus* Waterhouse (Marsupialia), with particular reference to its food habits. *Proceedings of the Zoological Society of London* 135: 183–207.

CERLING, T.E. & HARRIS, J.M. 1999. Carbon isotope fractionation between diet and bioapatite in ungulate mammals and implications for ecological and paleoecological studies. *Oecologia* 120: 347–363.

COULSON, M.H. 1989. The pangolin (*Manis temminckii* Smuts, 1832) in Zimbabwe. *African Journal of Ecology* 27: 149–155.

DEAN, W.R.J. 1978. Stomach contents of a specimen of *Proteles cristatus* from Angola (Carnivora: Protelidae). *Zoologica Africana* 13: 164.

FOX, L.R. & MORROW, P.A. 1981. Specialization: Species property or local phenomenon? *Science* 221: 887–893

GREENSLADE, P.J.M. 1973. Sampling ants with pitfall traps: Digging-in effects. *Insectes Sociaux* 20: 343–353.

HARTMAN, G. 2011. Are elevated δ^{15}N values in herbivores in hot and arid environments caused by diet or animal physiology? *Functional Ecology* 25: 122–131.

HEATH, M.E. & COULSON, I.M. 1997. Home range size and distribution in a wild population of Cape pangolins, *Manis temminckii*, in north-west Zimbabwe. *African Journal of Ecology* 35: 94–109.

HEATH, M.E. & COULSON, I.M. 1998. Measurements of length and mass in a wild population of Cape pangolins (*Manis temminckii*) in north-west Zimbabwe. *African Journal of Ecology* 36: 267–270.

HILDERBRAND, G.V., FARLEY, S.D., ROBBINS, C.T., HANLEY, T.A., TITUS, K. & SERVHEEN, C. 1996. Use of stable isotopes to determine diets of living and extinct bears. *Canadian Journal of Zoology* 74: 2080–2088.

HOBSON, K.A., GIBBS, H.L. & GLOUTNEY, M.L. 1997. Preservation of blood and tissue samples for stable-carbon and stable-nitrogen isotope analysis. *Canadian Journal of Zoology* 75: 1720–1723.

HÖLLDOBLER, B. & WILSON, E.O. 1994. *The ants*. Belknap Press, Massachusetts, USA.

JACOBSEN, N.H.G., NEWBERY, R.E., DE WET, M.J., VILJOEN, P.C. & PIETERSEN, E. 1991. A contribution of the ecology of the Steppe Pangolin *Manis temminckii* in the Transvaal. *Zeitschrift für Säugetierkunde* 56(2): 94–100.

JOOSSE, E.N.G. 1965. Pitfall trapping as a method for studying surface dwelling Collembola. *Zeitschrift fuer Morphologie und Oekologie der Tiere* 55: 587–596.

KASPARI, M., O'DONNELL, S. & KERCHER, J.R. 2000. Energy, density and constraints to species richness: Ant assemblages along a productivity gradient. *American Naturalist* 155: 280–293.

KELLY, J.F. 2000. Stable isotopes of carbon and nitrogen in the study of avian and mammalian trophic ecology. *Canadian Journal of Zoology* 78: 1–27.

KRUUK, K. & SANDS, W.A. 1972. The aardwolf (*Proteles cristatus* Sparmann) 1783 as a predator of termites. *East African Wildlife Journal* 10: 211–227.

LESAGE, V., HAMMILL, M.O. & KOVACS, K.M. 2002. Diet-tissue fractionation of stable carbon and nitrogen isotopes in phocid seals. *Marine Mammal Science* 18: 182–193.

LINDSEY, P.A. & SKINNER, J.D. 2001. Ant composition and activity patterns as determined by pitfall trapping and other methods in three habitats in the semi-arid Karoo. *Journal of Arid Environments* 48: 551–568.

LUBIN, Y.D. & MONTGOMERY, G.G. 1981. Defenses of *Nasutitermes* termites (Isoptera, Termitidae) against *Tamandua* anteaters (Edentata, Myrmecophagidae). *Biotropica* 13(1): 66–76.

MANLY, B.F.J., MACDONALD, L. & THOMAS, D. 1993. Resource selection by animals: Statistical design and analysis for field studies. Chapman & Hall, London.

MATSEBULA, S.N., MONADJEM, A., ROQUES, K.G. & GARCELON, D.K. 2009. The diet of the aardwolf, *Proteles cristatus* at Malolotja Nature Reserve, western Swaziland. *African Journal of Ecology* 47: 448–451.

MONTGOMERY, G.G. 1979. El grupo alimentico (feeding guild) del oso hormiguero. *Conciencia* 6: 3–6.

MUCINA, L. & RUTHERFORD, M.C. (eds). 2006. The vegetation of South Africa, Lesotho and Swaziland. *Strelitzia* 19. South African National Biodiversity Institute, Pretoria, South Africa.

NEWSOME, S.D., DEL RIO, C.M., BEARHOP, S. & PHILLIPS, D.L. 2007. A niche for isotopic ecology. *Frontiers in Ecology and the Environment* 5(8): 429–436.

NEWSOME, S.D., BENTALL, G.B., TINKER, M.T., OFTEDAL, O.T., RALLS, K., ESTES, J.A. & FOGEL, M.L. 2010. Variation in $\delta^{13}C$ and $\delta^{15}N$ diet-vibrissae trophic discrimination factors in a wild population of California sea otters. *Ecological Applications* 20(6): 1744–1752.

PARR, C.L., ROBERTSON, H.G., BIGGS, H.C. & CHOWN, S.L. 2004. Response of African savanna ants to long-term fire regimes. *Journal of Applied Ecology* 41(4): 630–642.

PIETERSEN, D.W. 2013. Behavioural ecology and conservation biology of ground pangolins (*Smutsia temminckii*) in the Kalahari Desert. M.Sc. Thesis, University of Pretoria, Pretoria, South Africa.

PIETERSEN, D.W., MCKECHNIE, A.E. & JANSEN, R. 2014a. Home range, habitat selection and activity patterns of an arid-zone population of Temminck's ground pangolins, *Smutsia temminckii*. *African Zoology* 49(2): 265–276.

PIETERSEN, D.W., MCKECHNIE, A.E. & JANSEN, R. 2014b. A review of the anthropogenic threats faced by Temminck's ground pangolin, *Smutsia temminckii*, in southern Africa. *South African Journal of Wildlife Research* 44(2): 167–178.

REDFORD, K.H. 1985. Feeding and food preference in captive and wild giant anteaters (*Myrmecophaga tridactyla*). *Journal of Zoology (London) A* 205: 559–572.

REDFORD, K.H. 1986. Dietary specialization and variation in two mammalian myrmecophages (variation in mammalian myrmecophagy). *Revista Chilena de Historia Natural* 59: 201–208.

REDFORD, K.H. 1987. Ants and termites as food: Patterns of mammalian myrmecophagy. IN: GENOWAYS, H.H. (ed.). Current Mammalogy volume I. Plenum Press, New York: 349–399.

RICHARDSON, P.R.K. 1987. Food consumption and seasonal variation in the diet of the aardwolf *Proteles cristatus* in southern Africa. *Zeitschrift für Säugetierkunde* 52: 307–325.

RICHARDSON, P.R.K. & LEVITAN, C.D. 1994. Tolerance of Aardwolves to defense secretions of *Trinervitermes trinervoides*. *Journal of Mammalogy* 75(1): 84–91.

RICHER, R., COULSON, I. & HEATH, M. 1997. Foraging behaviour and ecology of the Cape Pangolin (*Manis temminckii*) in north-western Zimbabwe. *African Journal of Ecology* 35: 361–369.

ROTH, J.D. & HOBSON, K.A. 2000. Stable carbon and nitrogen isotopic fractionation between diet and tissue of captive red fox: Implications for dietary reconstruction. *Canadian Journal of Zoology* 78: 848–852.

SAMWAYS, M.J. 1990. Species temporal variability: Epigaeic ant assemblages and management for abundance and scarcity. *Oecologia* 84: 482–490.

SCHOEMAN, C.S. & FOORD, S.H. 2012. A checklist of epigaeic ants (Hymenoptera: Formicidae) from the Marakele National Park, Limpopo, South Africa. *Koedoe* 54(1): 1–7.

SWART, J. 1996. Foraging behaviour of the Cape pangolin *Manis temminckii* in the Sabi Sand Wildtuin. MSc Thesis, University of Pretoria, Pretoria, South Africa.

SWART, J.M., RICHARDSON, P.R.K. & FERGUSON, J.W.H. 1999. Ecological factors affecting the feeding behaviour of pangolins (*Manis temminckii*). *Journal of Zoology* 247: 281–292.

SWEENEY, R.C.H. 1956. Some notes on the feeding habits of the ground pangolin, *Smutsia temminckii* (Smuts). *Annual Magazine of Natural History, 12th series* 9: 893–896.

TAYLOR, W.A. & SKINNER, J.D. 2000. Associative feeding between aardwolves (*Proteles cristatus*) and aardvarks (*Orycteropus afer*). *Mammal Review* 30: 141–143.

TAYLOR, W.A., LINDSEY, P.A. & SKINNER, J.D. 2002. The feeding ecology of the aardvark *Orycteropus afer*. *Journal of Arid Environments* 50: 135–152.

TIESZEN, L.L. & FAGRE, T. 1993. Effect of diet quality and composition on the isotope composition of respiratory CO_2, bone collagen, bioapatite, and soft tissues. IN: LAMBERT, J. & GRUPE, G. (eds.). Molecular archaeology of prehistoric human bone. Springer, Berlin Heidelberg New York.

TIESZEN, L.L., BOUTTON, T.W., TESDAHL, K.G. & SLADE, N.A. 1983. Fractionation and turnover of stable carbon isotopes in animal tissues: Implications for $\delta^{13}C$ analysis of diet. *Oecologia* 57: 32–37.

WEST, J.B., BOWEN, G.J., CERLING, T.E. & EHLERINGER, J.R. 2006. Stable isotopes as one of nature's ecological recorders. *TRENDS in Ecology and Evolution* 21(7): 408–414.

WILLIS, C.K., SKINNER, J.D. & ROBERTSON, H.G. 1992. Abundance of ants and termites in the False Karoo and their importance in the diet of the Aardvark, *Orycteropus afer. African Journal of Ecology* 30: 322–334.

ZAZZO, A., HARRISON, S.M., BAHAR, B., MOLONEY, A.P., MONAHAN, F.J., SCRIMGEOUR, C.M. & SCHMIDT, O. 2007. Experimental determination of dietary carbon turnover in bovine hair and hoof. *Canadian Journal of Zoology* 85: 1239–1248.

Table 1. Epigaeic ant and termite species captured in pitfall traps in eight vegetation types on Kalahari Oryx Game Farm between March 2011 and February 2012. Species forming part of the Temminck's ground pangolins' *Smutsia temminckii* diet are shaded in grey. The diel period during which most activity was recorded is indicated for each species. Numbers in non-boldface indicate species that form part of a morphospecies complex and although their presence at the study site was confirmed, they may not occur in all vegetation types indicated - totals for these species are for the entire morphospecies complex. Vegetation type codes are: DKS = Dwarf Karroid Shrubland; AMRT = *Acacia mellifera* - *Rhigozum trichotomum* Veld; AE = *Acacia erioloba* Veld; AM = *Acacia mellifera* Thicket; MV = Mountain Veld; MS = Mixed Savannah; DG = Duneveld Grassland; AH = *Acacia haematoxylon* Savannah. AFRC-za = AfriBugs collection morphospecies code.

ANT AND TERMITE SPECIES	**VEGETATION COMMUNITY**								**TOTAL**	**ACTIVITY PERIOD**
	DKS	**AMRT**	**AE**	**AM**	**MV**	**MS**	**DG**	**AH**		
FORMICIDAE										
Aenictinae										
Aenictus furibundus Arnold				**3**					**3**	Nocturnal
Cerapachyinae										
Cerapachys coxalis Arnold		**2**							**2**	Diurnal
Dolichoderinae										
Technomyrmex pallipes (F. Smith)		**1**	**24**	**22**	**146**	**330**	**2**	**233**	**758**	Nocturnal
Dorylinae										
Dorylus AFRC-za05	4				1			2	7	Nocturnal
Formicinae										
Anoplolepis steingroeveri (Forel)	**131**	**59**	**38**	**1**		**795**	**156**	**246**	**1426**	Both
Camponotus fulvopilosus (de Geer) [savannah form]		**56**	**11**	**47**	**2**	**28**	**39**	**25**	**208**	Diurnal
Camponotus mystaceus kamae Forel	**8**	**51**	**12**	**86**	**44**	**172**	**84**	**30**	**487**	Nocturnal
Camponotus namacola Prins	**2**								**2**	Diurnal
Camponotus AFRC-za20						**1**			**1**	Diurnal
Camponotus (*Myrmosericus*) AFRC-za34					**10**				**10**	Diurnal
Camponotus AFRC-za50 sp. nov.						**7**			**7**	Diurnal
Lepisiota imperfecta (Santschi)		2		1	2	12	18	8	43	Diurnal
Lepisiota AFRC-za15		2		1	2	12	18	8	43	Diurnal
Lepisiota AFRC-za19					**23**	**4**			**27**	Diurnal
Lepisiota AFRC-za20		**5**	**66**	**5**		**22**	**13**	**23**	**134**	Diurnal
Tapinolepis AFRC-za02	**30**	**101**	**2**	**7**	**8**	**111**	**60**	**6**	**325**	Diurnal
Myrmicinae										
Cataulacus intrudens (F. Smith)		**5**	**6**						11	Both
Crematogaster AFRC-za08		**44**	**8**	**17**	**3**	**5**			**77**	Both

Crematogaster AFRC-za12			**2**	**1**	**119**			**1**	**123**	Nocturnal
Meranoplus glaber Arnold	4	7	2		2	66	105	7	193	Nocturnal
Meranoplus spininodis Arnold	4	7	2		2	66	105	7	193	Nocturnal
Messor capensis (Mayr)	**6**		**3**						**9**	Diurnal
Monomorium damarense Forel	203	690	218	272	39	513	659	521	3115	Diurnal
Monomorium minor Stitz	**6**	**140**	**61**	**6**	**21**	**94**	**90**	**84**	**502**	Diurnal
Monomorium notulum Forel	203	690	218	272	39	513	659	521	3115	Diurnal
Monomorium rufulum Stitz	**48**	**2**	**5**	**50**	**15**	**292**	**3**	**2**	**417**	Diurnal
Monomorium setuliferum Forel	203	690	218	272	39	513	659	521	3115	Diurnal
Monomorium vaguum Santschi	203	690	218	272	39	513	659	521	3115	Diurnal
Myrmicaria fusca nigerrima Arnold				**2**	**2**				**4**	Both
Nesomyrmex vannoorti Mbanyana & Robertson	4	3	3		1		3	1	15	Diurnal
Ocymyrmex cavatodorsatus Prins				**2**		**2**	**1**	**12**	**17**	Diurnal
Ocymyrmex hirsutus Forel	**13**	**77**	**33**	**29**		**99**	**76**	**76**	**403**	Diurnal
Oligomyrmex AFRC-za01	4				1			2	7	Nocturnal
Pheidole tenuinodis Mayr	**525**	**1023**	**410**	**112**	**7**	**393**	**1573**	**454**	**4497**	Both
Pheidole AFRC-za10	8		8						16	Diurnal
Pheidole AFRC-za17	8		8						16	Diurnal
Pheidole AFRC-za25	203	690	218	272	39	513	659	521	3115	Diurnal
Tetramorium argentopilosum Arnold	4	3	3		1		3	1	15	Diurnal
Tetramorium flaviceps Arnold	65	69	79	72	73	171	103	47	679	Both
Tetramorium inezulae (Forel)	35	78	338	96	7	987	104	485	2130	Both
Tetramorium luteolum Arnold	65	69	79	72	73	171	103	47	679	Both
Tetramorium peringueyi Arnold	**1**				**3**	**1**			5	Diurnal
Tetramorium rufescens Stitz	**468**	**647**	**279**	**576**	**661**	**326**	**71**	**209**	**3237**	Diurnal
Tetramorium sericeiventre Emery	**140**	**355**	**129**	**6**	**279**	**99**	**5**		**1013**	Diurnal
Tetramorium sericium Arnold	35	78	338	96	7	987	104	485	2130	Both
Tetramorium simulator Arnold							**10**		**10**	Diurnal
Tetramorium AFRC-za12	203	690	218	272	39	513	659	521	3115	Diurnal
Tetramorium AFRC-za21	35	78	338	96	7	987	104	485	2130	Both
Tetramorium AFRC-za22	65	69	79	72	73	171	103	47	679	Both
Tetramorium AFRC-za23	65	69	79	72	73	171	103	47	679	Both
Ponerinae										
Anochetus levaillanti Emery			**2**		**3**	**2**	**2**		**9**	Diurnal
Pachycondyla elisae Forel			**1**		**4**				**5**	Both
Hypoponera perparva Bolton & Fisher	4				1			2	7	Nocturnal
TERMITIDAE										
Termitidae (unidentified sp.) 1		**12**	**4**	**4**		**1**	**10**	**4**	**35**	Both
Termitidae (unidentified sp.) 2				**4**	**33**	**34**	**76**	**21**	**168**	Both

Hodotermitidae										
Hodotermes mossambicus Hagen	**17**	**49**				**20**	**7**		**93**	Both
Nasutitermitinae										
Trinervitermes trinervoides Sjöstedt				**3**	**12**	**13**	**16**	**3**	**47**	Both
TOTAL NUMBER OF INDIVIDUALS	**1718**	**3478**	**1744**	**1424**	**1520**	**4600**	**3286**	**2500**		
TOTAL NUMBER OF SPECIES	**35**	**36**	**38**	**35**	**41**	**40**	**38**	**38**		

Table 2. Number and proportion of foraging bouts and standardised forage ratio for each ant and termite species preyed on by Temminck's ground pangolins *Smutsia temminckii* at Kalahari Oryx Game Farm. Standardised Forage Ratios range from zero to one, with values closer to one indicating that a species was strongly selected.

Species	**Number of foraging bouts**	**% of total observations**	**Standardised Forage Ratio**
Crematogaster AFRC-za08	31	21.5	0.580
Crematogaster AFRC-za12	20	13.9	0.243
Anoplolepis steingroeveri	69	47.9	0.070
Camponotus fulvopilosus	8	5.6	0.062
Trinervitermes trinervoides	16	11.1	0.045

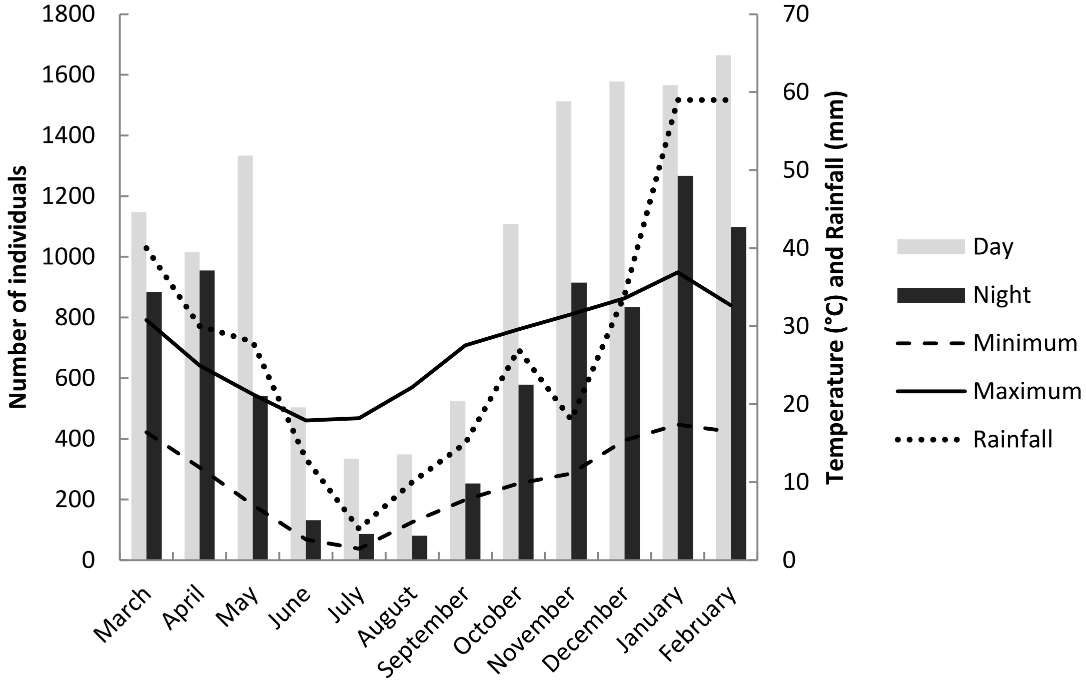

Figure 1. Absolute numbers of epigaeic ants and termites captured during day and night sampling at Kalahari Oryx Game Farm between March 2011 and February 2012, compared to the average monthly minimum and maximum temperatures and rainfall recorded at the same site.

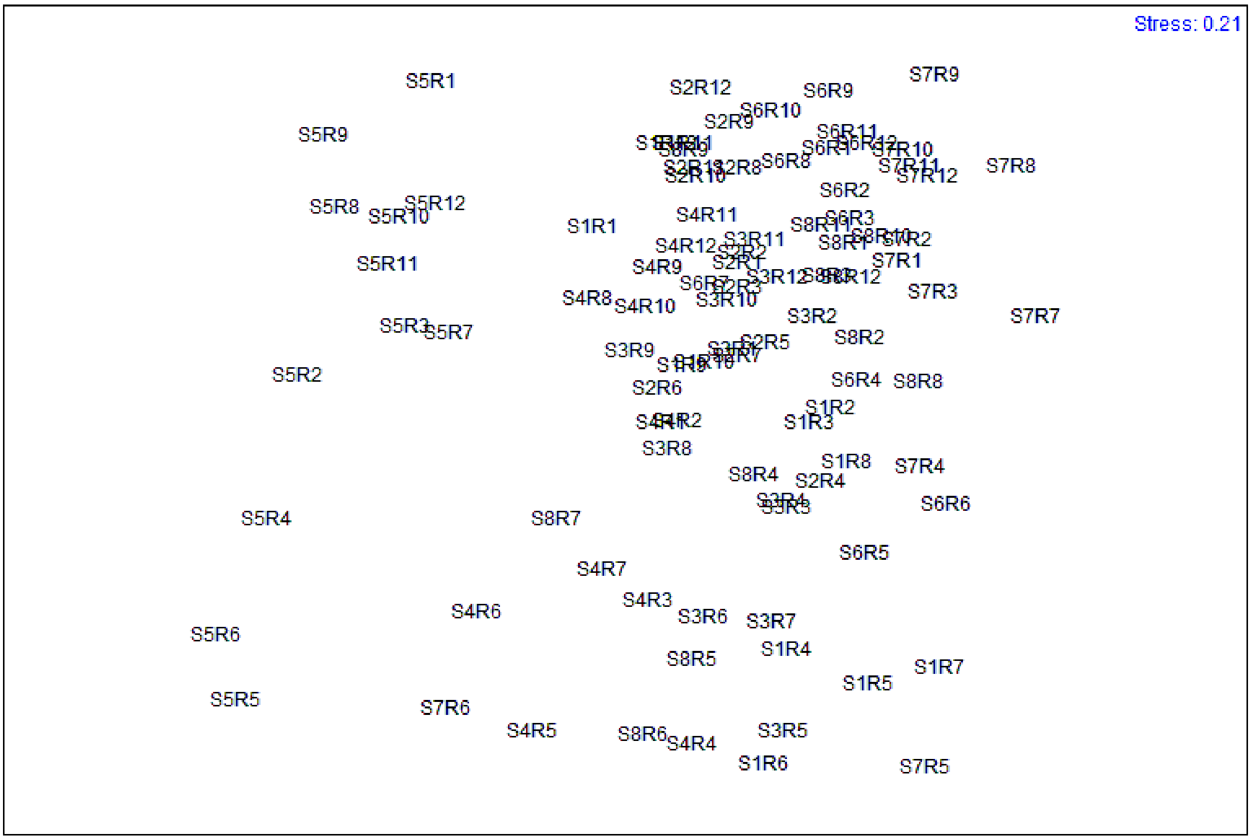

Figure 2. Multi-Dimensional Scaling plot of the monthly ant and termite community assemblages for the eight habitat types sampled on Kalahari Oryx Game Farm between March 2011 and February 2012. Data label acronyms are: S = Site Number, R = Replicate number.

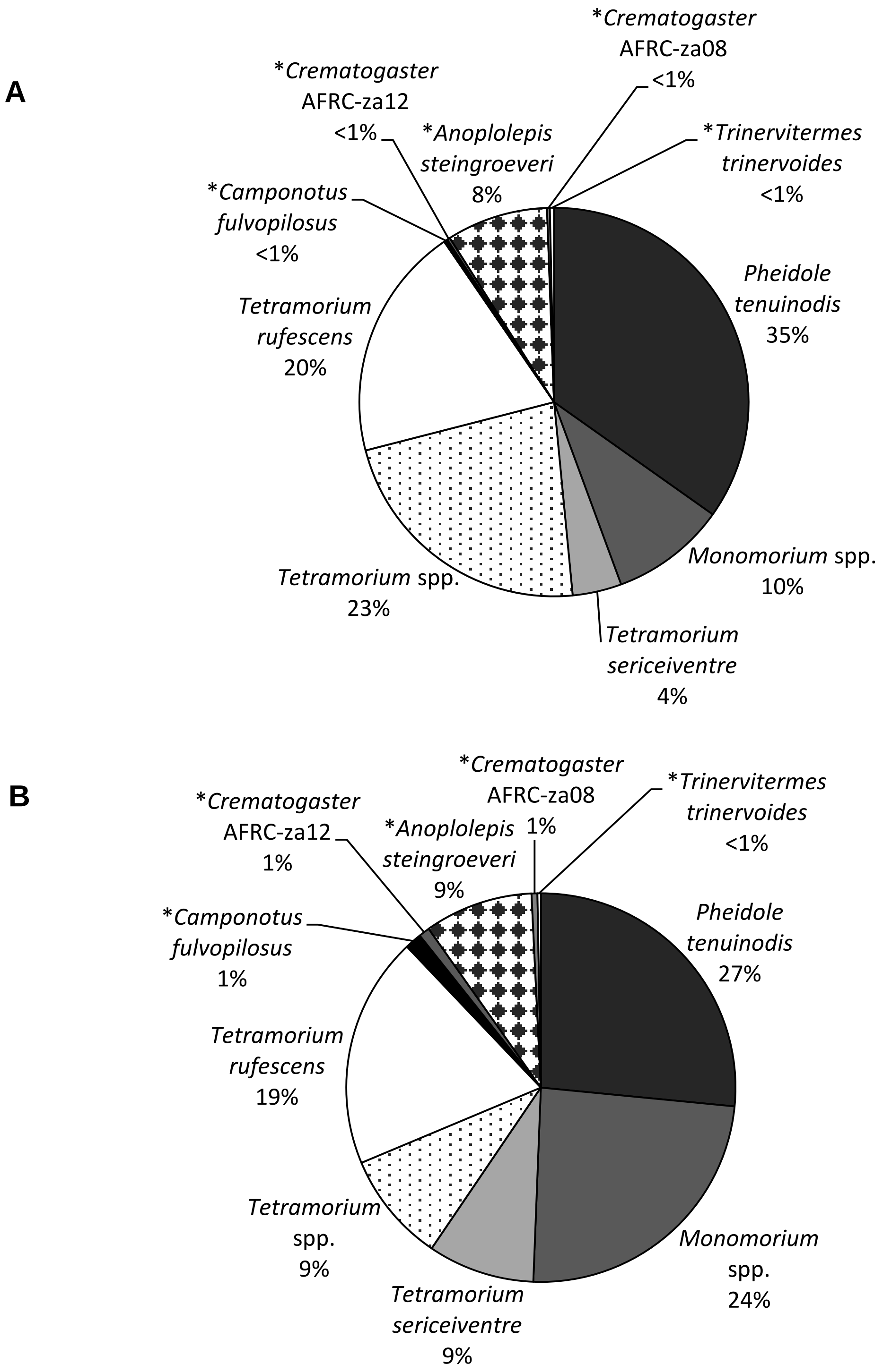

Figure 3. (**A**) Winter (May – Aug) and (**B**) Summer (Nov – Feb) variation in the relative abundance of the five most common ant species, and ant and termite species preyed on by Temminck's ground pangolins *Smutsia temminckii* on Kalahari Oryx Game Farm, pooled for eight vegetation types. Prey species are indicated with asterisks.

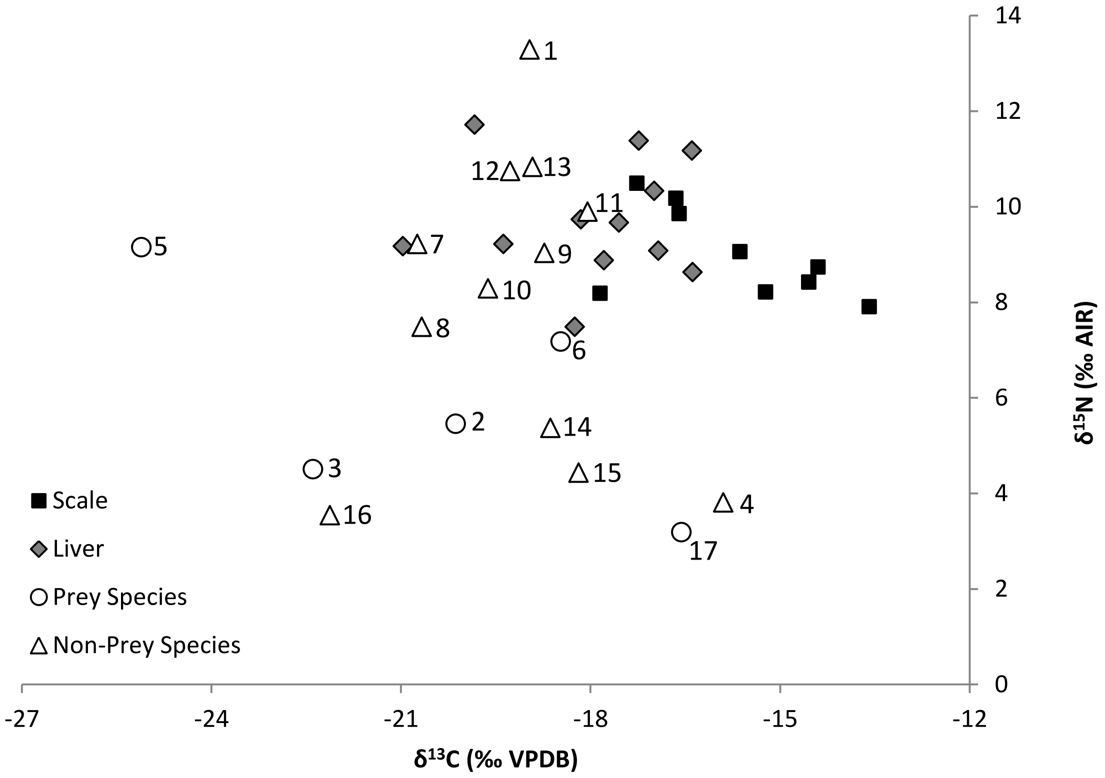

Figure 4. Stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) values for Temminck's ground pangolin *Smutsia temminckii* liver and scale samples (closed symbols), and observed and potential ant and termite prey species (open symbols). The ant and termite plots are numbered, and correspond to the following taxa: 1 = *Aenictus* AFRC-za03; 2 = *Anoplolepis steingroeveri*; 3 = *Camponotus fulvopilosus*; 4 = *Camponotus mystaceus kamae*; 5 = *Crematogaster* AFRC-za08; 6 = *Crematogaster* AFRC-za12; 7 = *Lepisiota* AFRC-za20; 8 = *Messor capensis*; 9 = *Ocymyrmex hirsutus*; 10 = *Pheidole tenuinodis*; 11 = *Tetramorium rufescens*; 12 = *Tetramorium sericeiventre*; 13 = *Tetramorium* spp.; 14 = *Hodotermes mossambicus*; 15 = Termitidae sp. 1; 16 = Termitidae sp. 2; 17 = *Trinervitermes trinervoides*.

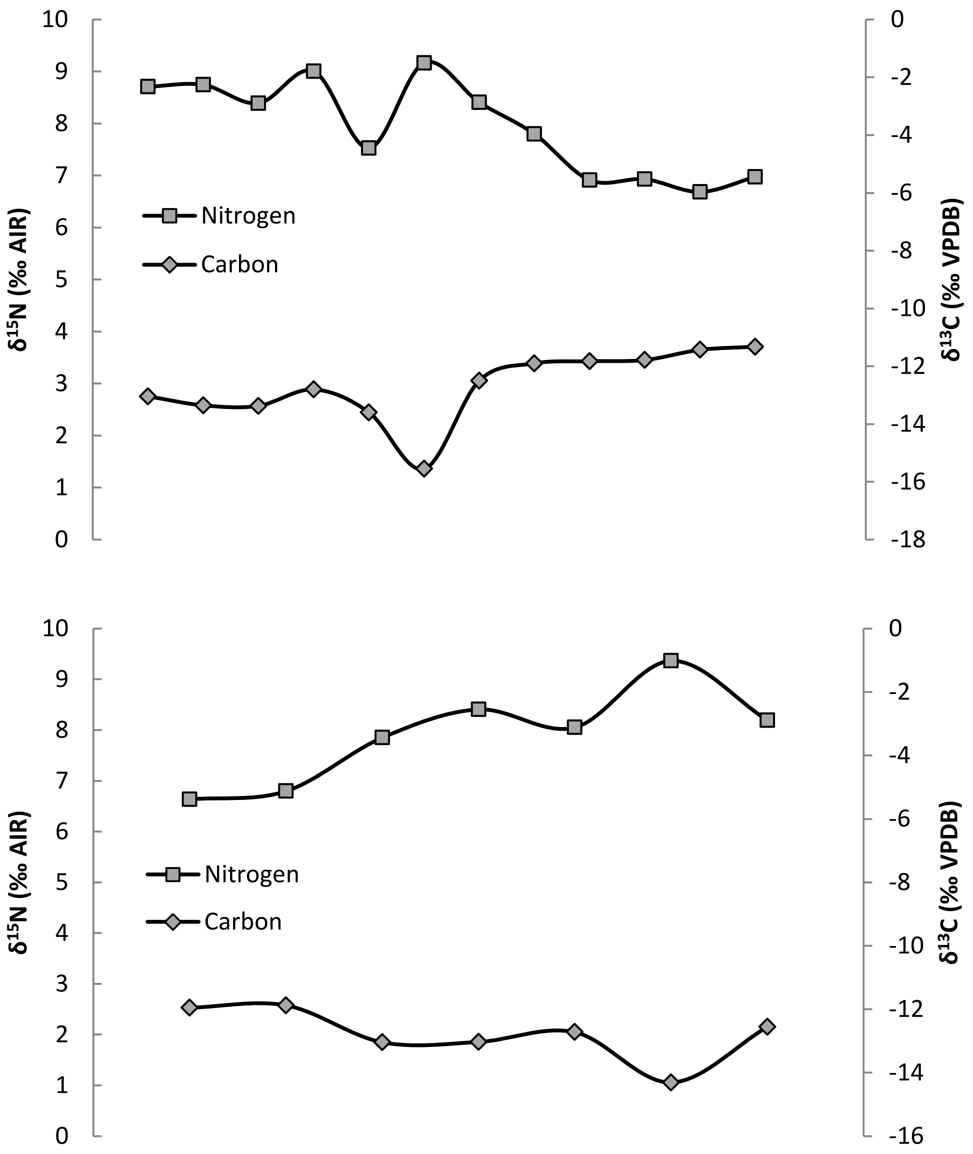

Figure 5. Sequential changes in δ^{15}N and δ^{13}C values discretely measured across a scale in two Temminck's ground pangolin *Smutsia temminckii* individuals (STEM 15 at top, STEM 50 at bottom). Scale age increases from left to right.