AN INVESTIGATION OF THE PALAEOECOLOGY AND PAST DISTRIBUTION OF TORTOISES (CHELONIANS) IN THE ARID INTERIOR OF SOUTH AFRICA: A TOOL TO AID PRESENT DAY CONSERVATION

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Declaration

I declare that the thesis hereby submitted by me for the Philosophiae Doctor Degree at the University of the Free State is my own, independent work and has not previously been submitted by me at another university or faculty. I furthermore cede copyright of the thesis in favour of the University of the Free State.

Sharon Holt

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Dedicated with love to my parents:

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Contents

Abstract

This dissertation focuses on the past and present ecology of land tortoises (Testudinidae) from the arid interior of South Africa, with special emphasis on the leopard tortoise (*Stigmochelys pardalis*). Aside from an Introduction and Conclusion, it comprises four chapters, each a stand-alone paper of which two have already been published and two others are being prepared for submission, dealing with different aspects of tortoise ecology and palaeoecology. It addresses an important anthropogenic threat to persistence of tortoise populations, and then investigates human-tortoise interactions that occurred in past Quaternary environments. This research also led to the creation of an extensive modern osteological tortoise collection which can be used as a comparative and reference collection for future researchers.

The first paper focuses on mortality profiles of tortoises that were collected along electrified farm fences. We have examined and modelled the impact that these fences have on a leopard tortoise population. Previous studies only reported on deaths due to these fences, but so far the long-term consequences for populations have not been investigated. Results show that fence-related mortalities are biased towards larger, breeding-age individuals, which in turn has significant negative effects on population projections and extinction risks. With the growing popularity of electrified fences for the protection of livestock and game from unwanted predators and theft, the tortoise populations are being affected negatively and this could lead to their demise in the near future if nothing is done about the situation.

The remaining three papers focus on human-tortoise interactions in the past, using material from the archaeological site of Wonderwerk Cave (Northern Cape Province) as a case study. In the second paper of the dissertation, bone mineral density (BMD) values were calculated for leopard tortoise limb bones using a densitometer equipped with software for small

animals. Values obtained were compared with published values for leporids (rabbits/hares), canids (dogs/wolves etc.) and marmots. Since the shape of tortoise bones differ from those of mammals, new scan sites had to be defined as this was the first time a reptile has been scanned.

The third paper reports the results of a second round of scanning that was undertaken also with the bone densitometer, but this time for the shell (carapace and plastron). As no tortoise shell has ever been scanned before, there were no values to compare our findings with. To overcome this, computed tomography (CT) scans on three different species of South African tortoise were compared with one another.

BMD values obtained from extant tortoises were then used to investigate survivorship of bones in an archaeological context, the Later Stone Age tortoise remains from Wonderwerk Cave, Northern Cape Province (~15,000 years BP to present). The results showed that bone density can be a key taphonomic agent in archaeological and palaeontological assemblages, as the denser parts of the bones will survive better than those that are less dense, and so can help predict which elements of a tortoise should preserve the best over time.

In the fourth paper, the results of analysis of the Earlier Stone Age (ESA) tortoise remains from Wonderwerk Cave were reported, spanning the period ~2.0 million years to ~0.5 million years BP. These remains were studied taxonomically, enabling identification of the tortoise remains as belonging to the leopard tortoise, making this assemblage the oldest occurrence of this species in an archaeological site in southern Africa. In addition, Geographic Information Systems (GIS) were used to plot the spatial distribution of the tortoise remains from all the ESA strata. Results showed that finds from the three strata with the largest samples were concentrated in squares implying that they represented bones from the same animal. Taphonomic analysis of the ESA remains, compared to data for other

Early- and early Mid-Pleistocene sites in Africa, suggest that the Wonderwerk Cave assemblage is primarily anthropogenic in origin with some evidence for carnivore activity.

This dissertation has contributed new and valuable information specifically on the threat faced by leopard tortoise populations due to electrified fences, and highlights the need for urgent attention. It has also provided the first bone mineral density values for tortoises, and information on species biogeography in the Pleistocene. The results presented herein open new opportunities for investigating tortoise (palaeo)-biogeography in southern Africa, and the value of such research to understand environmental change impacts on this animal group.

Introduction

1. Background to the Testudinidae

Modern land tortoises fall within the order Testudines (the turtles) that includes terrestrial tortoises (Testudinidae), marine turtles (Cheloniidae) and freshwater turtles (Trionychidae). In this work the term tortoise/s is used exclusively to refer to terrestrial forms and turtle/s to refer to freshwater and marine species. All members of the Testudines are characterized by a shell - either a hard bony shell or a soft cartilaginous one. They are members of the Cryptodira - chelonians whose head can be withdrawn into the shell and is protected by the forelimbs that retracts with the head, the neck skin can invaginate and the pelvis is not fused to the shell but attached by ligaments (Branch, 2008).

According to the fossil record, the earliest Testudinidae originated in Asia and from there dispersed during the Eocene (56.5 to 35.5 million years ago [Mya]), first to North America and Europe (Early Eocene), and later into Africa (Late Eocene) (Holroyd and Parham, 2003; Le et al., 2006; Hofmeyr et al., 2017). Based on mitochondrial and nuclear DNA sequence data, Hofmeyr et al. (2017) suggested that Testudinidae may have occupied Africa even earlier than attested by the oldest fossil Testudinid remains from Egypt, which date back to the Oligocene ca. 35.5 Mya.

This study focuses on members of the family Testudinidae in South Africa, with a specific emphasis on the leopard tortoise (*Stigmochelys pardalis*) (Figure 1). South Africa is home to ~30% of the world's total tortoise species, with three endemic tortoise Genera (*Chersina, Psammobates, Homopus*) and eight endemic or near-endemic species (angulate tortoise - *C. angulata,* Parrot-beaked dwarf tortoise - *H. areolatus,* Karoo dwarf tortoise - *H. boulengeri,* Greater dwarf tortoise - *H. femoralis,* Speckled dwarf tortoise - *H. signatus,* Lobatse hinge-back tortoise - *K. lobatsiana,* Natal hinge-back tortoise - *K. natalensis,* Geometric tortoise - *P. geometricus*), making it a Testudinid hotspot (Hofmeyr et al., 2014;

Rhodin et al., 2018), with more than half of the endemic species occurring in the Karoo Biome (Vernon, 1999).

Figure 1 – Leopard tortoise (*Stigmochelys pardalis*) (Photo: Rian Horn).

In the Red List compiled by the International Union for Conservation of Nature (Rhodin et al., 2018), it states that of all recognised species of tortoises and turtles in the world 20% are critically endangered or endangered and 51.9% are threatened (see Table 1 for the threat level of South African tortoises). Chapter 1 of this dissertation relates to the current threats facing the leopard tortoise in the interior of South Africa, primarily due to the erection of electrified fences, especially around privately-owned land.

Testudine remains are found in fossil hominin and archaeological sites in South Africa from the Early Pleistocene onwards. Currently, the earliest finds are from the site of Sterkfontein, Member 2 in the Cradle of Humankind (Gauteng Province) (ca. 4.2-3.3 Mya; Brain, 1981) followed by Makapansgat Limeworks site in Limpopo Province (ca. 2.5-3.0 Mya; Broadly, 1962). In addition, several slightly younger fossil hominin sites in the Cradle

Table 1 – The threat level of South African tortoise species (after Rhodin et al., 2018).

Species	**Latin name**	**Threat level**
Geometric tortoise	*Psammobates geometricus*	Critically endangered
Speckled Dwarf tortoise	*Homopus signatus*	Vulnerable
Karoo Dwarf tortoise	*Homopus boulengeri*	Near-threatened
Kwa-Zulu Natal Hinged-back tortoise	*Kinixys natalensi*	Near-threatened
Angulate tortoise	*Chersina angulata*	Least concern
Lobatse hinge-back tortoise	*Kinixys lobatsiana*	Least concern
Parrot-beaked Dwarf tortoise	*Homopus areolatus*	Least concern
Greater Dwarf tortoise	*Homopus femoralis*	Least concern
Leopard tortoise	*Stigmochelys pardalis*	Least concern
Speke's hinged-back tortoise	*Kinixys spekii*	Not evaluated
Eastern hinge-backed tortoise	*Kinixys zombensis*	Not evaluated
Serrated Tent tortoise	*Psammobates oculifer*	Not evaluated

of Humankind have yielded Testudine finds: Kromdraai A and B (ca. 2.0 Mya; Brain, 1981), Drimolen (ca. 2.0 to 1.8-1.6 Mya) (Broadley, 1962, 1997), Sterkfontein Member 5 (ca. 1.9-1.5 Mya; Brain, 1981), Swartkrans Member 1 (ca. 1.8 Mya), Member 2 (ca. 1.5 Mya) and Member 3 (ca. 1.0 Mya; Watson, 2004) as well as Elandsfontein in the Western Cape (ca. 1.0 and 0.6 Mya). The problematic issue of assigning these remains to early hominin activity is discussed in Chapter 4.

In terms of Genus/species identification, this has not been attempted for most of these early finds. For example, at Sterkfontein Members 2 and 5, Swartkrans Members 1, 2 and 3, and Kromdraai A and B, the tortoise remains are listed merely as “indet. Chelonian”, while at Makapansgat the finds were attributed to *Geochelone* sp. One exception is the site of Drimolen where an early form of tent tortoise, *Psammobates antiquorum,* was documented (Broadley, 1962, 1997). Braun et al. (2013) reported the presence of angulate tortoise (*Chersina angulata*) from the Middle Pleistocene hominin occupation layers at the site of Elandsfontein. Although not a Testudine, it is worth noting the identification of the marsh terrapin (*Pelomedusa*) at the site of Taung (ca. 2.5 or 2.0 Mya) (Wood, 1973). Chapter 4 of this dissertation presents an additional example of an Early-Middle Pleistocene tortoise assemblage from Wonderwerk Cave (Northern Cape Province) spanning the period ca. 2.0-0.5 Mya, while Chapters 2 and 3 describe the Holocene tortoise remains from the same site (15,000 BP to the present). The species identified in all layers at Wonderwerk Cave is exclusively the leopard tortoise (*Stigmochelys pardalis*), and the oldest finds from this site ca. 1.0 Mya, represent the earliest identification of this taxon in southern Africa.

2. Aims and rationale of the dissertation

The aims of this dissertation are to examine the past ecology, distribution and factors affecting survivorship of tortoises and their remains in the Northern Cape and Free State Provinces of South Africa, as an aid for conservation of tortoises in the region today.

The dominant vegetation type of the Northern Cape Province is Eastern Mixed Nama Karoo, along with lesser amounts of Upper Nama Karoo (Mucina and Rutherford, 2006). The dominant geology in the area is rocky Karoo dolerite interspersed with sandy to loamy red soils that overlie a shallow calcrete layer (Vorster, 2003). The area has a semi-arid continental climate (Climate-data.org), with a distinct cold and dry period during winter (June–August; -8 to 25°C) and a hot and rainy period during summer (December–February; 8 to 40°C). Four species of tortoise inhabit the Northern Cape region today (Figure 2): the greater padloper (*Homopus femoralis*), Kalahari tent tortoise (*Psammobates oculifer*), tent tortoise (*Psammobates tentorius*) and the leopard tortoise (*Stigmocelys pardalis*) (Boycott and Bourquin, 2000; Branch, 2008; Hofmeyr et al., 2014). Of these, only three species also occur in the adjacent Free State Province (a source of some of the modern samples used in this study): the greater padloper, the Kalahari tent tortoise and the leopard tortoise (Hofmeyer et al., 2014).

The main reason for choosing this dissertation topic is the endangered status of tortoises worldwide, including in South Africa (Hofmeyr et al., 2014; Rhodin et al., 2018). Tortoises are an important element in past and present ecosystems (Cobo and Andreu, 1988; Guzman and Stevenson, 2008; Gibbs et al., 2010; Froyd et al., 2014). For example, like other herbivores, they play a role in seed dispersal and open pathways in the landscape (Milton, 1992). Yet, as they are easy prey for both other animals and humans, tortoises are extremely endangered. As noted in 2018 by Mickey Agha, an ecologist at the University of California, Davis (https://news.mongabay.com/2018/09/as-turtles-go-so-go-their-ecosystems/): "*We must take the time to understand turtles, their natural history, and their importance to the environment, or risk losing them to a new reality where they don't exist. Referred to as a shifting baseline, people born into a world without large numbers of long-lived reptiles, such as turtles, may accept that as the new norm*."

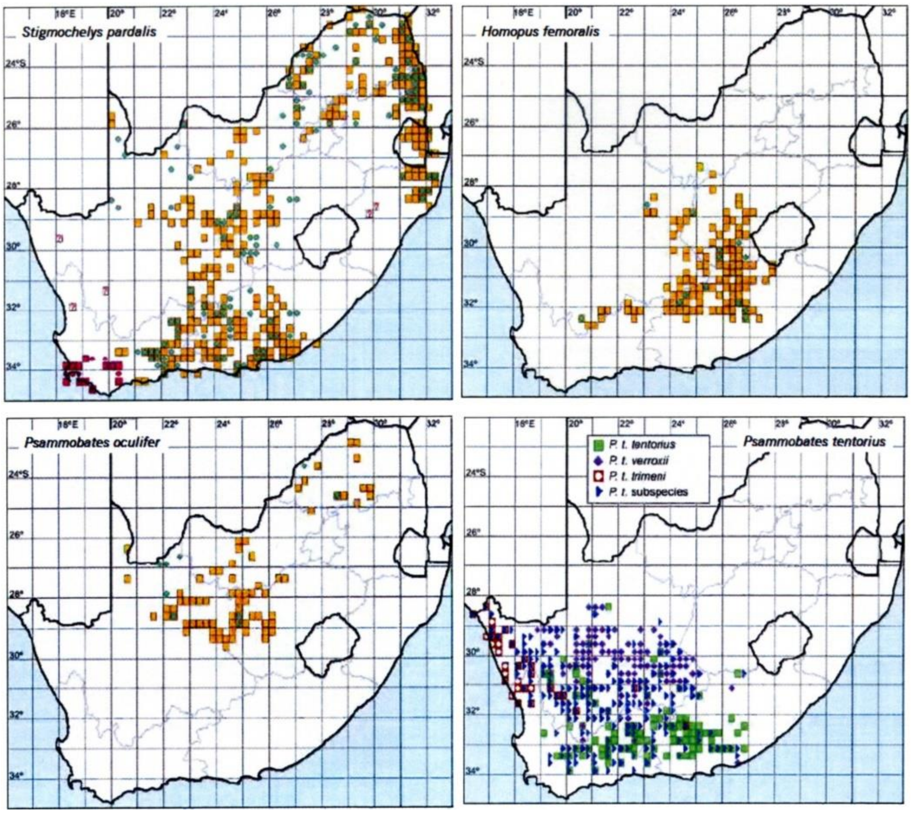

Figure 2 – Distribution of the four tortoise species in the research area covered in this dissertation (after Hofmeyr et al., 2014).

In South Africa, as elsewhere in the world, numerous species of birds (Branch and Els, 1990; Boshoff et al., 1991; Malan and Branch, 1992; Sampson, 2000), non-human primates (Hill, 1999) and mammalian carnivores (Lloyd and Stadler, 1998; Kamler, et al., 2012) are known to prey on tortoises, especially tortoise eggs, hatchlings and juveniles, although large raptors such as eagles may take bigger animals (Boshoff et al., 1991; Davies, 1994). Therefore, from the youngest age, animal predation impacts tortoise survivorship. There is also a human threat to tortoises that is not new as reflected in the abundance of their remains in archaeological sites all over the world (Connolly and Eckert, 1969; Schneider and Everson, 1989; Speth and Tchernov, 2002; Blasco, 2008; Blasco et al., 2011; Biton et al., 2017; Nabais and Zilhão, 2019) as well as in South Africa (e.g. Klein and Cruz-Uribe, 1983, 2000, 2016; Sampson, 1998; Avery et al., 2004, 2008; Thompson and Henshilwood, 2014a, 2014b). Furthermore, Klein and Cruz-Uribe (1983, 2000, 2016), demonstrated that tortoises in South Africa underwent a significant size diminution as a result of human over-exploitation. Currently, the leopard tortoise, although not seen as endangered in South Africa, is negatively affected by the erection of electrified fences along farm boundaries in the study region (Burger and Branch, 1994; Beck, 2010; Arnot and Molteno, 2017; Macray, 2017), such that greater attention needs to be given to this subject, as addressed in Chapter 1.

3. Bone Mineral Density (BMD) in tortoises

A particular focus of this dissertation has been on factors that influence tortoise bone preservation, since biases such as taphonomic effects can cloud our ability to uncover details about tortoise palaeoecology. Specifically, the effect of bone density mediated attrition on the preservation of different skeletal elements has been investigated, under the assumption that bones (or parts of bones) with higher bone density values will preserve at higher rates than bones with lower density values. To date, this issue has not been studied in tortoises, despite being a potentially critical taphonomic factor shaping fossil, archaeological and modern Chelonian bone assemblages (Binford and Bertram, 1977; Lyman, 1984, 2014). Under certain conditions, bone density mediated attrition may even lead to the total destruction of bone remains in a site and in the context of this study, will bias our understanding of the role Testudines played in the ecology of past landscapes and in the lives of past peoples. In Chapters 2 and 3 the datasets for bone mineral density values (BMD) that were developed for modern tortoises are given. In these chapters their relevance to archaeological assemblages is demonstrated in a case study derived from a ca. 2.0 million year long sequence from Wonderwerk Cave, Northern Cape Province (Horwitz and Chazan, 2015).

Another theme that has guided the research for this dissertation, is what the author considers as a methodological gap in the study of tortoise remains recovered in South African archaeozoological contexts. Although tortoise remains are extremely abundant in archaeological sites, species identification and their implications for the past biogeographic distribution of tortoise species has not been addressed. Moreover, the focus of much of the archaeozoological research on tortoises has been on the angulate tortoise (*Chersina angulata*) that is found in sites in the Cape Province (Sampson, 1998; Klein et al., 1999, 2004; Avery et al., 2004, 2008; Thompson and Henshilwood, 2014a, 2014b), with little attention paid to other species or other regions. The reason for this may be the bias in research that has targeted sites in the Cape Province, linked to the fact that it is by far the most common tortoise species inhabiting that region. This contrasts with most other regions of South Africa, where few studies of Testudines have focused on species identification (see the study by Sampson, 1998 which is an exception). Furthermore, most published faunal lists generated for archaeological and fossil sites in South Africa, in general, do not provide the number of identified specimens (NISP) or minimum number of individual counts (MNI) for tortoise remains, but simply list their remains as present (or absent). Again, this lack of detail makes it virtually impossible to generate and test hypotheses relating to tortoise palaeoecology in the region. The issue of species identification is addressed in Chapters 2, 3 and 4 in relation to the Wonderwerk Cave remains.

4. History of research

In order to achieve the aims of this dissertation, this research entailed several different steps.

(1) The first stage was to visit natural history collections in South Africa containing specimens of tortoise species that inhabit the interior of South Africa, with an emphasis on the three species found in the vicinity of Wonderwerk Cave today: the leopard tortoise (*Stigmochelys pardalis*), Kalahari tent tortoise (*Psammobates oculifu*) and the greater padloper (*Homopus femoralis*). The aim was to measure tortoise skeletons (limbs as well as shells) to enable me to develop morphological and metric characters that could be applied to identify tortoise species found in archaeological assemblages, since only selected osteological criteria have been published that are relevant to South African Testudines (e.g. Loveridge and Williams, 1957; Olsen, 1968; Sobolik and Steele, 1996; Lapparant du Broin et al., 2006).

Although five museum collections and one University collection in South Africa were visited (National Museum, Bloemfontein; Ditsong in Pretoria, East London Museum; McGregor Museum in Kimberley; Bay World in Port Elizabeth and the collection in the Archaeology Department, University of Cape Town), the vast majority of the collections comprised complete tortoise shells with the keratinous scutes still adhering, and lacked limb elements or else comprised whole tortoises kept in liquid from wet collections. These collections proved unsuitable for the aims of this study. Thus, a large part of the initial work for this dissertation entailed the collection of complete tortoise skeletons.

(2) To obtain tortoise skeletons, I advertised in local newspapers, an agricultural magazine (*Die Landbou Weekblad*) and contacted Nature Conservation offices in the Free State and Northern Cape Provinces. Since 2014, 237 partial and complete tortoises, representing seven species, have been collected in this manner. They were cleaned, prepared, acquisitioned and boxed, and relevant measurements were taken for this dissertation research. Table 2 presents the list of tortoises resulting from this work that are now held in the collection of the Florisbad Quaternary Research Department, National Museum, Bloemfontein. It must be emphasized that no live animals were killed for the purposes of this study.

Table 2 – The tortoise species collected for this project and housed at the Florisbad Quaternary Research Department, National Museum, Bloemfontein.

Common Species name	**Latin name**	**Total**
Leopard tortoise	*Stigmochelys pardalis*	197
Angulate tortoise	*Chersina angulata*	15
Geometric tortoise	*Psammobates geometricus*	17
Tent tortoise	*Psammobates tentorius*	2
Kalahari tent tortoise	*Psammobates oculifer*	3
Bell's hinged-back tortoise	*Kinixys belliana*	1
Parrot-beaked padloper	*Homopus areolatus*	2
Total		237

(3) A spin-off from the collection project, was that numerous live leopard tortoises (*Stigmochelys pardalis*), were also offered to the author. As a conservation measure, in consultation with the Mangaung Metropolitan Municipality and the Management Committee of Grant's Hill (Figure 3), it was decided to create a refuge area for leopard tortoises in this natural park (35 ha) situated within the urban area of the city of Bloemfontein (Schulze,

Figure 3 – Aerial view of Grant's Hill Conservation area (Taken from: Schulze, 2017).

2017). The Grant's Hill Park already had a few leopard tortoises inhabiting it and also falls within their natural biogeographic range.

Figure 4 – Photographs of releasing tortoises at Grant's Hill. a) Weighing of the larger tortoises with a pull scale, b) Documenting all tortoises, c) Releasing of the tortoises with volunteers in the background, d) Released tortoises with numbers painted on their shells.

For example, the carapace measurements taken on a live tortoise that was weighed could then be used to extrapolate live weight for the same species of tortoise found in the osteological collection. Moreover, once a correlation is established between carapace length/breadth, tortoise limb bone size and tortoise weight (for a specific species), it will be possible to use limb bone size of archaeological tortoises of the same species, to estimate their size and live weight. These measurements were taken to increase our database and will be used in future studies.

(4) In order to understand the past exploitation pattern of tortoises in the Northern Cape Province, the tortoise assemblage from the archaeological site of Wonderwerk Cave was selected as a case study. This site was chosen as it has the longest archaeological record of any site in the arid interior of South Africa and contains abundant faunal remains, including tortoises, spanning the entire ca. two million year-long sequence.

Wonderwerk Cave (27º50’44.7”S; 23º33’12.3”E) is situated in a low foothill of the Kuruman hills in the Northern Cape Province (Beaumont, 1990; Horwitz and Chazan, 2015; Ecker et al., 2017). The cave has yielded archaeological deposits that span the Oldowan as well as Earlier, Middle and Later Stone Age lithic industries, and include botanical and faunal remains (Beaumont, 1990; Chazan et al., 2008, 2012). Tortoise assemblages from all archaeological layers within Excavation 1 situated adjacent to the cave entrance were examined, beginning in the Stratum 12 Oldowan layer, dated to over 2.0 Mya and ending in the sub-recent Stratum 1, dating to the last 100 years. For the Holocene assemblage, most tortoise material had already been separated out from other taxa by Francis Thackeray as part of his dissertation research (Thackeray, 1984). For the Earlier Stone Age, tortoise remains were made available by James Brink and Liora Kolska Horwitz who are working on these faunal assemblages.

For all tortoise remains, skeletal elements were identified to bone (Loveridge and Williams, 1957; Sobolik and Steele, 1996; Olsen, 1968; Plug, 2014), sided where possible, and quantified (NISP counts and MNI estimates – see Grayson, 1984; Lyman, 2012). No MNE (Minimum number of Element) counts were made given the small sample sizes and high degree of fragmentation in the assemblages, that did not enable precise placement of each fragment within the skeleton. Identification of the species represented in the cave was determined using metric criteria developed based on investigation of modern collections, and on morphological criteria as published in the literature (Loveridge and Williams, 1957;

Sobolik and Steele, 1996; Olsen, 1968; Plug, 2014) and verified by myself on the museum collections. Nomenclature for bones follows Zangerl (1969). To assess the agent responsible for tortoise exploitation in the cave, taphonomic studies were undertaken to score burning, butchery and animal damage following criteria given in published literature (Stiner and Bar-Yosef, 2005; Blasco, 2008; Thompson, 2010; Blasco et al., 2011; Thompson and Henshilwood, 2014a; Andrews and Fernandez-Jalvo, 2016). Unfortunately, insufficient numbers of long bones were preserved so that no assessment could be made of size change over time, as in some previous studies (Klein and Cruz-Uribe, 1983, 2000, 2016).

As noted above, an innovative aspect of this research was to examine survivorship of tortoise remains in archaeological assemblages as they relate to bone density mediated attrition. This was done by quantifying the bone mineral density (BMD) values of individual bones in the tortoise appendicular skeleton and shell. BMD values were obtained for three tortoise species - leopard tortoise (*Stigmochelys pardalis*), angulate tortoise (*Chersina angulata*) and the greater padloper (*Homopus femoralis*), using two methods: bone densitometry and computed tomography (CT) scans. Although similar studies of BMD have been carried out on a variety of mammals (Brain, 1969; Behrensmeyer, 1975; Boaz and Behrensmeyer, 1976; Binford and Bertram, 1977; Lyman, 1984; Chambers, 1992; Kreuzer, 1992; Lyman et al., 1992; Elkin, 1995; Galloway et al., 1997; Lam et al., 1998, 1999; Pavao and Stahl, 1999; Stahl, 1999; Pickering and Carlson, 2002; Ioannidou, 2003; Munson and Garniewicz, 2003; Carlson and Pickering, 2004; Novecosky and Popkin, 2005; Symmons, 2005; Gutiérrez et al., 2010), birds (Dirrigl, 2001; Cruz and Elkin, 2003; Broughton et al., 2007), and fish (Nicholson, 1992; Butler and Chatters, 1994; Butler, 1996), this study is the first to estimate BMD in a reptile. The modern data set generated was used as a baseline against which to compare the survivorship of tortoise bones in all levels at Wonderwerk Cave

(Chapters 2 and 3). The findings can be applied to other fossil and archaeological tortoise bone assemblages worldwide.

(5) A second area of investigation relating to tortoise survivorship was an investigation of present-day tortoise survival in relation to electrified fences. The erection of electrified fences has become widespread over the last few years in the interior of South Africa as a means of keeping out unwanted predators, reducing stock theft and stopping costly game animals from escaping. The zoologist from the McGregor Museum in Kimberley (Beryl Wilson) has for several years, been monitoring the boundaries of the same electrified fences every 6 months to document and sometimes collect, dead animals. She alerted me to the large numbers of dead leopard tortoises that had been electrified, adjacent to three farm fences. Since 2014, all tortoise remains found along certain stretches of electrified fence bordering three farms located in the Northern Cape Province and Free State, were collected under permits given from the Department of Environment, Northern Cape and the Department of Economic Development, Tourism and Environmental Affairs, Free State to Beryl Wilson, and then prepared and acquisitioned into the National Museum’s collection. Chapter 1 presents the findings for the impact of electrified fences on leopard tortoise demography in the region.

5. Problems encountered in this research

The initial problem faced was the lack of a suitable osteological collection of complete tortoise skeletons, that had to be created as outlined above.

A second problem related to my work on BMD. I encountered a problem in finding a suitable bone densitometry machine and a micro-CT Scanner in the Bloemfontein area, that were equipped with the software for scanning and quantification of density for something as small as a tortoise. As such, bone densitometry scanning was undertaken at the University of Potchefstroom, 320 km away and CT scanning was done at NECSA in Hartebeestpoort, 460 km away. This led to time and financial constraints and so I was unable to scan all skeletal elements collected, but only a subset, while for the CT scanner the number of scan areas had to be limited and only density of the trabecular bone was quantified and not that of outer or inner cortical bones layer. The computed tomography (CT) scanning of the three species of tortoise at NECSA was also a first attempt at such work and a unique protocol had to be devised to do this.

This was, to my knowledge, the first time that tortoise bones have been scanned for BMD quantification. Since their bones differ from those of mammals, new suitable scan sites had to be chosen on each bone, including where to take measurements on the virtual slices.

A third problem was the lack of free access to farms in the region in order to collect all tortoises found dead along the electric fences. Consequently, samples used in this research are not as complete as hoped for and no study could be carried out on living populations on the same farms to compare to live population composition. Instead published data on the demography of living populations from other regions was used.

6. Layout of the dissertation

This dissertation consists of published and as yet unpublished papers on different aspects of past and present Testudines in the interior of South Africa.

Chapter 1

*Holt, S., Horwitz, L.K., Wilson, B., Codron, D. 2019. Leopard tortoise (*Stigmochelys pardalis Bell, 1928*) mortality caused by electrified fences in central South Africa and its impact on tortoise demography.* In preparation for submission.

In this paper the effect of electrified fences on the mortality rate of the leopard tortoise in two separate areas in the arid interior of South Africa was examined. Leopard tortoise remains were collected along electrified fences in these areas from 2014 to 2019 and measurements on the shells and bones were taken to determine the size of the individuals affected. Fence-related mortalities are expected to be biased towards larger individuals that cannot move freely underneath the lowest fence lines. To test this hypothesis, the size distribution of the electrocuted tortoise sample was compared with those of living leopard tortoise populations sampled elsewhere in southern Africa. Since survivorship of large, reproductively active adults is critical for Chelonian populations (e.g. Crowder et al., 1994), a population viability analysis was performed to estimate the possible influences of fence-related mortalities on this population. Population projections were derived from stochastic stage-structured matrix models, which reveal a significantly higher probability of population extinction when fence-related mortalities are considered.

Chapter 2

Holt, S., Codron, D., Horwitz, L.K., 2018. Bone Mineral Density in the Leopard Tortoise: Implications for Inter-Taxon Variation and Bone Survivorship in an Archaeozoological Assemblage. Quaternary International 495, 64-78.

In this paper, bone mineral density (BMD) scan values were obtained for the limb bones of a modern male leopard tortoise using a bone densitometer (DEXA) machine. In order to compare density patterns with other vertebrates, we examined density volumes (DV) for the leopard tortoise against those of published values for a range of mammals with adult body weights of up to ca. 8 kg. This included - foxes (*Vulpes* spp.), marmots (*Marmota* spp.), rabbits (*Sylvilagus floridanus* and *Oryctolagus cuniculus*) and hares (*Lepus* spp.), and three larger Canid species - wolf, dog and coyote (Lyman et al., 1992; Pavao and Stahl, 1999; Novecosky and Popkin, 2005). Results illustrated that bone density reflects the biomechanical adaptation of a species, with the tortoise DV values similar to those of other fossorial taxa.

Finally, the BMD values generated for the modern leopard tortoise were used to assess the survivorship of leopard tortoise limb bones from Late Pleistocene-Holocene layers at the site of Wonderwerk Cave. The data show a significant positive relationships between bone frequencies of bone elements in all layers of the Wonderwerk Cave sequence. Results indicate that this assemblage has undergone some degree of bone density-mediated attrition, probably influenced by burning and deposition time rather than animal agents. The data published in this paper is the first of this kind for a reptile, the leopard tortoise, and will thus contribute to the list of vertebrates for which such data has been published.

Chapter 3

*Holt, S., Horwitz, L.K., Hoffman, J., Codron, D., 2019. Structural density of the leopard tortoise (*Stigmochelys pardalis*) shell and its implications for taphonomic research. Journal of Archaeological Science: Reports 26 (2019) 101819.*

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This is a companion paper to that presented in Chapter 2. Here, bone mineral density (BMD) values were calculated for the shell (carapace and plastron) of the same leopard tortoise specimen studied in Chapter 2 using the same bone densitometer machine (DEXA). For comparison with the BMD data, computed tomography (CT) scans were taken of the shell of a leopard tortoise (*Stigmochelys pardalis*) and two other tortoise species that differ in shape and size - angulate tortoise (*Chersina angulata*) and the greater padloper (*Homopus femoralis*). The results indicate that the patterning of bone density is similar across shell elements and scan sites in all three species, although all values were lower in the greater padloper, which can be attributed to shape differences – a flat rather than domed shell. Significant differences were found among elements for BMD and density volume (DV), but not for bone mineral content (BMC).

In addition, the leopard tortoise BMD values were tested against data on shell elements found in the Late Pleistocene-Holocene at Wonderwerk Cave. For most strata there was a significant association with skeletal element survivorship, again demonstrating the role played by BMD in determining the skeletal composition of this assemblage. This study was the first of its kind for tortoises, and hopefully will be of use in the study of other fossil and archaeological tortoise bone assemblages.

Chapter 4

Holt, S., Codron, D., Birkenfeld, M., Horwitz, L.K. 2019. Early Pleistocene Tortoise Exploitation at Wonderwerk Cave, South Africa. In preparation for submission.

In this paper the ca. 400 tortoise remains from the Earlier Stone Age (ESA) layers of Wonderwerk Cave, Northern Cape Province were examined. The remains span the time period ca. 2.0 to 0.5 Mya. In this study skeletal element representation, the spatial distribution of remains, taphonomic modifications and species identification were investigated. Using morphological and metric criteria, the species represented in the Earlier Stone Age level dated to ca. 1.0 Mya was identified as leopard tortoise, making it the earliest definite identification of this species in southern Africa. This is the same taxon occurring in the Late Pleistocene-Holocene levels at the cave.

In addition, the role played by hominins versus other biotic and abiotic agents in the accumulation of this assemblage was discussed. Based on the skeletal element representation, presence of percussion fractures and extent of burning, it was concluded that the tortoises were most probably introduced into the cave by hominins.

The findings from this site are further discussed in relation to other Early Pleistocene Testudinid assemblages from other sites in Africa (and to a lesser extent sites in Europe), many of which have not been studied in such detail. The Wonderwerk assemblage therefore provides an important addition to our knowledge of the broad spectrum of resources exploited by early hominins and the different types of dietary strategies employed by them.

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Chapter 1

Holt, S., Horwitz, L.K., Wilson, B., Codron, D. 2019. Leopard tortoise (*Stigmochelys pardalis* Bell, 1928) mortality caused by electrified fences in central South Africa and its impact on tortoise demography. In preparation for submission.

Leopard tortoise (*Stigmochelys pardalis* Bell, 1928) mortality caused by electrified fences in central South Africa and its impact on tortoise demography

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Abstract

We examine here the impact of electrified fences in the Free State Province (Jacobsdal distict) and Northern Cape Province (Strydenburg district) on leopard tortoise (*Stigmochelys pardalis*) mortality and its implications for survivorship of this species. Data on leopard tortoise populations from other regions were used to create a model of a living population and then this was compared to our mortality data. The study show a strong selection bias towards larger (breeding age) individuals, which, given the life history of the species, should have strong (negative) consequences for populations. Then, we used size-structured matrix models to compare population growth rates of tortoises that are and are not affected by fencing. Population projections, taking into account variation in survivorship and re-productive rates across and within size classes, indicate substantially higher risk of negative population growth (and eventual extinction) in populations affected by electrified fences. These results confirm that fencing is a problem for the leopard tortoise population in this, and probably other, regions. We call for further work into these effects, as well as highlighting a need to urgently address this problem before its too late.

Keywords: Jacobsdal District (Free State); Strydenburg District (Northern Cape); tortoise conservation

1. Introduction

In the former Cape Province of South Africa, in accordance with Article 4 of Ordinance No. 26 of 1957, it was compulsory for farmers to join a government subsidized hunting club to control problematic predators in that area (Stadler, 2006). This was in addition to the installation on farms of government-subsidized jackal-proof fencing (Stadler, 2006; De Waal, 2007). However, from the 1990's on, local administrations disbanded these clubs (e.g. the *Oranjejag* in the Free State was disbanded in 1993) leading to a rise in livestock losses from predation (De Waal, 2007). Consequently, in this region, a large number of both livestock and wildlife farmers chose to erect electrified fencing around their farms, in order to keep costly game and livestock inside, to limit poaching, and to control predators (predominantly caracal (*Caracal caracal*) and black-backed jackal (*Canis mesomelas*)) (Bergman et al., 2013; Du Plessis, 2013). This has followed a worldwide trend, with electrified fences the preferred deterrent to protect animals on both farms and nature reserves in recent years (e.g. Linhart et al., 1982; Heard and Stephenson, 1987; Mayer and Ryan, 1991; Farmer, 2002; Koiko et al., 2008; Beck, 2010; Jori et al., 2011; Sapkota et al., 2014; Macray, 2017).

When touched by an animal or person, the electrified fence creates an electrical circuit via a power energizer that converts power into a brief, high voltage pulse with voltages of varying strengths (Beck, 2010). Electrified fences differ greatly in their structure that is usually determined by their objective (Arnot and Molteno, 2017a). They differ in total height, the number of electrified strands, height between the strands (though this usually varies from 30-300 mm),[1] voltage (modern energisers generate approximately 5000 volts)

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[1] Macdonald (nd) gives an indication of the amount of strands and their spacing for cattle and calves - 3 strands with 290; 600 and 900 mm above ground level; sheep and lambs (even topography) - 4 strands with 150; 335; 600 and 900 mm above ground level; sheep, lambs and goats (uneven topography) - 4 strands with 150; 290; 900 mm above ground level; pigs - 3 strands with 150; 335; 600 mm above ground level while security and game - 14 strands with 1 off-set and 150 mm above ground level and 150 mm between successive strands with off-set support on "top" and "3rd" from top strand.

and if the fence is electrified on one or both sides (Burger and Branch, 1994; Beck, 2010; Macray, 2017; Macdonald, nd). In addition, many electrified fences have a “trip-wire” - a low live wire that is placed just above the ground at 50-100 mm away from the fence, on either one or both sides, to prevent animals and/or predators from burrowing under and escaping or entering the protected area (Arnot and Molteno, 2017a).

In the *Nature Conservation Ordinance Act, Act 8 of 1969* for game/stock farms in South Africa, there is currently no formal national guideline or legislation for the design of electrified fences, although local policies may be found (e.g. Cape Nature, 2014). This is surprising given the high numbers of wild animals that are killed by them. Table 1 gives a compilation list of 36 animal species that are documented as having been electrocuted by fences in South Africa over the time period 1987 to 2010. The animals range from large mammals such as an adult bushbuck (*Tragelaphus scriptus*) to a broad spectrum of small reptiles (Burger and Branch, 1994; Beck, 2010; Arnot and Molteno, 2017a). Tortoises are among the most common reptiles electrocuted, and although publications list the Lobatse hinged tortoise (*Kinixys lobatsiana*), angulate tortoise (*Chersina angulata*) and even marsh terrapins (*Pelomedusa subrufa*), the leopard tortoise constitutes > 86% of all reptile mortalities (Burger and Branch, 1994; Beck, 2010). The reaction of most animals that come into contact with an electrified fence is to jump away after being shocked, which breaks the current (Burger and Branch, 1994; Beck, 2010; Macray, 2017). But in the case of tortoises, they tend to retract their head into their shell and remain stationary which means that they continue to be pulse electrocuted and eventually die. Moreover, as some tortoises urinate when distressed, this dampens the ground and contributes to the conduction of the current though the animal ultimately increasing suffering and the risk of death (Arnot and Molteno, 2017a).

Table 1 – Alphabetical list of all species electrocuted by fences in South Africa from 1994 to 2010.

Species	Common name	Reference
Mammals		
Atelerix frontalis	South African Hedgehog	Beck 2010
Canis mesomelas	Black-backed Jackal	Beck 2010
Cephalopus natalensis	Red Duiker	Beck 2010
Chlorocebus pygerythrus	Vervet Monkey	Beck 2010; Arnot & Molteno 2017
Crocuta crocuta	Spotted Hyena	Beck 2010
Galago moholi	Lesser Bushbaby	Beck 2010; Arnot & Molteno 2017
Genetta genetta	Small Spotted Genet	Beck 2010
Hystrix africaeaustralis	Porcupine	Beck 2010; Arnot & Molteno 2017
Manis temminckii	Pangolin	Beck 2010; Arnot & Molteno 2017; Burger & Branch 1994
Mellivora capensis	Honey Badger	Beck 2010
Oreotragus oreotragus	Klipspringer	Beck 2010
Orycteropus afer	Aardvark	Beck 2010
Oryx gazella	Gemsbok	Beck 2010
Otolemur crassicaudatus	Thick tailed Bushbaby	Beck 2010
Phacochoerus africanus	Warthog	Beck 2010
Potamochoerus larvatus	Bushpig	Beck 2010
Tragelaphus scriptus	Bushbuck	Burger & Branch 1994
Reptiles		
Chameleo dilepis	Flap necked Chameleon	Beck 2010; Arnot & Molteno 2017
Chersina angulata	Angulate Tortoise	Burger & Branch 1994
Dendroaspis polylepis	Black Mamba	Beck 2010
Dispholidus typus	Boomslang	Beck 2010
Kinixys belliana	Bell's Hinged Tortoise	Beck 2010
Kinixys lobatsiana	Lobatse Hinged Tortoise	Beck 2010; Arnot & Molteno 2017
Pelomedusa subrufa	Marsh Terrapin	Beck 2010; Burger & Branch 1994
Philothamnus	Spotted Bush Snake	Beck 2010
Psammobates oculifer	Kalahari Tent Tortoise	Beck 2010
Psammophis mossambicus	Olive Grass Snake	Beck 2010
Psammophis subtaeniatus	Stripe-bellied Sand Snake	Beck 2010
Python natalensis	Southern African Python	Beck 2010; Arnot & Molteno 2017
Stigmochelys pardalis	Leopard Tortoise	Beck 2010; Arnot & Molteno 2017; Burger & Branch 1994
Thelotornis capensis	Southern Vine Snake	Beck 2010
Varanus albigularus	Rock Monitor	Beck 2010; Arnot & Molteno 2017
Varanus n. niloticus	Nile Monitor	Burger & Branch 1994
Amphibians		
Schlerophrys (=Bufo) pantherinus	Leopard Toad	Beck 2010
Pyxicephalus adspersus	Giant Bullfrog	Beck 2010
Schlerophrys (=Bufo) rangeri	Raucous Toad	Beck 2010

The leopard tortoise (*Stigmochelys pardalis*) is thought to be the most susceptible member of the Testudinidae to being electrocuted as, given its large size, its body makes contact with the electrified wires whilst the smaller tortoises can walk freely underneath the lowest strand of wire and so usually escape electrocution (Arnot and Molteno, 2017a). Moreover, the leopard tortoise has the widest geographic distribution and covers greater distances per day than other tortoise species (Hailey and Coulson, 1996; Beck, 2010; Hofmeyr et al., 2014; Macray, 2017), increasing the likelihood of eventually coming into contact with electrified fences. The aim of this paper is to determine how rates of mortalities due to electrified fencing impacts leopard tortoise population viability. A strong negative impact on tortoise populations is expected because fence-related mortalities are likely bias towards larger size classes, i.e. animals of reproductive age. In animals with a Type III survivorship strategy, i.e. high intrinsic rate of juvenile mortality, survival of breeding-age adults are often the most important demographic element for population growth, as is the case for many Chelonians (e.g. Grobler, 1982; Crowder et al., 1994; Germano, 1994; Keller et al., 1998; Pike and Seigel, 2006).

2. The Leopard Tortoise

Amongst South African Chelonians, the leopard tortoise has the widest biogeographic distribution, and occurs from Montague in the south-western Cape, eastwards towards East London and then northwards through northern and north-eastern South Africa (Boycott and Bourquin, 2000). Historically they are absent from the Little Namaqualand and the Western region of South Africa (Branch et al., 1995; Boycott and Bourquin, 2000; Hofmeyr et al., 2014).

Female leopard tortoises can lay as many as 50 – 70 eggs per year in multiple clutches (Boycott and Bourquin, 2000; Branch, 2008). There are no specific data on hatchling survivorship for this species but most populations reported in the literature are biased towards larger sizes because of high adult longevity and low recruitment rates (e.g. Grobler, 1982; Hailey and Coulson, 1999; Hailey and Lambert, 2002). Leopard tortoise hatchlings weigh 23–50 grams and measure ~40–50 mm in length (SANBI website). Their growth rate is slow during their first year but then increases rapidly, allowing them to move longer distances to feed and become large enough not to be caught by small carnivores (Branch, 2008).

It takes about 7-8 years for a leopard tortoise to reach 1 kg in body weight but thereafter their body mass can double every 2-3 years (Branch, 2008). Adults have an average weight of between 10-20 kg but can grow even bigger, with the largest known leopard tortoise in South Africa, a female from the Eastern Cape, weighing 48.64 kg. There is significant variation in mean adult body size of leopard tortoises throughout their range (McMaster and Downs, 2006), with a trend for larger animals in drier areas (Hailey and Lambert, 2002; McMaster and Downs, 2006). Leopard tortoise females appear to be larger than males irrespective of habitat (McMaster and Downs, 2006) and also grow faster than males, reaching sexual maturity by 15 years[2] of age when growing starts slowing down (Branch, 2008). There is no published data on the age of reproductive maturity in male leopard tortoises, but McMaster and Downs (2006) report sexually active sub-adult males.

Whereas hatchling and juvenile mortalities are expected to be relatively high, sub-adults and adults have high survival rates (e.g. Hailey, 1990; Coulson and Hailey, 1999), approaching ~0.9 (90%). This represents a life history trade-off because it means that reproductive outputs are always high, compensating for high mortality rates amongst the very young i.e. hatchlings (due to predation or other factors). In this study, we use the above

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[2] Boycott and Bourquin (2000) give 10 years as the age of maturation in the leopard tortoise which is young and even 15 years given in Branch (2008) seems excessively young given that females of small-bodied species such as geometric tortoises mature at 10 years (Cape Nature https://www.capenature.co.za/fauna-and-flora/geometric-tortoise/) and large bodied tortoises are known to take longer to mature.

information about tortoise life history to compile size-based population projections that allow comparison of population viability with and without the effects of electrified fencing.

3. Materials

3.1 Study area

This study is based on the remains of dead tortoises collected along the electrified fences of two farms in the Jacobsdal district, Free State Province and one farm in the Strydenburg district, Northern Cape Province (Figure 1). The two farms near Jacobsdal (Farm 1 and Farm 2) are totally enclosed by electrified fencing but only the most western sections along the S892 secondary gravel road were accessible to the authors to collect tortoise remains road-side of the fences.

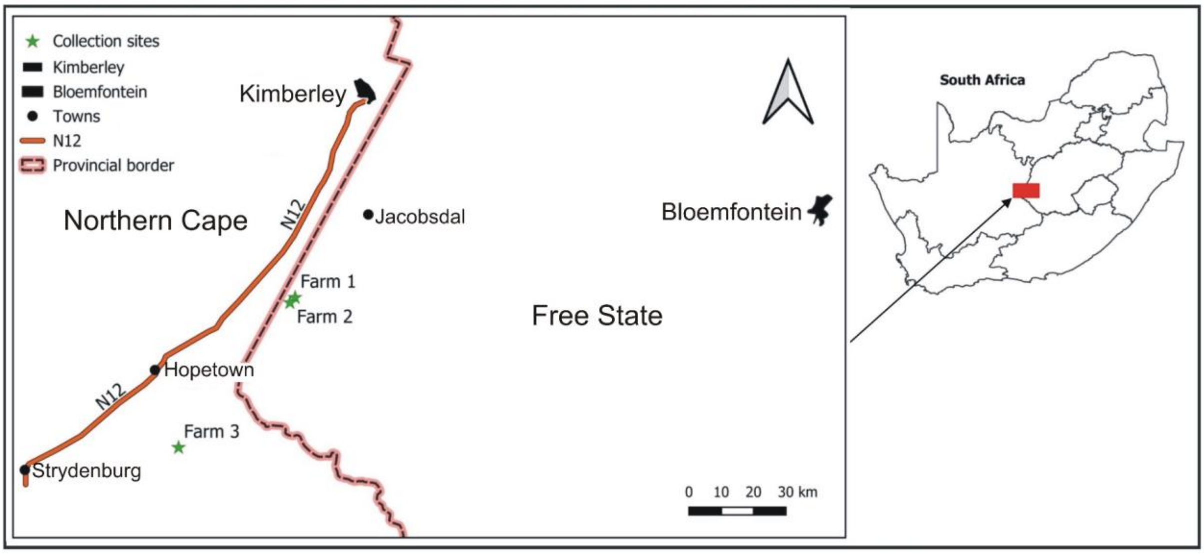

Figure 1 – Location map of the three farms where the dead tortoises were collected.

Both Jacobsdal farms are mixed sheep and game farm enterprises and the electrified fences were erected to keep predators out. The farm near Strydenburg (Farm 3) has a stretch of approximately 5.3 km of electrified fence abutting the S397 gravel secondary road.

The dominant vegetation type of the region covering all three farms is Eastern Mixed Nama Karoo, along with lesser amounts of Upper Nama Karoo (Mucina and Rutherford, 2006). The dominant geology in the area is rocky Karoo dolerite interspersed with sandy to loamy red soils that overlie a shallow calcrete layer (Vorster, 2003). The area has a semi-arid continental climate (Climate-data.org), with a distinct cold and dry period during winter (June–August; -8 to 25°C) and a hot and rainy period during summer (December–February; 8 to 40°C). The mean annual rainfall of Jacobsdal in the north is ±265 mm with Strydenburg further south receiving ±270 mm with the entire area receiving rain mostly in autumn. The former vast migratory herds of springbok (*Antidorcas marsupialis*) have been replaced by domestic stock, particularly sheep, goats, donkeys and cattle. Populations of naturally-occurring wild ungulates including steenbok (*Raphicerus campestris*), common duiker (*Sylvicapra grimmia*), springbok (*Antidorcas marsupialis*), blesbok (*Damaliscus pygargus*), black wildebeest (*Connochaetes gnou*) and gemsbok (*Oryx gazella*), are present, as well as various introduced valuable or rare species. A rich variety of rodents and reptiles also occur in the Nama-Karoo, but all large carnivores (>15 kg) in the region were extirpated by 1900 (Skinner and Chimimba, 2005), and smaller carnivores (jackals, foxes) are the dominant predators present.

Four species of tortoise inhabit both farming areas: the greater padloper (*Homopus femoralis*), Kalahari tent tortoise (*Psammobates oculifer*), tent tortoise (*Psammobates tentorius*) and the leopard tortoise (*Stigmochelys pardalis*) (Boycott and Bourquin, 2000; Branch, 2008; Hofmeyr et al., 2014).

3.2 Farm Samples

As part of a research program monitoring roadside bird species, one of the co-authors (B.W.) drove along the outside of electrified farm fences every 6 months (typically end of

January and end of July). She observed many tortoise mortalities resulting from electrified fences, in particular at Farms 1 and 2 in the Jacobsdal area. For this project, we collected all dead tortoises from outside of the fences of the three farms, over a period of 5 years (2014-2019). Unfortunately, access to the farms and the inner perimeters of the fences was not possible. The lowest stand height at all three farms ranged between 100-150 mm but this was not a constant due to terrain and especially after rains that may have increased or decreased the height.

A total of 152, partial or whole, tortoise skeletons were collected. Table 2 summarises the tortoises collected by area, farm and date. The remains were in different stages of decomposition, but where possible, they were collected as individual animals. They were skeletonised to enable measurement and are currently curated in the collection of the National Museum, Bloemfontein.

Table 2 – Date, farm and district with total numbers of tortoises collected.

Collection Date	Farm	District	Not collected	Rescued	Collected
Jul-14	Farm 1	Jacobsdal			7
Jul-14	Farm 2	Jacobsdal			1
Jan-15	Farm 1	Jacobsdal	8	1	29
Jan-15	Farm 2	Jacobsdal	9		1
Jun-15	Farm 3	Strydenburg			40
Jun-15	Farm 2	Jacobsdal			28
Jul-15	Farm 1	Jacobsdal			4
Jan-16	Farm 1	Jacobsdal			12
Aug-16	Farm 2	Jacobsdal			14
Aug-17	Farm 1	Jacobsdal			5
Aug-17	Farm 2	Jacobsdal			3
Jan-18	Farm 1	Jacobsdal			3
Jan-18	Farm2	Jacobsdal			1
Jan-19	Farm 1	Jacobsdal			4
Total			**17**	**1**	**152**

After an initial trip in July 2014, due to the abundant dead tortoises alongside the fence, the owner of Farm 1 was reported to Free State conservation authorities and an appointment was made by the conservation officials to inspect the farm fence structure. However, prior to the arrival of the officials, the farmer removed all the dead tortoises and dumped them all in a pit on an adjacent farm. These remains were accessed and counted, yielding a minimum number of 50 tortoises of various sizes. This pit included the carcasses from the inaccessible farm-side of the fence that B.W. was not able to collect during previous trips.

In June 2015 it was reported to B.W. that there were a large number of dead tortoises alongside the electrified fence of a third farm (Farm 3) in the Strydenburg district. In August 2015, in collaboration with the National Museum of Bloemfontein, a trip was undertaken to the farm and remains of 40 tortoises were removed from the fence perimeter bordering the gravel road. At this stage the electrified fence had been switched off following a request by conservation officials. Unfortunately the exact time span of the mortalities is unknown, but their condition ranged from skeletonised to reasonably fresh. All these skeletons are included in Table 2.

4. Methods

For all tortoises ≥ 20 mm in length (skeletonized electrified fence specimens), a flexible tape measure marked in millimeters was used to measure: straight carapace length (SCL), plastron length (PL), maximum plastron breadth (PB) and maximum carapace breadth (CB).

For specimens ≤ 20 mm in length, a digital caliper was used to measure straight carapace length (SLC2), plastron length (PL2), maximum plastron breadth (PB2) and maximum carapace breadth (CB2). The difference between the measurements taken with the calipers and the flexible tape measure is only the second number after the decimal such that the deviation is minimal. The SCL/SCL2 measurement was taken from the most anterior point of the nuchal to the most posterior point of the pygal by placing the tortoise on its back with the plastron facing upwards. The PL/PL2 measurement was taken from the most anterior point of the gular to the most posterior point of the xiphiplastron with the tortoise on its back. The PB/PB2 measurement was taken from widest points across the hypoplastron. The CB/CB2 measurement was taken on the widest axis of the carapace when placing the tortoise on its back with the plastron facing upwards, this location varied slightly between specimens (Figure 2). Not all the specimens collected could be measured as some were too fragmented. Appendix 1 gives carapace and plastron measurements for the electrified fence osteological specimens.

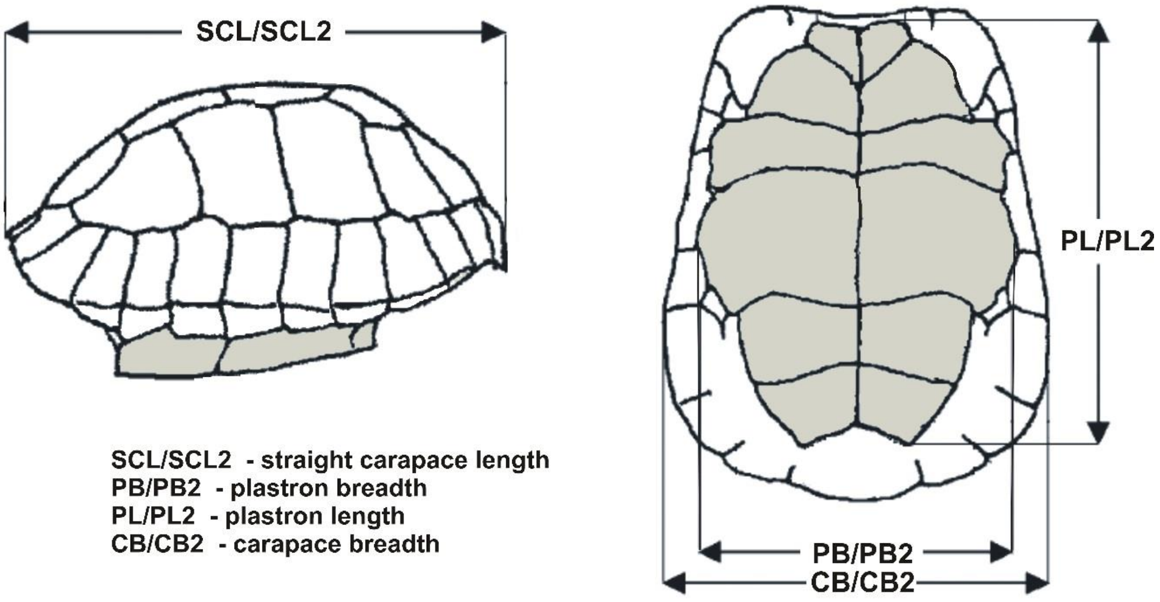

Figure 2 – Illustration showing measurements taken in mm with digital calipers and flexible measuring tape on the carapace (shown in white) and plastron (shown in grey shading).

4.4.1 Statistical Analyses

4.4.1.1 Comparative Size Distribution

To test our prediction that our tortoise sample is biased towards larger individuals due to the effects of electrified fencing on mortality, we compared their size distribution to that of four other populations of leopard tortoises from the literature. One sample derives from a field study of leopard tortoises in 5500 ha of farmland in the De Aar District in the Nama-

Karoo biome (McMaster and Downs, 2006). This field study covered the period October 1997 to April 1999, and included all seasons of the year. Altogether, they found 92 live tortoises in this study area, which they divided into three age classes based on body mass (hatchlings, sub-adults and adults), with males, weighing less than 5 kg and females less than 10 kg, considered as sub-adults. The adults comprised 62 tortoises (19 ♂ and 43 ♀), the sub-adults 26 tortoises (18 ♂ and 8 ♀) while only four hatchlings were documented. They reported a male to female ratio of 1:1.3 (all age classes combined).

A second data set used was generated from a field study by Hailey and Coulson (1999) conducted in the Sengwa Wildlife Research Area (Zimbabwe) from 1982 to 1992. The Sengwa data include a one-off live sample, and a dead sample (3rd data set) collected over 11 years. The researchers found that juveniles were almost twice as frequent in the live sample (41.3 %) than in the dead one (18.2 %) ($X^2 = 41.4$, $P < 0.001$). Juveniles were classified as any tortoise with a straight carapace length (SCL) of less than 180 mm but unfortunately they were not able to sex them. Adult males made up 57.7 % of the live animals but only 36.2 % of those found dead ($X^2 = 21.5$, $P < 0.001$). In both the live and dead samples, females were larger than males. Live females had a SCL of 279 mm ($n = 93$) and 249 mm ($n = 127$) in males, while in the dead sample, female SCL was 313 mm ($n = 155$) and 266 mm ($n = 88$) for males. They reported a significant sexual size dimorphism in their sample, with the mean asymptotic mass of females 1.7 times that of males. As in the other studies, males (0.80) had a higher annual survival rate than females (0.72). The sex ratios were male biased; 1.42:1 in the sample of dead tortoises and in the live sample 1.36:1. For statistical analysis, the living and dead samples were considered separately.

A fourth data set comes from Burger and Branch (1994), who collected size distributions of a dead sample from the Thomas Baines Nature Reserve, Eastern Cape Province.

A uniform size distribution could be created by binning all five datasets (the four published data sets and our data) in size classes of 50 mm increments, based on SCL/SCL2 or PL/PL2 ranging from 50 to 550 mm. Since the size classes were in 50 mm increments the small difference between the caliper and flexible tape were insignificant. The data were compared visually using histograms, and by testing for skewness of each distribution.

4.4.1.2 PVA and Matrix Model Projections

The quantitative effects of fence-related mortalities were studied using population viability analysis (PVA) of a leopard tortoise population not influenced by electrified fencing, and comparing those results to a PVA modified for elevated adult mortalities due to electrified fences representing our study population. The PVA's are based on stochastic size-structured matrix models used to simulate finite growth rates (λ) of each population (Lefkovitch, 1963; Caswell, 2001). We used five stage classes based on straight carapace length (SCL/SCL2) and/or plastron length (PL/PL2): class 1 = hatchlings ($\leq$ 40 mm), class 2 = juveniles (> 40 mm to $\leq$ 120 mm), class 3 = sub-adults (> 120 mm to $\leq$ 180 mm), class 4 = adults (> 180 mm to $\leq$ 350 mm), and class 5 = large adults (> 350 mm). These sub-divisions are based on work done by Kabigumila (2000) in northern Tanzania.

Baseline data for the life tables from which matrices were constructed are derived from the study of leopard tortoises in the Sengwa Wildlife Research Area, Zimbabwe (extrapolated from Figure 1 in Hailey and Coulson, 1999). Comparing the two samples allows an estimation of survival probabilities (*p*) of each stage class *i*.:

$$p_i = 1 - \frac{\frac{D_i}{11}}{D_i + L_i} \qquad \text{(eqn 1)}$$

where *D* and *L* represent the number of dead and live tortoises collected, respectively. Although this population lives in a very different habitat (subtropical Savanna) compared with our study area, the Sengwa data are the most complete life table information we could find for this species in the literature. Parameter estimates for Sengwa are also similar to estimates for other populations and species globally, and so we are confident these data can serve as a useful baseline for our study.

To incorporate mortalities due to electrified fencing, estimates of p_i were calculated as

$$p_i = 1 - \frac{\frac{D_i}{11}+M_i}{D_i+L_i+M_i} \qquad \text{(eqn 2)}$$

where Mi is the number of mortalities in each size class in our sample. To account for uncertainty in these estimates, survival probabilities were randomized ($\widehat{p_i}$) from a normal distribution with mean = p_i and sd = standard deviation of all p_i values, constrained such that $\widehat{p_i} | 0 \leq \widehat{p_i} \leq 1$ (see Table 3).

The Sengwa data (and ours) do not include hatchlings, i.e. individuals smaller than 40 mm (size class 1), and so p_1 was taken from other literature sources. Hatchling survival rates are seldom monitored in the field, but data do exist for other species, notably for the Eastern USA Gopher tortoise *Gopherus polyphemus* (Perez-Heydrich et al., 2012): this meta-analysis presents an average survival rate of 0.229 ± 0.4001 sd for hatchlings, an estimate which is similar to most other estimates for Chelonians we found in the literature.

Table 3 - Life table parameters estimated for the two tortoise populations in this study. Estimates for our population are derived by modifying the Sengwa population to include fence-related mortalities (see text for details).

		p_i		
Size class (*i*)	**SCL or PL (mm)**	**Unfenced**	**Fenced**	**m_i**
1 Hatchlings	<40	0.229 (0.4001)	0.229 (0.4001)	0
2 Juveniles	>40 to ≤120	0.980 (0.0226)	0.972 (0.1658)	0
3 Sub-adults	>120 to ≤180	0.970 (0.0226)	0.954 (0.1658)	0.04
4 Adults	>180 to ≤ 350	0.954 (0.0226)	0.865 (0.1658)	0.71
5 Large adults	>350	0.928 (0.0226)	0.613 (0.1658)	0.75

SCL = straight carapace length; PL = plastron length; p_i = survival probability (sd in parentheses); m_i = simulated size-specific fecundities.

For the size-structured matrix, survivorships were split into two parts: the probability of surviving and remaining in the same class ($p_{i,i}$) and the probability of surviving to the next class ($p_{i,j}$). To estimate $p_{i,j}$, we divided $\widehat{p_\iota}$ by the number of years spent in a particular class. For the leopard tortoise, our size structure is estimated to have time intervals of 1, 2, 2, 15, and >100 years for classes 1 to 5, respectively (see Figure 5c in Hailey and Coulson 1999). Based on this approach, $p_{i,i}$ is calculated as $\widehat{p_\iota}$ - $p_{i,j}$.

Fertilities (F) of each class were calculated as follows. First, a fecundity schedule (m_i) was simulated using the logistic expression

$$m_i = \frac{L}{1+e^{-r(i-i0)}} \qquad \text{(eqn 3)}$$

where L is an upper asymptote (the maximum fecundity rate; we set this at 0.75 to account for some proportion, i.e. 25%, of individuals that may not breed), r is a rate constant (arbitrarily set at 6), and i_0 is an inflection point, i.e. the stage class where m_i is equal to $\frac{L}{2}$. The fecundity schedule was constrained so that $m_i = 0$ for size classes 1 and 2 (Table 3). Further, by setting $i_0 = 3.5$, only a small portion of “sub-adults” are assumed to be reproductively active, a more realistic representation of most Chelonian populations while still accounting for the small number of sub-adult breeders that might occur because some individuals may progress to the adult stage class by the time of the “reproductive survey” (Crowder et al., 1994; Caswell, 2001). Fertilities, for classes 3 to 5 only, were then calculated as

$$F_i = m_i \widehat{p_\iota} R_0 p_{F,i} \qquad \text{(eqn 4)}$$

where p_F represents the proportion of females in each of the three reproductively-active size classes (0.49, 0.47, 0.95 and 0.5, 0.44, 0.89 for the unfenced and fenced populations, respectively), and R_0 is the number of offspring produced per individual per year (mean = 66.8 ± 29.2 sd; data from Branch, 2008; Boycott and Bourquin, 2000; Hofmeyr et al., 2014). In the stochastic model, randomized R_0 $(\widehat{R_0})$ is constrained to values > 0.

For projection of the matrix models, each matrix was multiplied by an abundance vector (**n**) t number of steps until reaching a stable distribution of size classes. The initial **n** was estimated by multiplying standardized survivorships (l_i) by an initial population size (N_0; arbitrarily set at 1 000),

$$l_1 = 1, \text{and } l_i = l_{i-1}\widehat{p_{i-1}} \qquad \text{(eqn 5)}$$

and

$$n_i = N_0 \frac{l_i}{\sum l_i}$$

where population growth rates (λ) for the two populations were compared using Monte Carlo comparisons over 10^4 iterations, to determine the probability that i) growth rate in the fence-influenced population is lower than the other, and ii) either population will experience a negative growth rate, i.e. $\lambda < 1$. All calculations, matrix model projections, and Monte Carlo comparisons were made using customized functions written in R v 3.5.2 (R Core Team 2015).

5. Results

5.1 Comparative Size Distribution

We only found leopard tortoises in the electrified fence assemblages although four species of tortoise inhabit the area. The other three species are the greater padloper (*Homopus femoralis*), Kalahari tent tortoise (*Psammobates oculifer*) and the tent tortoise (*P. tentorius*) (Boycott and Bourquin, 2000; Branch, 2008; Hofmeyr et al., 2014). We propose that they avoid being electrocuted by walking under the lowest strand of wire (in our research area lowest strand height was ~100-150 mm) since they are significantly smaller than the leopard tortoise (Table 4).

Table 4 – The size, weight and height of the four species of tortoise found in the study area (from Boycott and Bourquin, 2000).

Species	**Length SCL/SCL2 ♀**	**Length SCL/SCL2 ♂**	**Weight ♀**	**Weight ♂**	**Height ♀**	**Height ♂**
Homopus femoralis	154 mm	137 mm	652 g	511 g	70 mm	60 mm
Psammobates oculifer	121 mm	118 mm	489 g	319 g	76 mm	63 mm
Psammobates tentorius	131 mm	90 mm	450 g	150 g	79 mm	45 mm
Stigmochelys pardalis	300-450 mm (up to 700 mm)		10-20 kg (up to 40 kg)		300 mm	

Burger and Branch (1994) reported mortality data for 50 leopard tortoises killed due to electrified fences in the Thomas Baines Nature Reserve (Eastern Cape Province). They found that tortoises with a total length of 200-400 mm and a shell height of greater than 250 mm were most frequently electrocuted i.e. adults. Using Yate's-corrected chi-square test, we compared our frequency distributions with those of Burger and Branch (1994) and found a significant difference: ($X^2 = 18.898$, df = 6, $p < 0.01$). This difference may be attributed to the fact that in our sample we had a much higher percentage of larger individuals especially between 350 and 450 mm, and a lower percentage of smaller ones (between 200 and 300 mm) than reported by Burger and Branch (1994). Indeed, our fifth size class (old adults with carapace/plastron lengths over > 350 mm) comprise ~46% of our population. In the comparative published data sets, without the effect of fence-related mortalities, this size class only comprises ~7% of these samples.

In line with our predictions, our skeletonized sample had a bias towards larger size classes compared to both living and dead samples we used from the published literature (Figure 3). Indeed, our data were more right-skewed (1.264) compared to that from Hailey

Figure 3 - Comparative size distribution of leopard tortoises collected in this study with those from the literature.

and Coulson (1999) (0.704 and 0.436 for the dead and live samples, respectively) and also from Burger and Branch (1994) (0.887). Only the data on living leopard tortoises from the field study undertaken by McMaster and Downs (2006) had a similar right-skewed bias (1.402).

In our study we found that slightly more males (*n* = 83) were killed in the Jacobsdal and Strydenburg areas than females (*n* = 69) and this differs to other field studies carried out in South Africa where the majority of mortalities were female (Grobler, 1982; Mason et al., 2000; McMaster and Downs, 2009; Macray, 2017). However, since sexing was based on the plastron concavity, an element which was not always preserved in our disassociated skeletons, not all of our dead tortoises were sexed.

5.2 PVA and Matrix Model Projections

The PVA's and matrix model projections revealed that rates of population growth are generally positive whether electrified fencing was, or was not, a source of mortality (Table 5). Nevertheless, populations influenced by fencing experienced lower growth rates in ~90% of model simulations. Two striking results emerge from these projections. The first is that the 95% confidence limits for population growth rate (λ) of the fence-afflicted population includes negative growth (values < 1), and the second is that with fence-induced mortality, the risk of negative growth increased 52-fold, from 0.11% to 5.76%. In short, these results provide both relative and absolute evidence that electrified fences are an extinction threat.

Table 5 - Summary statistics for λ derived from 104 iterations of stochastic size-structured matrix models

Population	Mean (95% CI)	*p* (smallest)	*p* (neg growth)
Unfenced	1.332 (1.175 to 1.489)	0.1057	0.0011
Fenced	1.170 (0.969 to 1.371)	0.8943	0.0576

p (smallest) = probability of having a lower λ; *p* (neg growth) = probability of λ < 1.

6. Discussion

It is clear that electrified fences lead to an upward bias in mortality amongst larger leopard tortoises (Figure 3). Our comparative size distribution data show a right-skewed bias like that of the population studied by McMaster and Downs (2006). However, both differ from two other published datasets which show a left-skewed bias. The reason for this is perhaps two-fold. The latter two studies (by Burger and Branch, 1994 and Hailey and Coulson, 1999, respectively), were undertaken on nature reserves that are located in very different biomes to the Northern Cape-Free State farms (Savanna biome), while the McMaster and Downs (2006) study, also undertaken on a farm, was located in the same Nama-Karoo biome as our three farm samples. In addition, mean home range estimates for leopard tortoise adults are the same for these two farm-related samples, but differs significantly for the other published data sets from the Eastern Cape Province and Zimbabwe: 205.41 ha in the Nama Karoo of the Northern Cape Province (McMaster and Downs, 2013), 57.56 ha in the valley thicket of the Eastern Cape Province (Mason and Weatherby, 1996), with far smaller ranges of 35.42 ha in KwaZulu-Natal (Wimberger et al., 2009), 26 ha in Zimbabwe (Hailey and Coulson, 1996) and 13.49 ha in Swaziland (Monadjem et al., 2013). Moreover, leopard tortoise daily movement differs by habitat and region. They move further daily distances in the Karoo (up to 8 km per day - McMaster and Downs, 2009), and in some instances, even exhibit nomadic behaviour (Rall, 1985)[3] while in the Valley Thicket Biome of the Eastern Cape they move only ca. 100 m per day (Mason and Weatherby, 1996) and in Swaziland ca. 50 m per day as recorded by Monadjem et al. (2013). Taken together, these data demonstrate that daily movement and home range are associated with seasonal resource availability, especially lack of a permanent water source (Drabik-Hamshare and Downs 2017), and is highest in areas where water availability is low and/or unpredictable e.g. Karoo. We propose that the higher rates of adult leopard tortoise mortalities associated with electrified fences in the Karoo may then be related to their greater mobility in these regions and thus a higher likelihood of encountering fences.

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[3] However, recently, Drabik-Hamshare and Downs (2017) reported that the overall mean distance moved by leopard tortoises in the Karoo was only 257.7 (± 3.64) m per day. The difference in their results to that of McMaster and Downs (2009) may primarily relate to sample size and seasonality of field work.

High mortality rates of adults associated with electrified fences will likely impact negatively on the local tortoise population dynamics, this since leopard tortoises take a long time to grow, specifically larger-sized breeding adults are being targeted, and the female leopard tortoise only attains sexual maturity at ca. 15 years of age (Branch, 2008). At this age, the leopard tortoise will be large enough to be caught in the lowest strand of an electrified fence (usually less than 200 mm). Thus, high death rates amongst animals older than 15 years of age may result in local population extinction within several years. The model we used does have limitations and although our survivorship data was based on a populations from Sengwa in Zimbabwe, all the tortoise populations in the literature have similar adult and sub-adult survival rates. Nevertheless, there is a need to conduct more detailed studies of this and other fence-affected populations. This need is made ever more urgent because, given their slow growth to reach sexual maturity, if the population is pushed into negative growth it will be extremely difficult to turn it around.

Rhodin et al. (2018) lists all 360 currently recognized species of extant and recently extinct turtles and tortoise (Order Testudines) in the world. Their combined analysis indicates that 20% are critically endangered and 51.9% are threatened. In their appendix, they list the leopard tortoise as least concern, as do Baker et al. (2015). This situation will surely change in the near future if the mortality rate keeps on rising due to the demand to erect electrified fences.

Researches have come up with a variety of solutions to reduce mortalities of non-targeted species by electrified fences, while the fence will still fulfill its function for the farmer/nature reserve. Some of the steps that have been suggested that can be taken when constructing an electrified fence are listed below:

- Large rock aprons can be packed at the base of the fence to construct a physical barrier. This barrier should be high enough to stop animals climbing over it and should stop other animals burrowing underneath it. These rocks can be easily and cheaply obtained, especially if the farm is located in a rocky terrain (Beck, 2010; Arnot and Molteno, 2017a, 2017b). However, Macray (2017) does not see these rock aprons as a solution but rather as an obstacle and notes that tortoises who can climb over these aprons will get stuck between the apron and the fence while crows can use the apron to drop small tortoises on to crack their shells.

- Mesh wire can be used on the lower part of the fence instead of electrified strands of wire. This will prevent small predators from getting in under the fence and in combination with a rock barrier as mentioned above, can keep these animals out (Arnot and Molteno, 2017a, 2017b).
- Raising the lowest strand of wire to 250 mm (Burger and Branch, 1994; Beck, 2010; Arnot and Molteno, 2017a, 2017b; Macray, 2017) to prevent animals brushing against it. This will let most leopard tortoise pass freely under the fence, only the very large ones will be affected (Arnot and Molteno, 2017a).
- In accordance with above mentioned procedure, the trip wires should be at least 400-500 mm away from the main fence, allowing smaller tortoises to walk underneath the trip wire before they come into contact with the main fence as this will permit them to follow the fence without coming into contact with the trip wire (Beck, 2010; Arnot and Molteno, 2017a, 2017b).
- Physical checks of fences, where staff patrol the fence regularly and remove tortoises from the fence. However, this could be costly (Macray, 2017).
- A timer switch can be connected to the electrified fence, allowing it to be switched off during the mornings and afternoons when tortoises are most active and be switched on during the night when predators such as black-backed jackal (*Canis mesomelas*) and caracal (*Felis caracal*) are most active (Beck, 2010; Arnot

and Molteno, 2017a, 2017b). It can also allow a tortoise who comes into contact with the fence, time to recover and move away from the fence (Burger and Branch, 1994; Macray, 2017).

- Related to this is reducing the use of electrified fencing during the mating season and distancing it from water sources. This last recommendation directly relates to our findings and those of Drabik-Hamshare and Downs (2017), namely that leopard tortoises move greater distances on a daily scale and have larger territories in more xeric environments that lack permanent water sources. Thus, the probability of their coming into contact with an electrified fence is higher than in wetter regions with lush vegetation where leopard tortoises are not reliant on access to water.

Clearly, the trend to erect electrified fencing in South Africa is on the rise given the cost of predation on livestock (domesticated and wildlife animals) which is estimated in excess of one billion Rand per year (Kerley et al., 2017), while the estimated cost of livestock theft was R509 million in 2014 (Lombard et al., 2017). Thus, leopard tortoises, especially those inhabiting arid environments that have the largest home ranges and daily movement ranges, are at highest risk of encountering electrified fences. Intervention by conservation groups is urgently needed to protect these populations.

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Chapter 2

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Bone mineral density in the leopard tortoise: Implications for inter-taxon variation and bone survivorship in an archaeozoological assemblage

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ABSTRACT

In this study we present data on bone mineral density (BMD) values for the cranial and post-cranial skeleton of the leopard tortoise (*Stigmochelys pardalis*). We found significant inter and intra-skeletal variation in different values of BMD within this species. The intra-skeletal, but not inter-skeletal pattern, was comparable to that of terrestrial mammals of similar size, despite differences in bone structure. Overall, the tortoise has bone density that is intermediate between that of leporids (rabbits/hares) on the one hand and canids (dogs/wolves etc.) and marmots on the other. In this study we have used random effects to test regression models of BMD and demonstrate their value over the simple linear regression models that are currently in use.

Finally, we applied the modern leopard tortoise proxy data to test whether different parameters of BMD impact survivorship of tortoise bones in the Holocene strata from Wonderwerk Cave (Northern Cape Province, South Africa). Results indicate that this assemblage has undergone some degree of bone density-mediated attrition, probably influenced by burning and deposition time rather than animal agents.

1. Introduction

Archaeozoological assemblages are affected by pre- and/or post-depositional processes that cause differential destruction or fragmentation of bone elements, a factor which can influence the interpretation of skeletal element representation in a faunal assemblage. Numerous natural factors have been identified as determining the differential survivorship of bones in a faunal assemblage including: burial rate and environment, chemical composition of the bone, as well as the intrinsic properties of the bone (age of animal, size, shape and weight of the bone) (e.g., Klein and Cruz-Uribe, 1984; Von Endt and Ortner, 1984; Lyman, 1994; Hedges, 2002; Peres, 2010). Of these, bone mineral density (BMD) is perhaps the most salient factor (e.g., Lyman, 1984; Pavao and Stahl, 1999; Ioannidou, 2003; Lam et al., 2003; Symmons, 2004; Broughton et al., 2007), and may be a determining factor of bone survivorship in itself, or else plays a role in the resistance of skeletal elements/parts to actions of biotic or abiotic agents.

Pioneering taphonomic studies on bone density were carried out by several researchers in the 1960's and 1970's (e.g., Brain, 1967, 1969; Behrensmeyer, 1975; Binford and Bertram, 1977), but it was Lyman (1982, 1984) who introduced quantitative values of bone mineral density (BMD) for different bones and formalized such investigations by applying dual photon absorptiometry (DPA) to determine BMD of artiodactyls; domestic sheep (*Ovis aries*), white-tailed deer (*Odocoileus virginianus*) and pronghorn antelope (*Antilocapra americana*). Since Lyman's publications, numerous studies have applied DPA, Dual Energy X-Ray Absorption (DEXA or DXA, e.g. Pickering and Carlson, 2002) and more recently computed tomography (CT) scanning, to provide structural density values for different taxa, while simpler approaches have used immersion of bones in water with the volume of displaced water noted (e.g., Fish and Stein, 1991; Elkin, 1995). Although there has been much debate as to whether DPA, DXA or CT gives the most valid results (Lam et al., 2003; Stiner, 2004; Lam and Pearson, 2005), all methods have been used to compare skeletal elements and to predict their survivorship (Dirrigl, 2001). The advantage of CT scanning is that it provides a precise assessment of the cross-sectional area of the scan sites and for example, excludes the medullary cavity from density calculations, while with DPA (or DXA) a cross-sectional shape adjustment has to be made (Lam et al., 2003).

The basic assumption in taphonomic studies is that skeletal element abundance will correlate positively with bone density, with elements having higher BMD preserving better than those with lower BMD values (e.g., Lyman, 1994; Symmons, 2004; Faith et al., 2007). Bone density is then one of the key taphonomic processes influencing skeletal

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representation. However, its impact on skeletal element preservation may be both direct and indirect, the latter being mediated by other attritional factors. These factors may include a spectrum of animal and/or anthropogenic activities which may result in selective destruction of bone elements (e.g., Binford, 1978; Brain, 1981; Lyman, 1985; Blumenshine, 1988; Marean, 1991; Marean and Spencer, 1991; Munson and Garniewicz, 2003; Faith et al., 2007; Gaudzinski-Windheuser and Niven, 2009; Kuhn, 2011), the size of the element, age of the animal (e.g., Nicholson, 1996) as well as geological/sedimentary (Stiner et al., 2001; Baxter, 2004) or local ecological conditions as has been shown, for example, by Conard et al. (2008) in their analysis of the faunal remains from the Geelbek Dunes (Western Cape Province, South Africa). Consequently, interpreting bone survivorship data relative to BMD values must take into account all potential taphonomic processes that may have acted on an assemblage.

Structural density values for a wide range of different mammalian taxa are available in the literature (Brain, 1969; Behrensmeyer, 1975; Boaz and Behrensmeyer, 1976; Binford and Bertram, 1977; Lyman, 1984; Kreutzer, 1992; Chambers, 1992; Lyman et al. 1992; Elkin, 1995; Galloway et al., 1997; Lam et al., 1998, 1999; Stahl, 1999; Pavao and Stahl, 1999; Pickering and Carlson, 2002; Ioannidou, 2003; Munson and Garniewicz, 2003; Carlson and Pickering, 2004; Symmons, 2005; Novecosky and Popkin, 2005; Gutiérrez et al., 2010). Similarly, there is a fair amount of published data for birds (Dirrigl, 2001; Cruz and Elkin, 2003; Broughton et al., 2007), and fish (Nicholson, 1992; Butler and Chatters, 1994; Butler, 1996). So far, however, archaeozoological investigations based on bone density studies have overlooked reptiles, although this animal class (especially tortoises) are abundant in many archaeological sites worldwide. Moreover, many recent studies have focused specifically on tortoise exploitation by humans (e.g., Klein and Cruz-Uribe, 1983; Sampson, 1998, 2000; Klein and Cruz-Uribe, 2000; Speth and Tchernov, 2002; Avery et al., 2004; Stiner, 2005; Blasco, 2008; Blasco et al., 2011; Thompson and Henshilwood, 2014a, 2014b; Blasco et al., 2016; Klein and Cruz-Uribe, 2016; Biton et al., 2017).

Examination of BMD values of animals within the same vertebrate class, and BMD values for a number of skeletal elements of a single animal or closely related group (e.g., Pavao and Stahl, 1999; Dirrigl, 2001; Novecosky and Popkin, 2005), has shown that it varies intra- and inter-specifically with age, sex, nutrition, genetics and function (e.g., Lyman, 1982; Ioannidou, 2003; Gutiérrez et al., 2010). Since the structure and growth pattern of reptilian bone differs from that of other vertebrates (e.g., Enlow, 1969; Haines, 1969; De Ricqlès, 1976), we considered that investigations of bone mineral density in this class will contribute to a more general understanding of bone density patterns across vertebrate groups.

In this paper we present BMD values for the African leopard tortoise (*Stigmochelys pardalis*) derived from dual photon absorptionmetry, which will be the first such data set for a reptile. We investigated the extent of differences in bone density within and between reptile bones, and how these patterns differ in comparison to similarly-sized terrestrial vertebrates. To further explore the utility of tortoise bone density as a taphonomic tool in archaeozoology, we present a case study in which we interrogated relationships between bone density and skeletal part preservation in a large assemblage of Holocene leopard tortoise remains (dating to ca. 12,200 BP to ca. 1910 AD) from the site of Wonderwerk Cave (Northern Cape Province, South Africa).

1.1. *Structure of reptile versus other terrestrial vertebrate bone*

For us to open a discussion on tortoise bone density patterns, it is important to consider these animals in comparison to other vertebrates. In vertebrates, long bones develop from cartilaginous precursors (endochondral bone formation). The cartilage is totally replaced by bone in the diaphysis (shaft) but as long as the cartilaginous region of the epiphysis remains mitotically active, the bone can continue to lengthen. Although longitudinal bone growth in birds and mammals ceases when the epiphyses ossify with sexual maturity, in most reptiles, such as tortoises, longitudinal bone growth continues during most of their lifespan (Haines, 1969). Growth rate appears to slow down after reaching sexual maturity and in the later stages of life, but it probably never stops completely (Avery, 1994).

The compact bone microstructure of many reptiles lacks the typical structure found in mammals of outer and inner circumferential lamellae enclosing a middle layer of Haversian systems (Enlow, 1963, 1969; Ahmed et al., 2017). In reptiles, such as tortoises, the secondary rebuilding of the primary cancellous bones that occurs in mammalian long bones, due to resorption as well as secondary redeposition of newly formed trabeculae, is lacking or very limited. Instead, the primary arrangement of the cancellous medulla is retained even in mature individuals. As a result of compact, periosteal bone being directly converted into cancellous medullary bone (without the reformation of the trabeculae involved), cancellous bone is present in tortoises on most of the endosteal surfaces of the diaphyseal cortex. Thus in Chelonidae (and Crocodilia), although the outer shaft is a well ossified shell of periosteal bone, medullary trabeculae are widespread in most areas of the bone including the shaft and form an internal meshwork of bone (Bellairs, 1969; Enlow, 1969). The shaft grows in thickness by adding bone to the outer surface of the periosteal shell, the inner surface being corresponding resorbed (Bellairs, 1969; Enlow, 1969; Avery, 1994). In addition, most reptiles experience annual cyclical growth patterns and their bone cortices show alternating zones of fibrolamellar tissue and lamellar tissue as the animal experiences periods of rapid growth (osteogenesis) or decreased growth rates (avascular regions) (Castanet et al., 1993). Such a pattern of growth is not found in most mammals and birds (Chinsamy-Turan, 2005).

Finally, the low values for bone mineralization (i.e. the large volume fraction of pores in their bone structure) for tortoise bone relative to other mammals (such as a cow femur, deer antler, whale tympanic bulla), are associated with high values for fracture toughness, but low values of elasticity (Young's modulus) and intermediate values of bending strength (Currey, 1984). Indeed, Currey's findings indicated that tortoise (and crocodile) long bones had lower modulus values than those found in birds and mammals although preliminary findings reported in a more recent study (Erickson et al., 2002), found higher Young's modulus values with both reptiles falling within the range of birds and mammals. The implication of the unique reptilian pattern of bone growth and bone composition for BMD studies is that overall BMD values are expected to be low relative to most other vertebrates due to the presence of cancellous bone on the endosteal surfaces of the diaphyseal cortex. Moreover, due to their low elasticity and bending strength, under medium to high stress (as reported by Currey, 1984), it is expected that tortoise bones will fracture rather than bend or distort.

1.2. *Patterning in tortoise skeletal element representation*

The skeleton of terrestrial tortoises, like that of all Testudines, is unique to vertebrates (though superficially paralleled by armadillos) in that it includes a shell comprising numerous fused bones; with an upper shell - the carapace, and a lower shell termed the plastron, which are joined together along each side of the body by sutures (between the middle peripheral bones as well as the hypoplastron), in an area called the bridge. Together they house and shield the soft tissues and skeleton as well as sheltering the retractable limbs and cranium (Thomson, 1932; Pritchard, 1979). Notably (and unlike in armadillos), the vertebral column (except for the first seven cervical vertebrae) and rib cage are fused to the carapace along the neural and pleural bones respectively. Also, unlike in other tetrapods, the scapula sits inside the ribcage, and the proximal part of the limb girdles (pelvis, coracoid and scapula), rests against the carapace (Pritchard, 1979). Though offering considerable protection, the shell makes tortoises heavier and less nimble than other tetrapods of similar body length and so relatively easy to catch.

The physical structure of an animal and its size influences not only how it is caught, but also how it is killed, which skeletal elements are transported back to a site and how its carcass is processed and consumed. With respect to tortoises, it is logical that as prey they would be introduced into archaeological sites intact given their generally small size, the fact that they can be caught without being wounded, and that their limbs and meat-rich parts of their carcass are attached to their shell. Moreover, since they can be kept alive as a "living larder" for long periods of time without food or water (e.g. the exploitation of Galapagos tortoises as a fresh meat and water supply for ships on long voyages, as noted in Darwin, 1839: entry for September 23rd' 1835), there is additional advantage in bringing live animals back to a site for consumption at a later date.

Generally, tortoises are cooked whole in their shell either by boiling or heating on a fire (e.g. http://www.nairaland.com/2624436/experience-eating-tortoise-first-time) following which the limbs and meat are removed. Worldwide, the majority of tortoise remains found in archaeological sites are fragmented pieces of shell, though post-cranial elements are usually also well represented (e.g., Klein and Cruz-Uribe, 1983; Speth and Tchernov, 2002; Halkett et al. 2003; Stiner, 2005Blasco, 2008; Blasco et al., 2011, 2016; Biton et al. 2017), implying that whole animals were exploited. This pattern of paleo-skeletal representation is further attested by evidence for cooking whole tortoises in their shells, following which the limbs and other bones were cut or chewed off (e.g., Speth and Tchernov, 2002; Blasco, 2008; Blasco et al., 2011, 2016). Perhaps the most famous consumer of such a meal was Charles Darwin (1839) who, with respect to Galapagos tortoises, notes in *Voyage of the Beagle,* entry for 8th October 1835:

"While staying in this upper region, we lived entirely upon tortoise-meat: the breast-plate roasted (as the Gauchos do carne con cuero), with the flesh on it, is very good, and the young tortoises make excellent soup, but otherwise the meat to my taste is indifferent."

Thus, tortoises consumed by people are expected to be represented by all body parts, with evidence for burning - primarily on the exterior surface of the shell, as well as cut marks, especially on the inner surface of the shell resulting from meat removal (e.g., Blasco et al. 2011; Thompson and Henshilwood, 2014a; 2014b) and characteristic fracturing of the shell on the marginals in order to pry it open (e.g., Thompson and Henshilwood, 2014a; 2014b; Biton et al., 2017), while limbs may exhibit cut or chew marks. The dimensions and sex ratios of tortoises taken by people, is determined by the size range and demography of the natural population in the vicinity of the site which in turn, is influenced by environmental conditions and exploitation pressure (e.g., Klein and Cruz-Uribe, 1983, 2000; Willemsen and Hailey, 1999; Stiner et al., 2001; Fernández-Chacón et al., 2011).

A range of non-human predators are also known to take tortoises. Raptors smash open their shells by dropping them from a height and their roosts contain fragmented shell and post-cranial remains (Van Lawick-GoodalI, 1970; Avery, 1984; Sampson, 2000). Other birds, such as ravens prey on juvenile tortoises and peck holes in their shell (Boarman, 2003) while gulls are known to prey on hatchlings whose shells are still soft (Branch and Els, 1990). Carnivores, such as bears, hyaenas and honey badgers, consume tortoises (Smuts, 1979; Llyod and Stadler, 1998; Avery et al., 2004; Peterhans and Singer, 2006; Lovich et al., 2014) as do baboons, though they are only able to break open the shell of small individuals (Hill, 1999). As summarized by Thompson and Henshilwood (2014a, 2014b), these non-anthropogenic agents will result in characteristic bone accumulations that differ from those assembled by people in skeletal elements represented as well as surface modifications.

2. Materials and methods

2.1. Bone density measurement

A total of thirteen skeletal elements, comprising the limb bones, pelvic girdle, skull and mandible, of an adult male leopard tortoise were scanned using a Hologic Discovery W duel x-ray (DEXA) bone densitometer, at the Centre of Excellence for Nutrition at the North West University, Potchefstroom. Although CT scanning may be a more promising method as proposed by Lam et al. (1998, 2003), we used DEXA for compatibility since most previously published studies on mammals have used either DPA or DEXA. Notably, Lam et al. (1999) reported that the highest correlations in BMD were found between data sets derived using the same method, irrespective of the morphological or other similarities between taxa analysed. Furthermore, although a prime advantage of CT scanning is that it automatically takes into account the volume of the marrow cavity relative to the cortical and trabecular bone, this issue is less relevant for scans of tortoise bones that lack a well-defined marrow cavity.

Limb bones from the left side of the skeleton were used in this study. The leopard tortoise (specimen NMBF 2434) was collected in August 2016 near the town of Jacobsdal (Free State Province) and was killed through contact with an electric fence and was in good health with no visible pathologies on the bones or the shell. Allometric relationships between body mass and carapace length, and between body mass and carapace height, based on measurements of 26 specimens of live adult male leopard tortoises collected in the Bloemfontein region (Free State Province, South Africa), were used to estimate the body mass of NMBF 2434 which was ± 8.8 kg. Bulk BMD was measured using the APEX System Software Version 2.3.1, and the small animal software option was used. For scanning, the bones were submerged in water, but as the smaller, lighter bones floated we had to use a container filled with grains of rice in which the bones were fully submerged. Bones were scanned using the high resolution option. The densitometer was calibrated before the scanning started to ensure that systematic scanner error was absent.

A total of 52 scan sites were identified on the 13 bones based on locations used by Lyman (1984), Kreutzer (1992) and others for mammals, with additions and modifications of scan sites to suit the unique features of tortoise anatomy (Fig. 1). For each bone scanned, at least three density readings were obtained - on the proximal, mid-shaft and distal ends respectively. To obtain density values, the following protocol was followed. The densitometer gave a perfect outline of the scanned bone after which the APEX System software was used to define the selected scan sites individually. The instrument provides the average bone mineral content (BMC) of the scanned area measured in grams/cm (Elkin, 1995) and computes bone mineral density (BMD, i.e. BMC/area) in g cm^{-2}, for a defined region of the bone to obtain a "linear density" (Kreutzer, 1992; Lyman et al., 1992). Linear density treats all bones as flat objects (Kreutzer, 1992). However, since bones are not flat and each bone differs in these parameters, some cross-sectional shape-adjustment needs to be made. We followed Lyman (1982, 1984) who used caliper measurements of bone length, width and depth to arrive at bone volume. For each bone, we took four measurements of depth (SD) along the scan site as well as greatest bone length (GL) and greatest width (Bd) (SI Table 1). We used four measurements of SD for the variation and irregularities in bone thickness. The four SD measurements obtained were then averaged using medians, which were then multiplied by GL and Bd to derive a volume (in cm^3). Density volume (DV) was then calculated as BMC/volume in g cm^{-3}.

2.2. Data analysis

Most recent investigations consider patterns in both BMD and DV. Although Lyman (1994) and Kreutzer (1992) have argued that DV is a more accurate measure since it takes the 3D shape of different bones into account, here we present both datasets and an analysis of the relationship between the two metrics, based on a mixed effects linear model (MELM) with BMD as covariate and Bone as a random effect. Incorporation of the random effect ensures that correct error terms are compared, given that multiple points (i.e. non-independent data series)

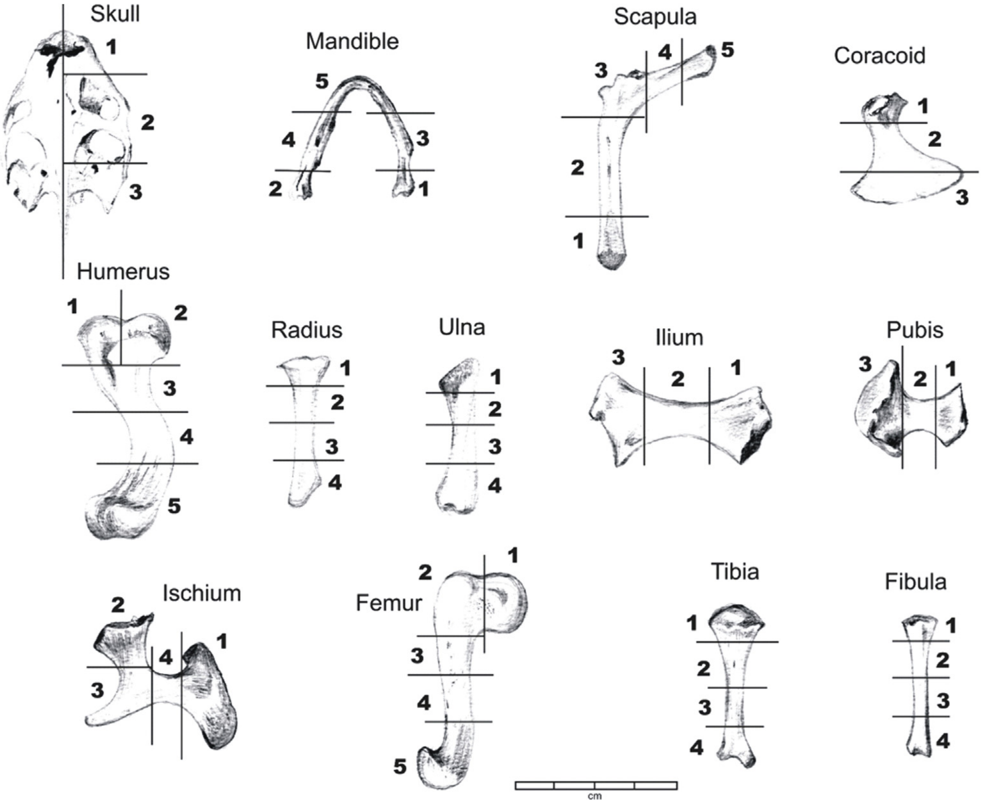

Fig. 1. The scan sites on the leopard tortoise bones.

were scanned on each bone.

To compare bone density patterns with other vertebrates, we examined density volumes (DV) for the leopard tortoise against those of published values for a range of mammals with adult body weights of up to ca. 8 kg, i.e. foxes (*Vulpes* spp.), marmots (*Marmota* spp.), leporids, including rabbits (*Sylvilagus floridanus* and *Oryctolagus cuniculus*) and hares (*Lepus* spp.), as well as three larger canid species - wolf, dog (Labrador size) and coyote (Lyman et al., 1992; Pavao and Stahl, 1999; Novecosky and Popkin, 2005; data included as online supplementary material, SI Tables 2–3). We carried out two types of analyses. First, we investigated whether tortoises differed in average DV from other mammals of similar body weight, using a MELM with Species as a main effect and Scan Site as a random effect (as above, accounting for the fact that multiple measures from the same bone were being compared). Ranked data were used in the MELM because residuals were not normally distributed (Shapiro-Wilks test). Tukey's HSD post hoc test was used for multiple comparisons. We then investigated whether within-bone density patterns were similar in the tortoise and other mammals, using Spearman's Rank correlations to compare the pattern in the tortoise with each of the mammal species in turn. These intra-bone correlations were performed for humeri (SI Table 2) and femora (SI Table 3) only, as these bones had similar numbers of scan sites in more or less the same locations as the tortoise bones. One distinction was in the proximal femur which in canids, marmots and leporids had three scan sites, while the tortoise only had two. Consequently, to facilitate comparison, data for scan sites FE 1–2 in the other mammals were combined and averaged. All statistical tests were carried out in R v 3.4.2. (R Core Team, 2015).

3. Results

3.1. Leopard tortoise BMD

Table 1 gives the bulk BMD values for scan sites of an adult leopard tortoise. The raw values for BMD, average BMC (SI Table 1) and area for each scanned skeletal element are the results as measured automatically by the densitometry machine. The two main density metrics (BMD and DV) were significantly related, even after accounting for multiple measures being taken per bone (MELM $F_{1,50} = 9.793$, $p = 0.003$). However, the relationship was not very strong (marginal $r^2 = 0.156$), consistent with results of previous studies which concluded that the two metrics represent different types of measurements (Lam et al. 2003). These differences are clearly portrayed when BMD and DV values for each bone and scan site are plotted in ascending rank order (based on median values for each bone) and compared (Fig. 2). For instance, whereas the fibula and ulna have the lowest median BMD of all bones, these bones (especially the fibula) have among the highest DV medians. By contrast, the femur and humerus have the highest median BMD

Table 1
Bone mineral density (BMD) values for the leopard tortoise.

Element	Scan sites				
	1	2	3	4	5
	BMD [g/cm^2]	BMD [g/cm^2]	BMD [g/cm^2]	BMD [g/cm^2]	BMD [g/cm^2]
Skull	0.457	0.35	0.497		
Mandible	0.392	0.342	0.525	0.493	0.457
Scapula	0.327	0.603	0.504	0.527	0.485
Coracoid	0.523	0.374	0.122		
Humerus	0.433	0.796	0.957	0.872	0.681
Radius	0.49	0.585	0.529	0.315	
Ulna	0.309	0.399	0.391	0.237	
Ilium	0.53	0.565	0.315		
Pubis	0.466	0.42	0.286		
Ischium	0.258	0.471	0.539	0.4	
Femur	0.739	0.618	0.722	0.78	0.686
Tibia	0.487	0.584	0.505	0.37	
Fibula	0.301	0.399	0.411	0.294	

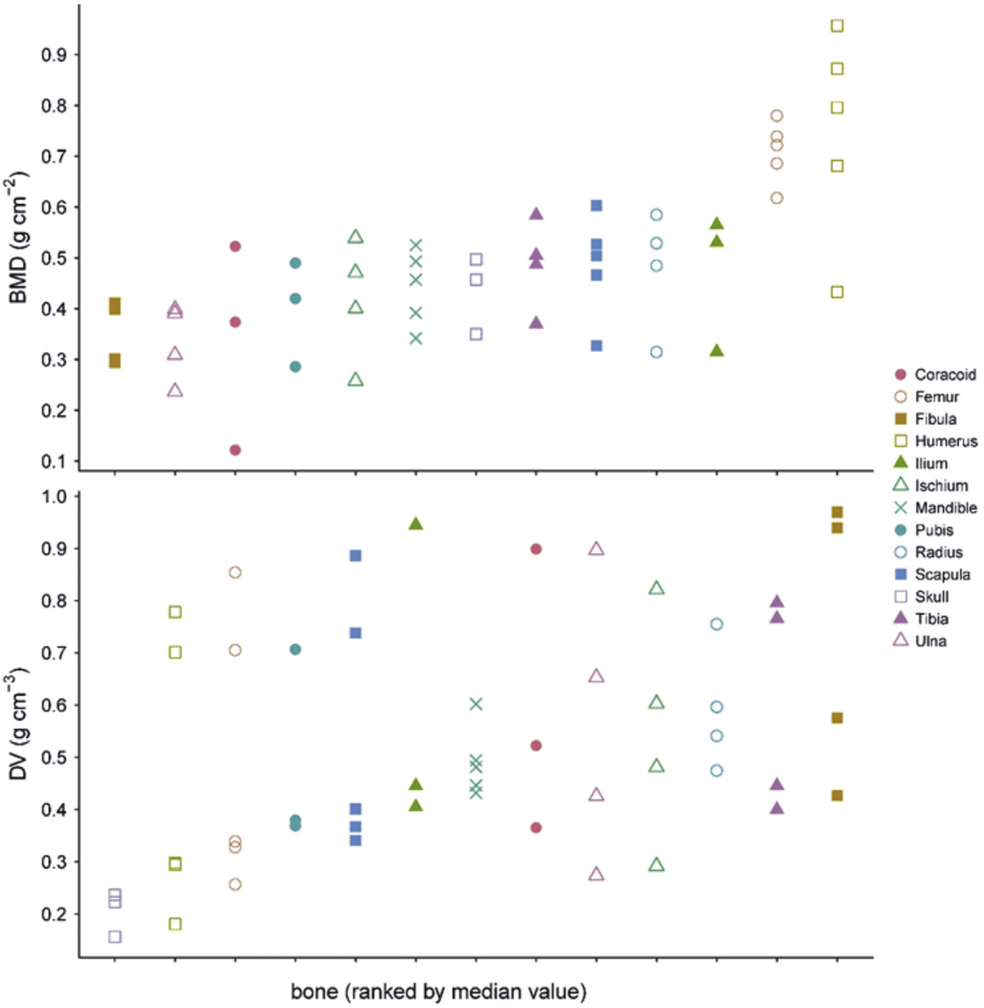

Fig. 2. Comparison of the BMD and DV values of all the scan sites on all the leopard tortoise bones.

values, but among the lowest median DV values.

Based on the DV values for the scan sites, it is clear that the fibula has the densest portions of bone with the proximal section of the shaft the thickest, followed by the distal shaft portion, then the distal end while the proximal end has the least dense value (see Fig. 1 for scan sites). The ilium shaft has the second highest DV value for all the scanned bones. The bone with the lowest DV values is the skull. The humerus exhibits the most variation in DV values, with the proximal shaft section having the highest value and the tuberosity section of the humerus the lowest value.

Comparing the bone areas that were scanned, for DV it can be expected that the densest parts - the fibula proximal shaft and ilium shaft - will be the most abundant bones in archaeological assemblages and that some sections of the humerus should be well preserved. It can also be speculated that the skull will be the least preserved. However, the BMD values give a different order of ranking with the four highest values found in the distal end of the ilium (scan site 3), followed by the acetabulum area of the scapula (scan site 3); the proximal humerus (scan sites 1 and 2) and the anterior part of the proximal femur (scan site 2). Our case study below explicitly addresses these predictions.

The poor association between DV and the other two measures of bone density (BMC, BMD) found in the leopard tortoise may result from variation in the thickness and shape along the shaft of the bone that was not adequately accounted for in our reconstruction of bone volume at each scan site.

3.2. *Reptile versus other vertebrate bone*

Given the very different size and shape of bones of the different vertebrates, we focused on DV for this part of the study. The density volumes (DV) of leopard tortoise bones is shown in Fig. 2, in comparison to values for several similar-sized mammal species (foxes, marmots, rabbits and hares), as well as three larger canid species - wolf, dog (Labrador size) and coyote. Visually it appears that tortoises have lower DV values than marmots and canids, but higher values compared with lagomorphs. Indeed, differences across species are significant ($F_{11,441} = 86.302$, $p < 0.0001$), and post hoc tests revealed that tortoise DV is significantly higher than all leporid species, and significantly lower than all canid species included here ($p < 0.0001$ to < 0.01, except for *V. velox* for which $p = 0.078$). By contrast, tortoise bone DV is not significantly different from that of the two marmot species ($p = 0.490$ to 0.741).

Tortoises also differed from mammals in terms of DV values between bones: there was no correlation between the inter-bone DV pattern of tortoises compared with all mammal species included here (Spearman's correlation coefficient, $R_s, = -0.236$ to 0.391, p 0.235 to 0.901). Thus, whereas the lowest DV values for the tortoise were found in the humerus, femur, and pubis, and the highest values in the tibia and fibula, mammal DV was particularly high in the humerus and pubis, but comparatively low in the scapula, tibia (*Canis* spp. excluded), and fibula (Fig. 3). Intra-bone variation in DV was, however, generally similar between the tortoise compared with canids and marmots

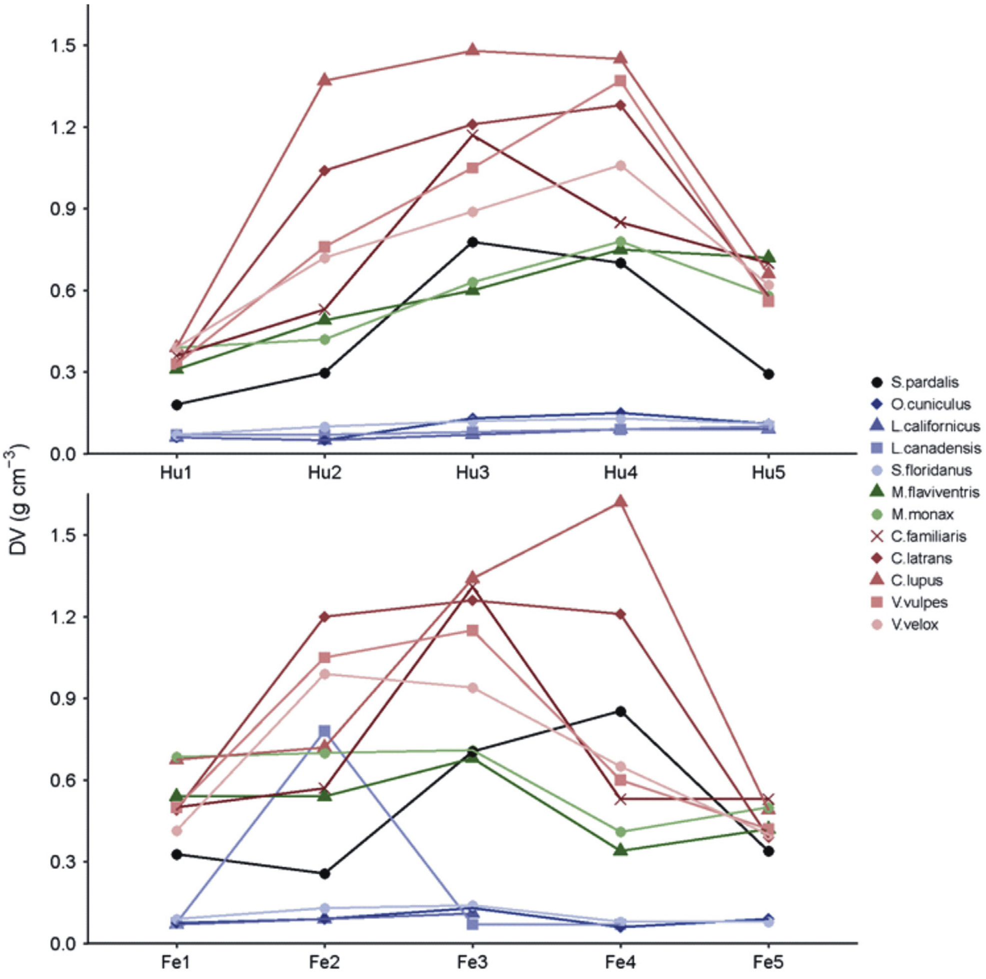

Fig. 3. Bone density comparisons of the humerus (top) and femur (bottom) between tortoise, hare, marmot, dog, fox and coyote. Data for other taxa taken from Pavao and Stahl (1999); Lyman et al. (1992); Novecosky and Popkin (2005).

(Fig. 4). In all these taxa, the humerus DV was lowest at scan site 1, increased towards the centre of the bone, and then decreased again at scan sites 4 and 5. The pattern in the tortoise was significantly correlated with that of the canids (R_s, = 0.9, p = 0.038), but not to the two marmot species (R_s = 0.5 and 0.8, p = 0.391 and 0.104, respectively). Leporids, in contrast, showed a pattern of humeral DV values generally increasing from scan site 1 to scan site 5, which was clearly different from the tortoise-canid-marmot pattern (R_s = 0.245 to 0.8, p = 0.104 to 0.694). The femur of tortoises and canids showed similar trends to each other, with the lowest DV at the extremities and higher DV in the middle portions of the bone. However, statistical correlations between taxa were weak and were therefore not significant in any comparison, including between tortoises and marmots, and tortoises and rabbits ($R_s = -0.626$ to 0.7, $p = 0.188$ to 0.873).

3.3. Discussion

This analysis reveals that bone density patterns in tortoises differ from those of other terrestrial vertebrates, both in terms of the distribution of DV values along a bone, and in absolute terms. However, these differences are not consistent for all tortoise-mammal comparisons. For example, tortoises and canids appear to share a similar trait in that highest densities occur in the middle of the humerus, but leopard tortoise DV values are more similar, in absolute terms to marmots, whereas, overall, DV values in canids and rabbits are higher and lower, respectively, than those of tortoises.

Lyman et al. (1992) used live weight of 19 species of mammals that were log-transformed for testing correlations between body mass and bone density, but he found no correlation. Variation in bone density in mammals may be due to locomotor and behavioural variation between species and this explanation may account for the similarities found between the leopard tortoise and marmot humeri. Of the 11 vertebrates compared here, only the marmots and the tortoise are adapted for digging and our findings suggest that locomotion and limb function may account for the similarity in the structural density of their bones. Lyman et al. (1992) predicted that fossorial animals would have denser phalanges, metapodials and distal limb elements, and this is shown in our data. Comparing the density volume of the marmots and the tortoise with one another, there is only one scan site on the humeri of the tortoise where the density exceeds that of the marmots. If locomotion/biomechanics determines similarity, this may account for differences between the marmot and the tortoise as they dig in a different manner. Lyman (1984) indicated that there are small differences in the bone density of species of the same genus and that there are slightly bigger differences between the bone densities of genera of the same family, a finding supported by the DV values for leporids ad canids shown in Fig. 3. Finally, leporids have significantly lower DV values when compared to other vertebrates shown in Fig. 3 and this too is probably related to differences in limb function, since leporids are bipedal hoppers characterised by reduced function in their forelimbs (Alexander et al., 1981; Williams et al., 2007).

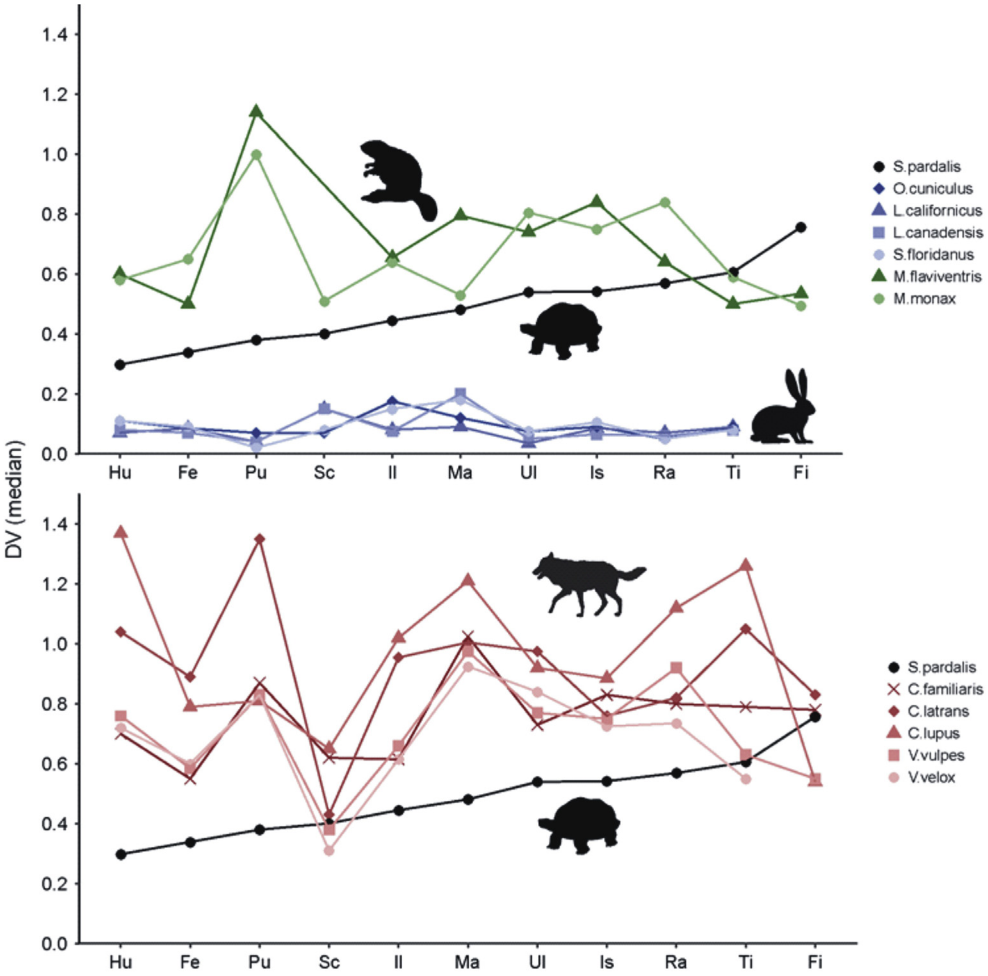

Fig. 4. Intra-bone variation in DV between tortoise, hare, marmot, dog, fox and coyote. Data for other taxa taken from Pavao and Stahl (1999); Lyman et al. (1992); Novecosky and Popkin (2005).

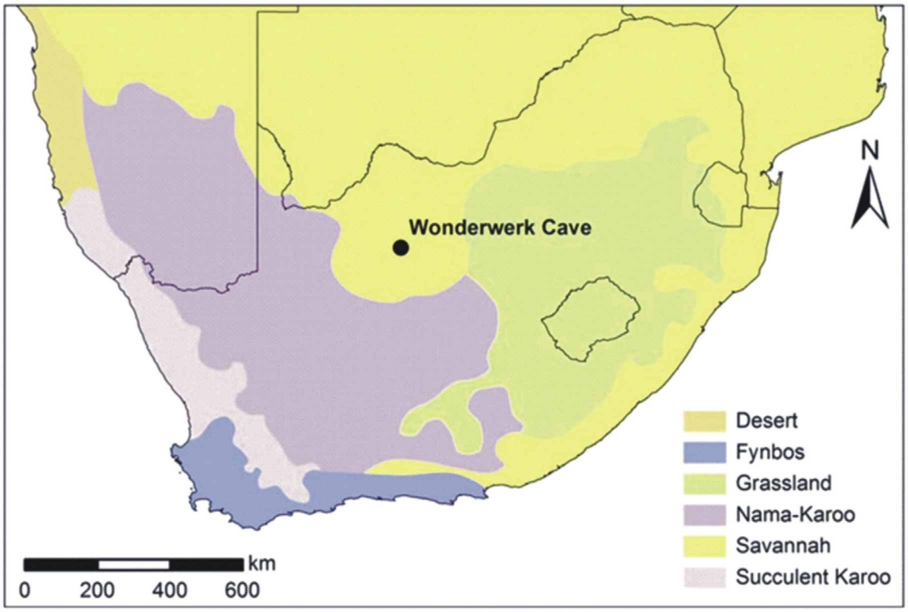

Fig. 5. Map of South Africa showing the location of Wonderwerk Cave within the savannah biome.

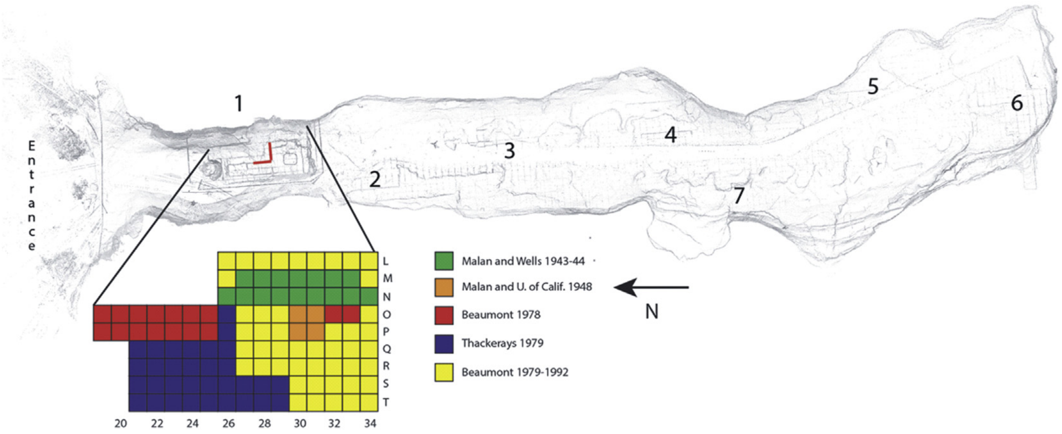

Fig. 6. Areas excavated in Excavation 1 at Wonderwerk Cave (Modified after Horwitz and Chazan, 2015:Fig. 2).

Table 2
Beaumont and Thackeray spits defined, including dates for stratums (Taken from Ecker et al., 2017).

Stratum	Boundary age cal. BP	Beaumont spits	Thackeray spits
1–2	Last 100 years	1, 2	1, 2a
2b-3a	190–2700	3UP, 3MID	2b, 3aI, 3aII
3b	2060–4800	3LR	3b
4a	4300–5400	4aUP, 4aMID	4aI, 4aII, 4aIII, 4aIV
4aLH	4900–5890	4aLWR	4aLH
4b	5550–6500	4bTUFA5, 4bTUFA6	4bI, 4bII
4c	5960–9800	4cUP, 4cLR	4cI, 4cII
4d	8600–12200	4d (top & base)	4dI, 4dII

4. Case study of Wonderwerk Cave

The results derived from the modern leopard tortoise described above were used to test the extent to which bone mineral density may have impacted skeletal element survivorship in the archaeozoological assemblage recovered from the Holocene layers of Wonderwerk Cave, Northern Cape Province, South Africa (Fig. 5).

4.1. Background to the cave and excavations

Wonderwerk Cave (27°50′44.7″S; 23°33′12.3″E) is a massive dolomitic cavity about 140 m long, situated in a low foothill of the Kuruman hills (Beaumont, 1990; Horwitz and Chazan, 2015; Ecker et al., 2017).

Table 3
The total number of bones (bold), and sections/scan sites (italic), analysed per stratum at Wonderwerk Cave.

Element	Stratum								Total
	1–2	2b-3a	3b	4a	4aLH	4b	4c	4d	
Humerus	**2**	**17**	**28**	**9**	**4**	**3**	**35**	**11**	**109**
scan site 1	*1*	*8*	*15*	*4*		*2*	*10*	*3*	*43*
scan site 2	*1*	*9*	*19*	*8*		*3*	*11*	*1*	*52*
scan site 3	*1*	*15*	*26*	*9*	*3*	*3*	*26*	*8*	*91*
scan site 4	*2*	*11*	*22*	*8*	*4*	*2*	*27*	*10*	*86*
scan site 5	*1*	*6*	*16*	*5*	*4*	*2*	*20*	*5*	*59*
Scapula	**1**	**12**	**17**	**6**		**6**	**26**	**4**	**72**
scan site 1			*3*	*1*		*1*	*2*	*1*	*8*
scan site 2	*1*	*12*	*16*	*6*		*6*	*23*	*4*	*68*
scan site 3	*1*	*13*	*17*	*6*		*7*	*26*	*4*	*74*
scan site 4	*1*	*12*	*16*	*4*		*6*	*17*	*2*	*58*
scan site 5		*2*	*7*	*2*		*2*	*8*	*1*	*22*
Coracoid		**4**	**3**			**1**	**4**	**1**	**13**
scan site 1		*3*	*3*			*1*	*5*	*1*	*13*
scan site 2		*4*	*3*				*4*	*1*	*12*
scan site 3		*1*							*1*
Ilium		**8**	**7**	**7**	**1**	**4**	**17**	**1**	**45**
scan site 1		*8*	*7*	*7*	*1*	*4*	*17*	*1*	*45*
scan site 2		*7*	*7*	*7*	*1*	*4*	*13*	*1*	*40*
scan site 3		*2*		*2*		*3*	*4*		*11*
Ischium		**1**	**1**				**1**		**3**
scan site 1		*1*							*1*
scan site 2		*1*	*1*				*1*		*3*
scan site 3		*1*					*1*		*2*
scan site 4							*1*		*1*
Femur	**1**	**10**	**10**	**11**		**2**	**16**	**4**	**54**
scan site 1		*5*	*5*	*7*		*1*	*9*	*3*	*30*
scan site 2		*5*	*7*	*7*		*2*	*12*	*4*	*37*
scan site 3		*4*	*9*	*10*		*2*	*12*	*4*	*41*
scan site 4	*1*	*7*	*10*	*8*		*2*	*13*	*4*	*45*
scan site 5	*1*	*7*	*9*	*7*		*2*	*10*	*3*	*39*
Total	**4** (*11*)	**52** (*144*)	**66** (*218*)	**33** (*108*)	**5** (*13*)	**16** (*55*)	**99** (*272*)	**21** (*61*)	**296**(*882*)

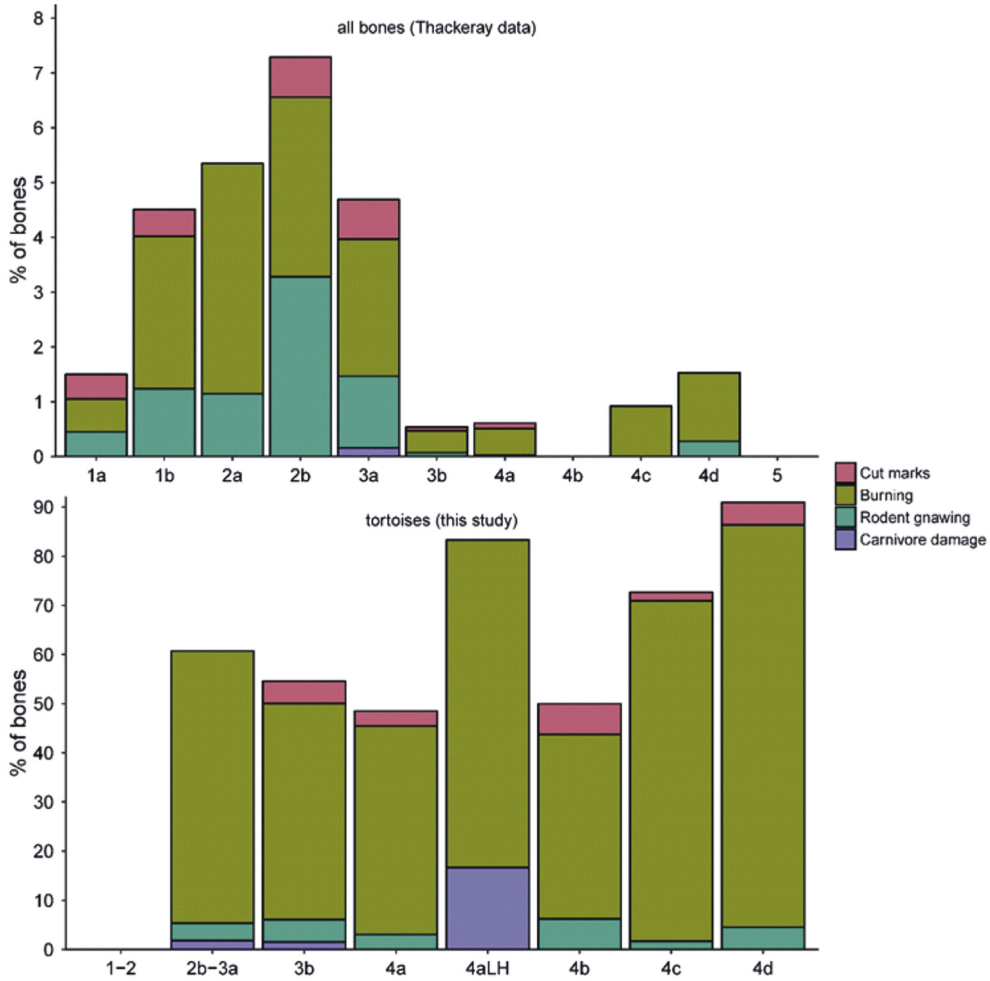

Fig. 7. Comparison of the frequencies of the different types of damage found on all bones examined by Thackeray (top histogram) compared to those documented in this study solely on tortoise cranials and post-cranials (bottom histogram). The totals of the tortoise bones per stratum can be found in Table 3 while Thackeray's bone totals are as follows: 1a (664), 1b (1617), 2a (262), 2b (274), 3a (1836), 3b (1490), 4a (2902), 4b (755), 4c (217), 4d (720) and 5 (374).

The cave has yielded archaeological deposits stretching back ca. 2.0 Ma years and includes Oldowan as well as Earlier, Middle and Later Stone Age lithic industries, botanical and faunal remains.

Excavations in the cave began in 1943 when, B.D. Malan and L.H. Wells made the first test excavations in two locations - ca. 30.5 and 61 m in from the cave entrance (Thackeray, 1983; Beaumont, 1990). In 1948 B.D. Malan returned with two members of the University of California African Expedition (Southern Section) and excavated additional squares O-P 30–31 near the cave entrance, but this work was never published (Thackeray, 1983). Between 1974 and 1977, K.W. Butzer undertook a sedimentology and geochemistry study of earlier collections (Butzer et al., 1979; Butzer, 1984a; 1984b). Beginning in 1978 an extensive excavation, known as Excavation 1, was undertaken by Peter Beaumont, archaeologist of the McGregor Museum, Kimberley, who was joined by two doctoral students, Francis and Anne Thackeray, in 1979 (Thackeray, 1983; Beaumont, 1990; Ecker et al., 2017). Fig. 6 illustrates the squares excavated by these different researchers in Excavation 1, located adjacent to the cave entrance.

In Excavation 1, Beaumont and the Thackeray's excavated 48 m^2 of Later Stone Age (LSA) deposit. They recognised four main LSA layers (Strata 1 through 4), with several sub-phases labelled a, b, c, etc. The excavation grid was laid out in square yards (each square 1 yard = 0.92 m), while the deposit within each square was excavated in 5 or 10 cm spits. Beaumont and the Thackeray's labelled their spits differently, and these were correlated by Ecker et al. (2017) to form the unified stratigraphic picture listed in Table 2 together with associated radiocarbon ages. A total of 3669 tortoise bones were documented in this study of the Holocene strata from Wonderwerk Cave. Of these, 296 were limb bones and 3373 were carapace and plastron parts. According to Beaumont and Vogel (2006:218), all deposit removed from the cave was dry sieved through a 1 mm or smaller mesh which has resulted in good recovery of even small skeletal elements.

4.2. Material and methods

All the LSA tortoise remains from Wonderwerk Cave were previously sorted by Dr Francis Thackeray when he analysed the faunal remains from these levels for his PhD (Thackeray, 1984, 2015). However, he did not list the tortoise remains by skeletal element, attempt species identification or provide any biometric or morphological information (Thackeray, 1984, 2015). For the current study, all tortoise material from Strata 1–4 was re-sorted and identified by skeletal element. Carapace and plastron remains were separated, but often the fragments were too small or too broken to determine to which they belonged and were therefore placed in a joint "carapace" category. A special effort was made to distinguish elements such as the gulars, pygals and nuchals since these were used for species identification and demonstrated that the Wonderwerk Cave tortoises all belong to the leopard tortoise (*Stigmochelys pardalis*).

A total of 296 limb elements from eight different LSA strata were analysed in this study (see Table 3). Sample sizes differ, with the largest collection amounting to almost 100 bones from Stratum 4c (99 bones)

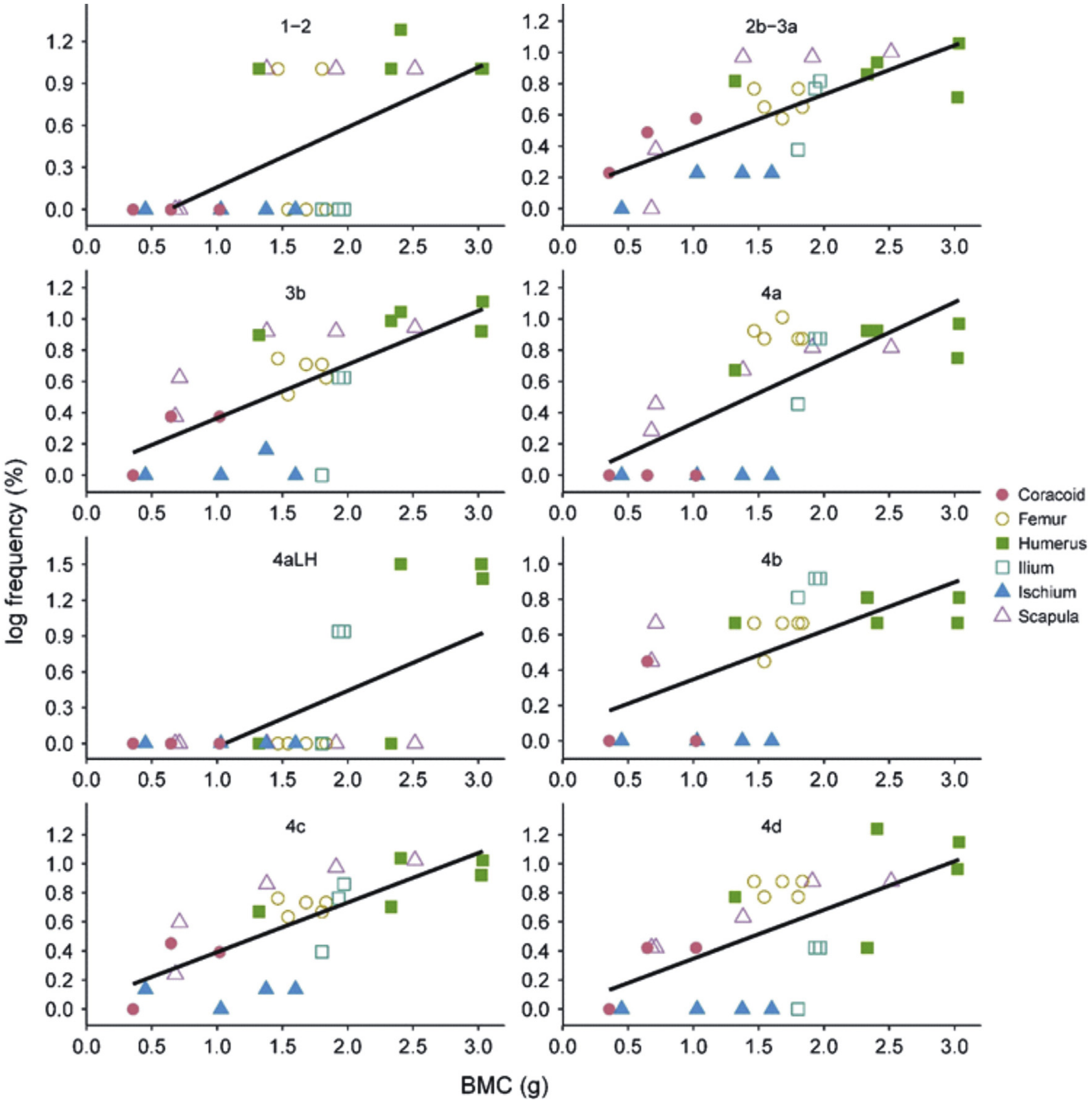

Fig. 8. Wonderwerk Cave tortoise density values by element and stratum (BMC).

and the smallest comprising only four bones (Stratum 1–2).

Concerning the general taphonomic history of the Wonderwerk Cave Holocene fauna, Thackeray (1984, 2015) observed that leopards (*Panthera pardus*) may "have temporarily used the Wonderwerk Cave in the mid-Holocene" (Thackeray, 2015:738). However, as shown in Fig. 7, carnivore damage was identified only in Strata 3a and 4a and was minimal; found on 0.16% and 0.3% of the 1836 and 2902 bones examined in each of these samples respectively (Thackeray, 1984: Table 71). Gnawing by rodents (small rodents and porcupines) was evident in only six of the eleven layers studied (Fig. 7). The highest gnaw damage for small rodents was found in Stratum 2b where it was present on 2.19% of the bones but evident on fewer than 1% of the remains in all other layers. Porcupine damage was identified on 1.14% of the faunal remains in Stratum 2a and on 1.09% in Stratum 2b, but in the other four layers it was evident on less than 1% of the remains (Thackeray, 1984: Table 71). Slightly higher proportions of the bones exhibited cut marks and/or burning (Fig. 7); the highest frequencies are 0.73% cut marked bones in Stratum 2b and 4.20% burnt bones in Stratum 2a (Thackeray, 1984: Table 70). These results led Thackeray (1984, 2015) to conclude that people were the main agents of bone accumulation in all layers.

Our examination of modifications specifically present on tortoise post-cranial and cranial remains (Fig. 7) mirrors this pattern, with burning the most common modification in all strata. In contrast, cut marks, rodent and carnivore damage are not found in all strata and when present, occur in very low frequencies, implying that the input of non-anthropogenic agents in modifying this assemblage was small.

4.3. Statistical methods

We evaluated the relationship between BMD values and frequency occurrences of limb elements, and regions/parts of these elements for all strata at Wonderwerk Cave. Although all the skeletal elements of the leopard tortoise were scanned, not all available BMD values could be used for Wonderwerk Cave as no skull, mandibles, radii, ulnae, tibiae or fibulae were found in the material sorted by Thackeray. Random samples (bags) of the unidentified fraction of the faunal assemblage from the Holocene layers were checked by us and none of the tortoise bones listed above were found, such that we are confident that their absence is not a methodological artefact. Moreover, given that these skeletal elements are consistently missing in all layers, the statistical probability of none of them showing up in the sample due to poor sorting is low.

Frequency occurrences were defined as the percentage each bone

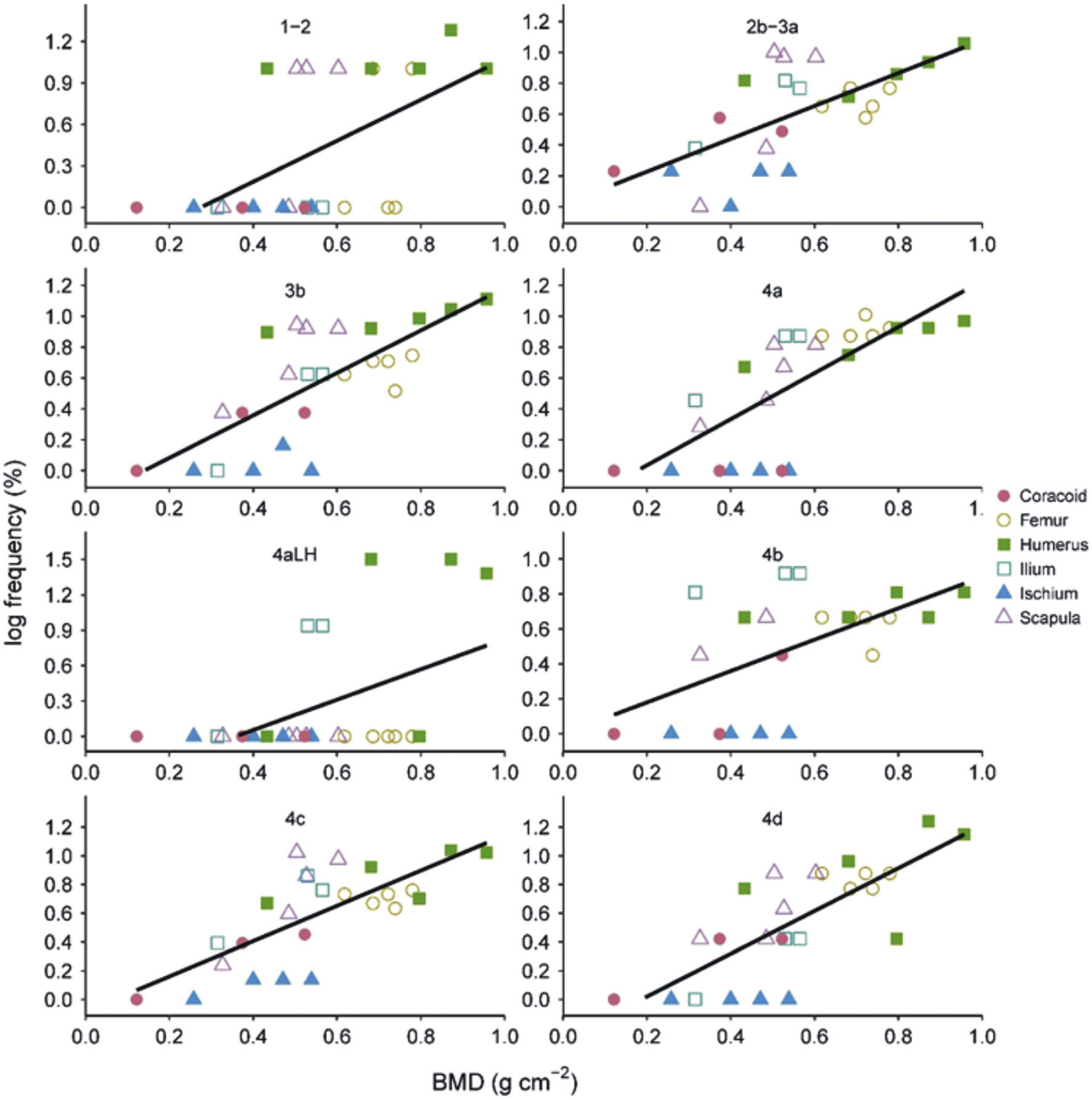

Fig. 9. Wonderwerk Cave tortoise density values by element and stratum (BMD).

part made up the total in a given assemblage, where each assemblage was defined as the set of bones recovered from one of eight LSA strata. Relationships were evaluated for each assemblage (Stratum) separately, as well as for each of the three bone density metrics described above (BMC, BMD, and DV). Our initial approach to these relationships follows those widely used in the literature, namely, to apply simple linear regression models (SLR) with the respective bone density metrics as covariates. However, this approach does not account for the fact that different bones may differ in preservation rates due to properties other than density such as bone size, shape and weight (Lyman, 1984). Moreover, SLR does not account for the fact that multiple measures were taken for each bone, so that the data series are non-independent.

To overcome the constraints of simple linear regression models (SLR), we re-evaluated the relationships using MELMs, in which we included "Bone" (femur, humerus, scapula, etc.) as a random effect. In both cases, i.e. SLR and MELM, assumptions of parametric tests, in particular normality of residuals, were not met (Shapiro-Wilks $p > 0.05$), and so frequency occurrence data were $\log_{10}$-transformed. Significance of the bone density covariate was estimated based on the F-distribution (two-tailed α-level = 0.05), and that for the random effect Bone on a X^2-distribution. Strength of the relationships are indicated by r^2 values (in SLR), and marginal r^2 (in MELM); in the case of the latter, conditional r^2 values are used to estimate the predictive power of models when Bone is included as a random effect.

4.4. Results

Simple linear regression models (SLR) revealed significant positive relationships between both BMC (Fig. 8) and BMD (Fig. 9) with the frequencies of bone elements in all layers of the Wonderwerk Cave sequence (Table 4). The strength of these effects ranged from weak ($r^2 = 0.218$ for BMD in Stratum 4b) to moderate ($r^2 = 0.580$ for BMD in Stratum 4d; see Table 2). However, results for two of the eight assemblages are to be treated with caution: i) in Strata 1–2 all bone elements present are represented by only a single specimen, except in the case of the distal humerus shaft where $n = 2$; and ii) in Stratum 4aLH, 20 of 25 element types included in this study are absent, and therefore the data includes primarily zeroes.

Density volume (DV) (Fig. 10) was not significantly related to frequency occurrences in any of the Wonderwerk Cave layers studied ($p = 0.361$ to 0.837). This is not surprising given the marked differences found between bone density measurements in the modern leopard tortoise, using BMC, BMD and DV. The percentage survivorship of skeletal elements in all Wonderwerk Cave strata, irrespective of sample

Table 4
Regression models evaluating the effect of the various bone density metrics on frequency occurrences of different skeletal elements and parts of bones in the various strata of the Wonderwerk Cave sequence.

Layer	SLR				MELM						
	df	*F*	*p*	r^2	*df*	*F*	*p*	X^2_{Bone}	p_{Bone}	r^2_{marginal}	$r^2_{\text{conditional}}$
BMC (g)											
1–2	1,23	13.236	0.0014	0.3653	1,23	6.782	0.0160	3.489	0.0618	0.2232	0.5391
2b-3a	1,23	25.846	0.0000	0.5291	1,21	20.189	0.0002	1.939	0.1638	0.4814	0.6242
3b	1,23	19.509	0.0002	0.4589	1,22	10.083	0.0044	12.342	0.0004	0.2054	0.7623
4a	1,23	24.277	0.0001	0.5135	1,19	13.054	0.0018	22.444	0.0000	0.1338	0.8890
4aLH	1,23	17.207	0.0004	0.4280	1,18	12.179	0.0026	0.850	0.3564	0.3620	0.4723
4b	1,23	12.721	0.0016	0.3561	1,21	9.322	0.0061	18.515	0.0000	0.1474	0.8231
4c	1,23	29.944	0.0000	0.5656	1,23	22.368	0.0001	7.985	0.0047	0.4404	0.7512
4d	1,23	15.165	0.0007	0.3974	1,22	10.982	0.0032	12.986	0.0003	0.2236	0.7615
BMD (g cm^{-2})											
1–2	1,23	10.916	0.0031	0.3219	1,22	4.861	0.0384	3.274	0.0704	0.1814	0.4852
2b-3a	1,23	18.519	0.0003	0.4460	1,20	14.016	0.0012	2.305	0.1290	0.3993	0.5772
3b	1,23	27.374	0.0000	0.5434	1,22	20.561	0.0002	14.901	0.0001	0.3432	0.8179
4a	1,23	29.546	0.0000	0.5623	1,19	15.160	0.0009	21.384	0.0000	0.1544	0.8964
4aLH	1,23	7.157	0.0135	0.2373	1,23	6.690	0.0167	5.063	0.0244	0.2267	0.5517
4b	1,23	6.412	0.0186	0.2180	1,20	7.141	0.0145	21.451	0.0000	0.1105	0.8386
4c	1,23	27.134	0.0000	0.5412	1,23	25.669	0.0000	11.125	0.0009	0.4508	0.7992
4d	1,23	31.725	0.0000	0.5797	1,23	15.167	0.0007	6.840	0.0089	0.3508	0.7268
DV (g cm^{-3})											
1–2	1,23	0.121	0.7316	0.0052	1,18	2.198	0.1552	9.714	0.0018	0.0368	0.6151
2b-3a	1,23	0.830	0.3717	0.0348	1,18	3.365	0.0828	6.978	0.0082	0.0667	0.5434
3b	1,23	0.230	0.6362	0.0099	1,18	6.850	0.0174	22.973	0.0000	0.0502	0.8325
4a	1,23	0.043	0.8371	0.0019	1,18	6.391	0.0210	33.294	0.0000	0.0242	0.9136
4aLH	1,23	0.793	0.3823	0.0333	1,19	2.783	0.1121	6.619	0.0101	0.0593	0.5086
4b	1,23	0.092	0.7647	0.0040	1,18	1.361	0.2585	21.329	0.0000	0.0105	0.8229
4c	1,23	0.868	0.3611	0.0364	1,18	7.144	0.0154	16.136	0.0001	0.0750	0.7596
4d	1,23	0.364	0.5522	0.0156	1,18	7.863	0.0117	20.973	0.0000	0.0634	0.8154

SLR = simple linear regression; MELM = mixed effects linear model, with "Bone" included as a random effect; BMC = bone mineral content; BMD = bone mineral density; DV = density volume.

size, best matches the results obtained for bone density in the modern tortoise using BMC and BMD values.

Including ‘Bone’ as a random effect in MELMs revealed a similar trend, in that the effect of BMC and BMD on bone frequencies was significant ($p < 0.05$) in all assemblages/layers. The strength of these effects again varied from weak to moderate (marginal $r^2 = 0.111$ to 0.481 for Stratum 4b). The random effect “Bone” was also significant in five of the eight strata in the case of BMC, and in six strata in the case of BMD. In layers where the random effect was non-significant, this result was only marginal ($p \sim 0.07$), probably reflecting low statistical power especially in the anomalous case of Strata 1–2 (see above). Interestingly, whereas DV and frequency occurrence were not related in the SLR models, DV had a significant ($p < 0.05$) effect on frequencies in four of the eight strata in MELM, indicating that accounting for different preservation rates (and biases) amongst bone types is important when evaluating taphonomic effects of density. Moreover, the strength of the models improved substantially for all density metrics when the variance across bone types was accounted for (conditional $r^2 = 0.472$ to 0.914).

4.5. Discussion

Our findings suggest that survivorship of tortoise bones in the Holocene strata at Wonderwerk Cave was significantly impacted by bone mineral density. As predicted from BMD and BMC values, the humerus caput and greater trochanter of the femur were the most common bones in the archaeological assemblage while the coracoid and pubis were the least. Notably, several skeletal elements that are missing in the Wonderwerk Cave assemblage (cranial, mandible, radius, ulna, tibia and fibula as well as metacarpals and metatarsals) are among those with lowest overall values for BMD, as shown in Table 1, offering a good case for bone density-mediated attrition as a primary factor. The role played by other agents (humans, carnivores, rodents, geology) in explaining these missing skeletal elements, is far less significant. Human activities, such as butchery and discard of the head and distal limbs during carcass processing or following cooking, cannot be ruled out since the missing elements are those poor in meat compared to the upper limbs and shell which are represented in the Wonderwerk Cave assemblage. Such an explanation would imply that the missing elements were discarded either, in an as yet unexcavated part of the cave or outside the cave, such that it cannot be tested. Moreover, given their relatively small size and low weight and meat value (as well as the argument presented above as to why live tortoises would have been preferentially introduced into the site), there would be little reason for people to have dismembered these missing skeletal elements at the original tortoise find spot in the field. An alternative agent who may be responsible for their absence are carnivores, such as leopards who inhabited the cave, who could have gnawed off and digested the small and quite fragile head and distal limb bones. This, since these elements protrude from the shell and would be accessible even if the shell was not broken open. This explanation would necessitate the presence in the Wonderwerk Cave assemblage of at least some of these elements exhibiting acid etching, which is not the case. A final argument against carnivores, rodents or humans as the main agents responsible for the observed patterning in skeletal element representation, is the consistency of the BMD results for all strata irrespective of the intensity of their activities. As illustrated in Fig. 7, evidence for carnivore, rodent and even human modifications is uneven between strata and aside from burning, of low intensity. Thus, the most parsimonious explanation is that BMD in itself was the primary agent in modifying skeletal element survivorship. Given the large numbers of burnt bones, it cannot be excluded as a factor and may have served to bias preservation of the denser elements. Finally, the correlation between BMD and skeletal elements decreased in significance from the lowest to the uppermost strata, suggesting that time of deposition (and/or depth of deposit) has also played a role in bone preservation at this site.

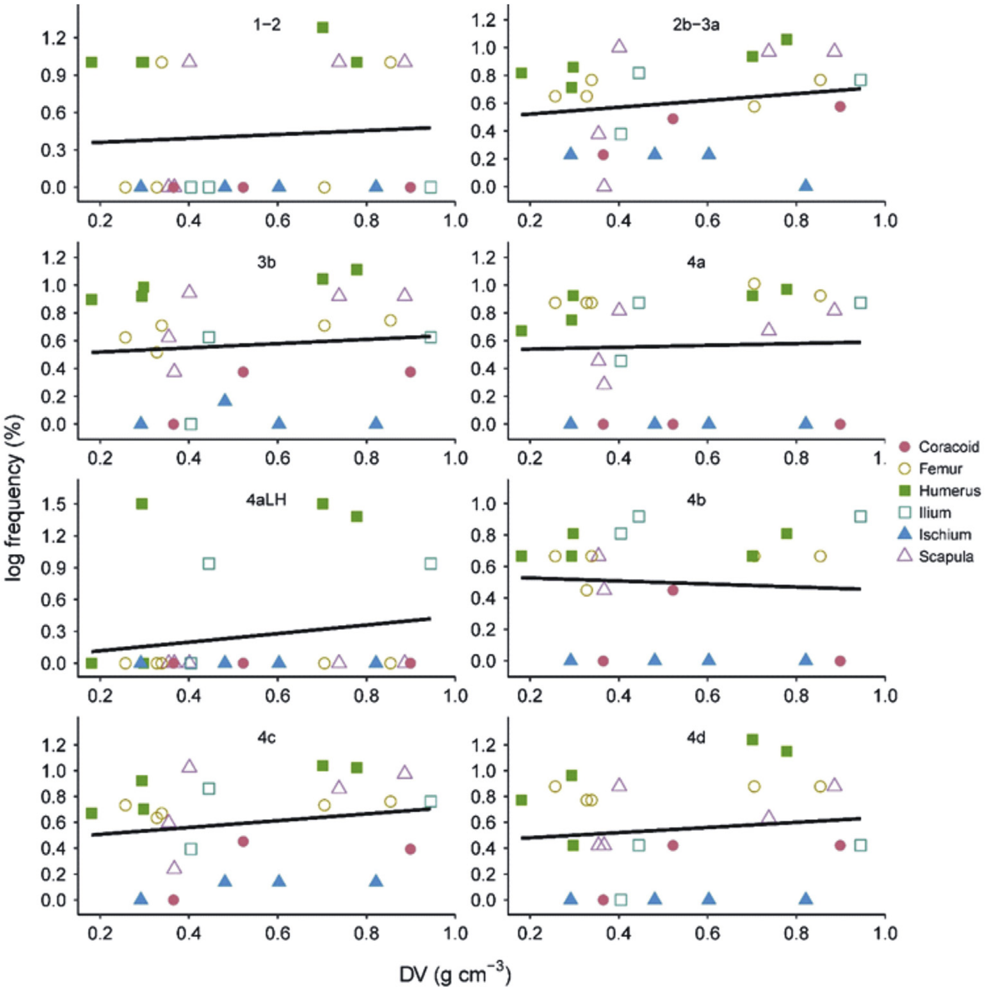

Fig. 10. Wonderwerk Cave tortoise density values by element and stratum (DV).

5. Conclusion

This study demonstrates that the inclusion of random effects in the regression models is not only a more valid statistical approach than the traditionally used SLR, but that these more complex models improve our understanding of taphonomic events. Future studies could build from this concept in efforts to identify which (non-random) processes act alongside BMD to influence preservation rates of different skeletal elements. As mentioned above, bone size, shape and weight are important parameters to consider (Lyman, 1984) and this is why it is extremely important to include bone as a random effect in models.

Although this investigation only examined BMD in one tortoise specimen, the results indicate that despite differences in growth patterns, reptile bones behave in the same manner as those of other vertebrates such that the differential survivorship of their skeletal elements in archaeological assemblages, as demonstrated here for the Holocene strata at Wonderwerk Cave, is also influenced by density-mediated attrition.

Finally, inter-species variation in BMD of different terrestrial vertebrates offers insights into bone function and biomechanics. This study illustrates the potential application of this method as a taphonomic proxy to gain further understanding of palaeofaunal assemblages in the future.

Acknowledgments

We dedicate this paper to James Brink on the occasion of his 60th birthday. James has played a positive role for us, as a valued colleague and research collaborator and we offer him our warm wishes for the coming years. We would like to acknowledge the Palaeontological Scientific Trust (PAST) for their financial support towards SH's PhD research and to thank the Centre of Excellence for Nutrition at the North West University for permission to undertake the bone density scans and Magda Uys who did the scanning. Special thanks to Beryl Wilson of the McGregor Museum, Kimberley who helped to collect the dead tortoises that are now curated in the National Museums collection including the specimen used in this article and to Linda Wheeler who made the sketches of the tortoise bones. We thank the two anonymous reviewers for their useful comments which helped to improve this paper.

Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.quaint.2018.04.020.

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Chapter 3

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Structural density of the leopard tortoise (*Stigmochelys pardalis*) shell and its implications for taphonomic research

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ABSTRACT

We investigated bone mineral density values of the shell (carapace and plastron) of a modern leopard tortoise (*Stigmochelys pardalis* Bell, 1828) to assess its impact on survivorship of the different skeletal elements. We found significant differences among elements for bone mineral density and density volume, but not for bone mineral content.

We then compared these findings with those obtained using computed tomography (CT) scans of shells of three modern tortoise species that differ in size and shape; the leopard tortoise, greater padloper (*Homopus femoralis*) and angulate tortoise (*Chersina angulata*). Results indicate that the patterning of bone density is similar across shell elements and scan sites in all species, although all values were lower in the greater padloper, which we attributed to shape differences – a flat rather than domed shell.

Finally, we correlated the frequency of shell elements from the Holocene leopard tortoises recovered at the site of Wonderwerk Cave (South Africa) using, as a proxy, the densitometry values obtained from the modern leopard tortoise. For most strata there was a significant association with skeletal element survivorship demonstrating the role played by bone mineral density in determining the skeletal composition of this assemblage.

1. Introduction

There are 13 species of terrestrial tortoises in southern Africa today (Boycott and Bourquin, 2000; Branch, 2008; Hofmeyr et al., 2014). Their exploitation by humans dates back to the Early Pleistocene, as attested to by findings from archaeological sites at Sterkfontein, Swartkrans and Makapansgat (Broadley, 1962, 1997). In the subsequent Middle and Late Pleistocene tortoises were exploited even more intensively (e.g. Klein et al., 1999, 2004; Klein and Cruz-Uribe, 2000, 2016; Thompson and Henshilwood, 2014a, 2014b; Discamps and Henshilwood, 2015), with their remains especially common in Holocene hunter-gatherer and pastoralist sites (Klein and Cruz-Uribe, 1983, 2016; Sampson, 1998; Avery et al., 2004). In these later cultures, tortoises appear to have played an important role not only in human diet, but also in their material culture, being used as containers and for the manufacture of ornaments (Avery et al., 2004).

Taphonomic studies of tortoise bone assemblages worldwide have explored how these reptiles were exploited by past peoples, focusing mainly on patterns of skeletal element representation, burning and butchery (e.g. Speth and Tchernov, 2002; Stiner, 2005; Blasco, 2008; Blasco et al., 2011; Stiner and Munro, 2011; Thompson and Henshilwood, 2014a, 2014b; Blasco et al., 2016; Biton et al., 2017). While numerous factors have been identified that may affect the preservation of bone in archaeological and palaeontological contexts (e.g. Lyman, 1994; Haglund and Sorg, 2001; Allison and Bottjer, 2011), the role played by bone mineral density (BMD) in the differential preservation of skeletal elements (e.g. Lyman, 1984; Kreutzer, 1992; Lam and Pearson, 2004) has only been addressed for reptiles in one study, that of Holt et al. (2018) who investigated BMD of leopard tortoise limbs. Shell fragments, however, are the most common tortoise remains found in archaeozoological assemblages, such that factors influencing *their* representation warrant in depth research.

Here we present a detailed analysis of density variation in tortoise shell, including bones of both the carapace and plastron. Using data

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obtained from bone densitometry, we have documented variations in bone mineral density across and within elements of the shell of the modern African leopard tortoise (*Stigmochelys pardalis* Bell, 1828), and explored whether these variations are related to other properties of the shell, such as thickness. Results were then compared with density data obtained from computer tomography (CT) scans of three modern South African tortoise species that differ in size and shape (leopard tortoise, greater padloper [*Homopus femoralis*], angulate tortoise [*Chersina angulate*]), in order to assess whether, and how, interspecific differences in morphology may have influenced bone density variation throughout the shell. Finally, we investigated relationships between density and relative abundance of shell elements of Later Stone Age leopard tortoises remains (dating to ~12,200 BP to ~1910 CE) from the site of Wonderwerk Cave (Northern Cape Province, South Africa), to study the taphonomic role of bone density in element survival.

2. Biology of tortoise shell

2.1. Shell form

Terrestrial tortoises (family Testudinidae) have a shell which offers protection and support for the soft tissues and skeleton, provides shelter for the retractable limbs and cranium (Thomson, 1932; Pritchard, 1979), and plays a role in thermoregulation (Cordero, 2017). Numerous studies have shown that overall shell morphology is shaped by both environment and phylogeny (Claude et al., 2003; Scheyer, 2007; Scheyer and Sander, 2007), while sexual dimorphism is also evident in both the form and size of the shell (Thomson, 1932; Boycott and Bourquin, 2000; Pritchard, 2008; Branch, 2008).

The shell is comprised of a dorsal part (carapace) and a ventral part (plastron), both made up of bone plates covered with keratinous scutes whose margins do not align with those of the sutures of the underlying bone plates (Fig. 1; Pritchard, 1979; Scheyer, 2007; Branch, 2008). There is marked inter-specific variation in the numbers of bone plates in carapace and plastron (e.g. Thomson, 1932; Boycott and Bourquin, 2000; Pritchard, 2008), while abnormal numbers and arrangements of bone plates also occur (Farke and Distler, 2015).

In this study, shell nomenclature used follows Zangerl (1969) with the general composition of a tortoise shell outlined below.

2.1.1. Carapace

The ribs and vertebrae of the tortoise (except the first seven cervical vertebrae which are mobile) are fused to the carapace (Sobolik and Steele, 1996). On average, the carapace comprises 19 paired bones, from anterior to posterior and on each side - 8 costal bones and 11 peripheral bones as well as 10 unpaired bones - 8 neural bones, the nuchal bone (the most anterior bone) and the pygal (the most posterior bone). Between the last neural bone and the pygal are the two bones of the suprapygal 1 and 2 which are not fused to a vertebra (notably the number of superpygal bones varies among species). In tortoises, the neural arches of the vertebrae are fused to the neural bones of the shell and in some species, supernumerary neural bones are common (Farke and Distler, 2015). Tortoises have 8 cervical vertebrae (of which only the 8th is fused to the carapace), 10 thoracic vertebrae (all fused to the neural bones of the carapace), 2–3 sacral vertebrae (whose lateral processes are not fused to the carapace) and 12 (or more, depending on sex and species) caudal vertebrae, which form the tail and are mobile. The costals and neurals of the carapace develop as a mixture of dermal and endoskeletal bone, while some carapace elements, such as the nuchal, pygal, suprapygals and peripherals are dermal in origin (Scheyer, 2007; Hirasawa et al., 2015; Cordero, 2017).

2.1.2. Plastron

This forms the ventral part of the shell and is composed of four paired bones, from anterior to posterior: epiplastron, hyoplastron, hypoplastron and xiphiplastron, and one unpaired bone - the entoplastron, whose form is species-specific. The plastron elements are all dermal in origin and are the earliest bones of the shell to ossify (Sobolik and Steele, 1996).

In all tortoises, the carapace and plastron are joined by sutures between the middle peripheral bones (#3 – #8) in an area called the bridge (Fig. 1; Boycott and Bourquin, 2000; Scheyer, 2007; Branch, 2008). While the shell is developing, there are gaps at the sutures in both the carapace and plastron; that facilitates ongoing growth of the shell. The sutures close as the animal ages, with growth only ceasing in very old individuals when the bony shell becomes completely ossified (Branch, 2008; Pritchard, 2008). The shell of the leopard tortoise, the species focused on in this paper, comprises 59 skeletal elements, divided into 50 carapace bones (1 nuchal, 8 neurals, 2 suprapygals, 1 pygal, 16 costals, 22 peripherals) and 9 bones of the plastron (2 epiplastrons, 1 entoplastron, 2 hyoplastron, 2 hypoplastron, 2 xiphiplastron).

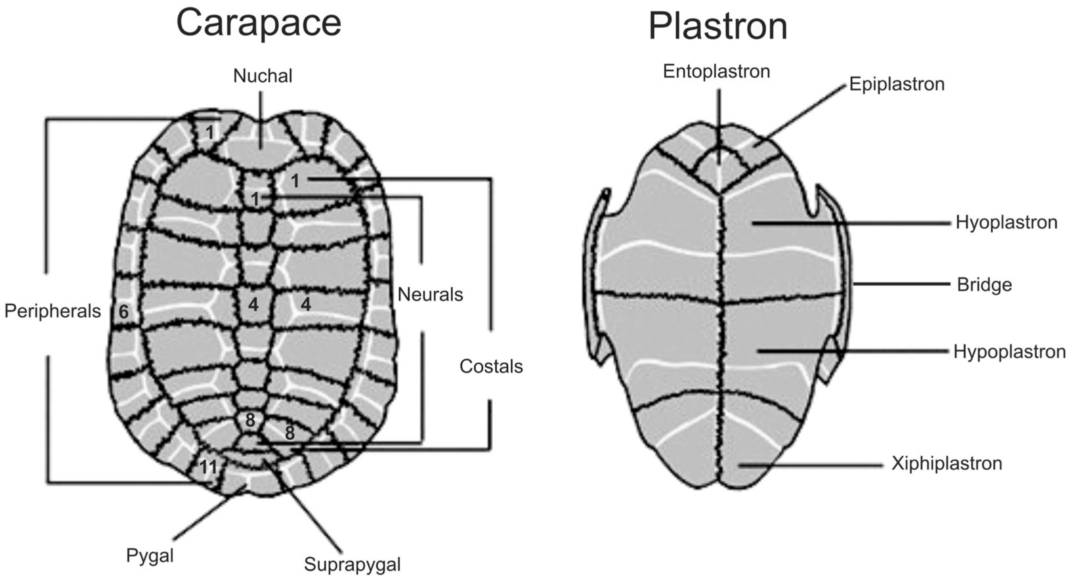

Fig. 1. A tortoise shell with the different bone plates of the carapace and plastron marked by black lines and the keratinous scutes by white lines.

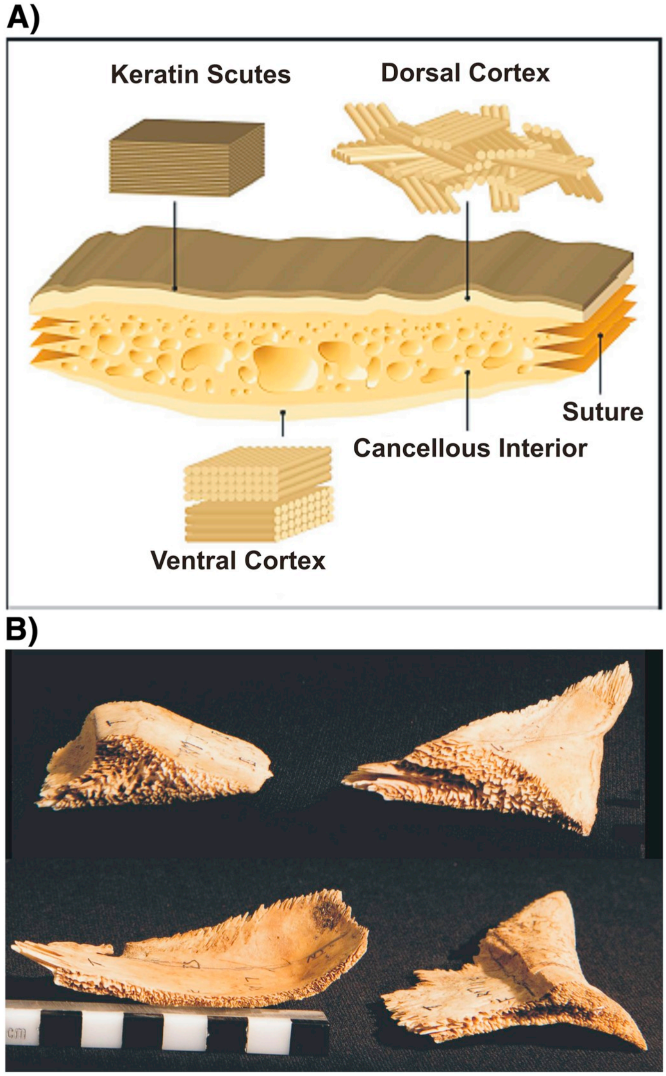

Fig. 2. a. Schematic cross-section of a tortoise carapace plate showing its microstructure (modified after Achrai and Wagner, 2013: Fig. 11).

Fig. 2b. Side view of leopard tortoise peripherals showing differences in thickness. (from left to right) Top row peripherals #'s 1 and 3. Bottom row peripherals #'s 7 and 11.

2.2. Micro-structure of the shell

Studies have shown that the microstructure of the bone comprising the shell is influenced by both phylogenetic and functional constraints (Hailey and Lambert, 2002; Scheyer and Sánchez-Villagra, 2007). The bone has a diploe structure with relatively dense, well-developed exterior lamellar cortices (compact bone) on the dorsal and ventral surfaces of the shell, respectively. The compact bone contains few large voids but has numerous lacunae containing bone cells (osteocytes), but the voids are relatively under-supplied by blood vessels. Sandwiched between the cortices is a more porous layer of cancellous (trabecular) bone, made up of thin islands of bone divided by large voids that are randomly distributed and which serve as sites for blood-cell generation (Fig. 2; Scheyer, 2007; Krauss et al., 2009; Rhee et al., 2009; Achrai et al., 2014; Achrai and Wagner, 2017). Porosity levels differ between the relatively denser exterior cortices and the interior trabecular layer. For example, Rhee et al. (2009) reported 65.5% porosity in the cortices of the common box turtle, *Terrapene Carolina*, versus 6.86% porosity for the trabecular layer.

Achrai and Wagner (2013) reported that in the red-eared terrapin (*Trachemys scripta elegans*), each cortex layer (ca. 0.25–0.5 mm thick) had a slightly different fibrillar organization. The outer dorsal cortex displays a disordered structure for both the osteon network and the fibrillar structure in which it is embedded, a structure which they interpret as playing a role in redirecting crack propagation. In contrast, the ventral cortex is stiffer and exhibits two parallel and perpendicular fiber sub-layers. Each sub-layer is oriented anterio-posteriorly and medio-laterally, a structure which is advantageous in a basal layer that provides structural support. Both cortices are stiffer and have higher mineral contents than the interior cancellous layer (ca. 2 mm thick). Average mineral content (measured as ash content) for the ventral cortex was ~60 ± 3 wt%, ~for the dorsal cortex ~60 ± 4 wt% but only ~50 ± 4 wt% for the interior trabecular layer (Achrai and Wagner, 2013: Table 1). However, despite differences in the textural morphology of the different layers in *Terrapene carolina* and *Trachemys scripta elegans*, the exterior compact bone layers (cortices) and the bony closed-cell walls of the interior trabecular layer, possess comparable hardness and Youngs modulus values (an index of elasticity) (Rhee et al., 2009; Achrai et al., 2013; Achrai and Wagner, 2017). Moreover, in each bone plate, they found an increasing gradient of mineralization from the unmineralized suture towards the bulk bone in the middle of the plate (Achrai and Wagner, 2013).

Thus, the overall composite structure makes the shell both strong and durable, enabling it to withstand predator attacks, protect the soft inner tissues and endure blunt shock such as from falls or being

Table 1

Best-supported models ($\Delta AIC_c = 0$) of factors describing variation in densitometry-based measures of shell density across and within elements. Effect slopes are shown as means with 95% CI in parentheses.

Variable	Model	*n*	*K*	r^2m	Effect	*F* or X^2	*p*	Slope	VCA (% explained)
BMC	Thickness	86	6	0.356	CP	1.285	0.260	C: 6.286 (3.380 to 9.192); P (5.303 (−0.140 to 10.746)	
					CP/Elemen	0.000	0.999		20.7
					Within elements				79.3
BMD	Thickness + Element	86	4	0.752	Thickness	237.029	< 0.0001	0.085 (0.074 to 0.096)	
					Element	5.337	0.021		27.0
					Within elements				73.0
DV	Thickness + Element	86	4	0.494	Thickness	75.894	< 0.0001	−0.008 (−0.010 to 0.007)	
					Element	5.108	0.024		26.6
					Within elements				73.4

n = number of observations; *K* = number of parameters in model; r^2m = marginal r^2 value; BMC = bone mineral content (g); BMD = bone mineral density (g mm^{-2}); DV = density volume (g mm^{-3}); Element = bone element (random effect); CP = carapace or plastron; Thickness = width of element at density scan site, in mm (log_{10}-transformed); *F* or X^2 = relevant statistic for fixed (CP, Thickness) or random (Element) effects, respectively; VCA = variance components analysis differentiating variance explained by between-element from within-element (residuals) differences.

smashed, i.e. compressive, low frequency fatigue and impact loadings (Magwene and Socha, 2013; Achrai and Wagner, 2017). However, as noted in the studies cited above, there are notable differences in mineral content between the two cortices and the cancellous layer, as well as between the sutures and zones of bulk bone. It is expected that this intra-shell variation will influence shell breakage and preservation patterns in archaeological assemblages.

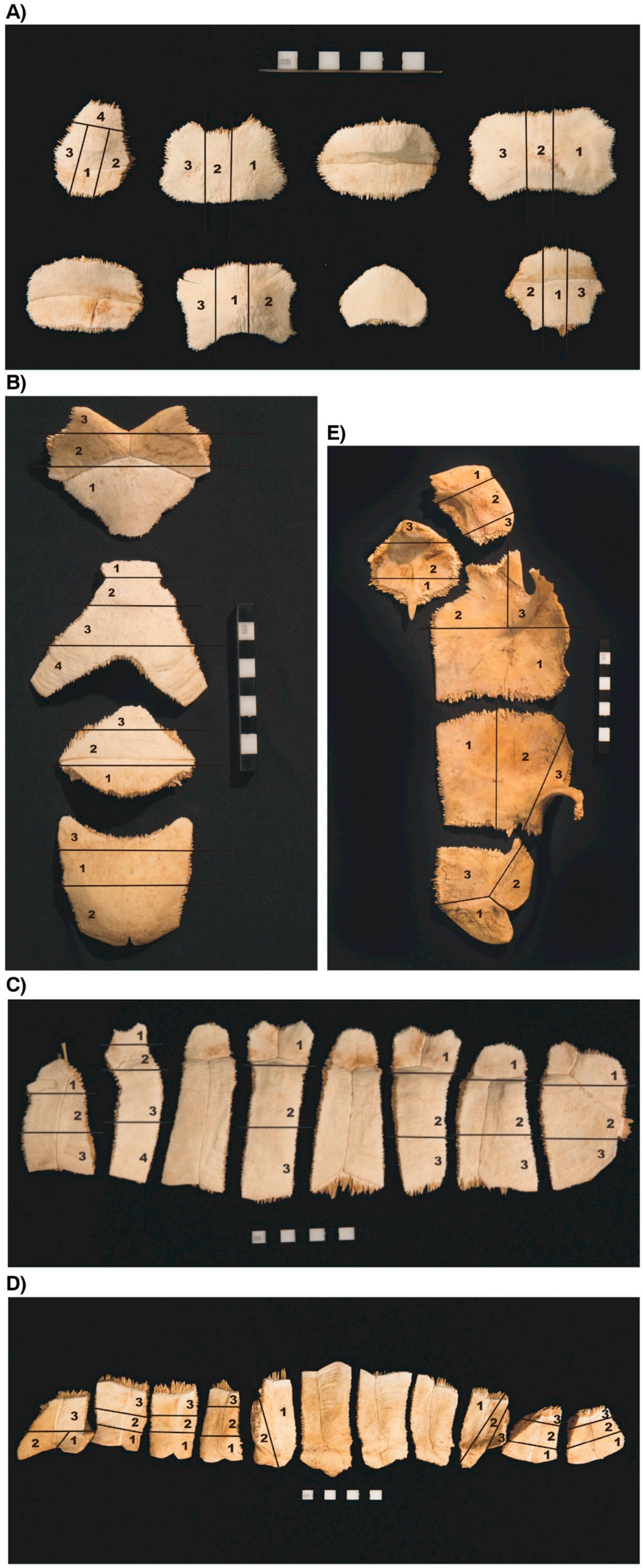

Fig. 3. a. Scan sites marked on the leopard tortoise neurals. Top row from left to right are neurals #'s 1, 2, 3 and 4. Bottom row from left to right are neurals #'s 5, 6, 7 and 8.
Fig. 3b. Scan sites marked on (from top to bottom) the leopard tortoise nuchal, suprapygal 1, suprapygal 2 and pygal bones.
Fig. 3c. Scan sites marked on the leopard tortoise costals. From left to right are costals #'s 8, 7, 6, 5, 4, 3, 2 and 1.
Fig. 3d. Scan sites marked on the leopard tortoise peripherals. From left to right are peripherals #'s 11, 10, 9, 8, 7, 6, 5, 4, 3, 2 and 1.
Fig. 3e. Scan sites marked on the leopard tortoise plastron bone plates. From top to bottom are the epiplastron, entoplastron, hyoplastron, hypoplastron and xiphiplastron.

3. Materials and methods

3.1. Bone densitometry

The bone density of the leopard tortoise shell was measured using a Hologic Discovery W duel X-ray (DEXA) bone densitometer, housed at the Centre of Excellence for Nutrition at the North West University, Potchefstroom. This method was chosen so that the results would be consistent with those already obtained by us for the appendicular skeleton of the same specimen ([NMBF 2434], a healthy adult leopard tortoise male from Jacobsdal, Free State Province) weighing ~8.8 kg that had died through contact with an electric fence (Holt et al., 2018).

For this study we selected 28 skeletal elements from the right side of the carapace and plastron for scanning. Given limitations of time, we omitted the 4th and 6th costals, the 4th to 6th peripherals, and 3rd, 5th and 7th neurals, since these have a similar form (size, shape and thickness) as their adjoining elements (see Fig. 3c–d). To ensure that each bone plate was placed in its correct anatomical position when scanned, they were numbered and their orientation marked to indicate their anterior and posterior aspects as well as the part of the bone that was closest to the neurals (top) or furthest (bottom).

Measurements and calibrations were made using APEX System Software Version 2.3.1, set to 'high' resolution for 'small-bodied' animals. For scanning, we used a container filled with grains of rice in which the skeletal elements were fully submerged. For each element the densitometer was calibrated before scanning.

In this study we identified a total of 86 scan sites on 28 skeletal elements following the unique features of tortoise shell anatomy (Fig. 3e). On each bone scanned, at least three density readings (the top, middle and bottom of each bone), were obtained. The densitometer yielded a perfect outline of the scanned element, after which the APEX System software was used to define the selected scan sites individually.

We investigated three measures of density, each of which has a slightly different meaning. The Bone Mineral Content (BMC) is a direct measure of bulk mineral density (in g) of the scanned area, whereas the other two measures, Bone Mineral Density (BMD) and Density Volume (DV), take into account the area and volume of the scan site, respectively. BMD (in g mm^{-2}) is estimated by the software (APEX System Software Version 2.3.1.) as BMC per area of the two-dimensional plane, representing the "linear" density of the bone (Kreutzer, 1992; Lyman et al., 1992). We estimated the volume of each scan site taking the area multiplied by bone thickness to calculate DV (=BMC/volume, in g mm^{-3}). Thickness was measured using a digital caliper positioned at various points (n = 4) along the relevant scan site: multiple measures were necessary because of the irregular shape of the bones. For data analysis, we used the median thickness for each scan site. All measurements are presented in supplementary Table S1.

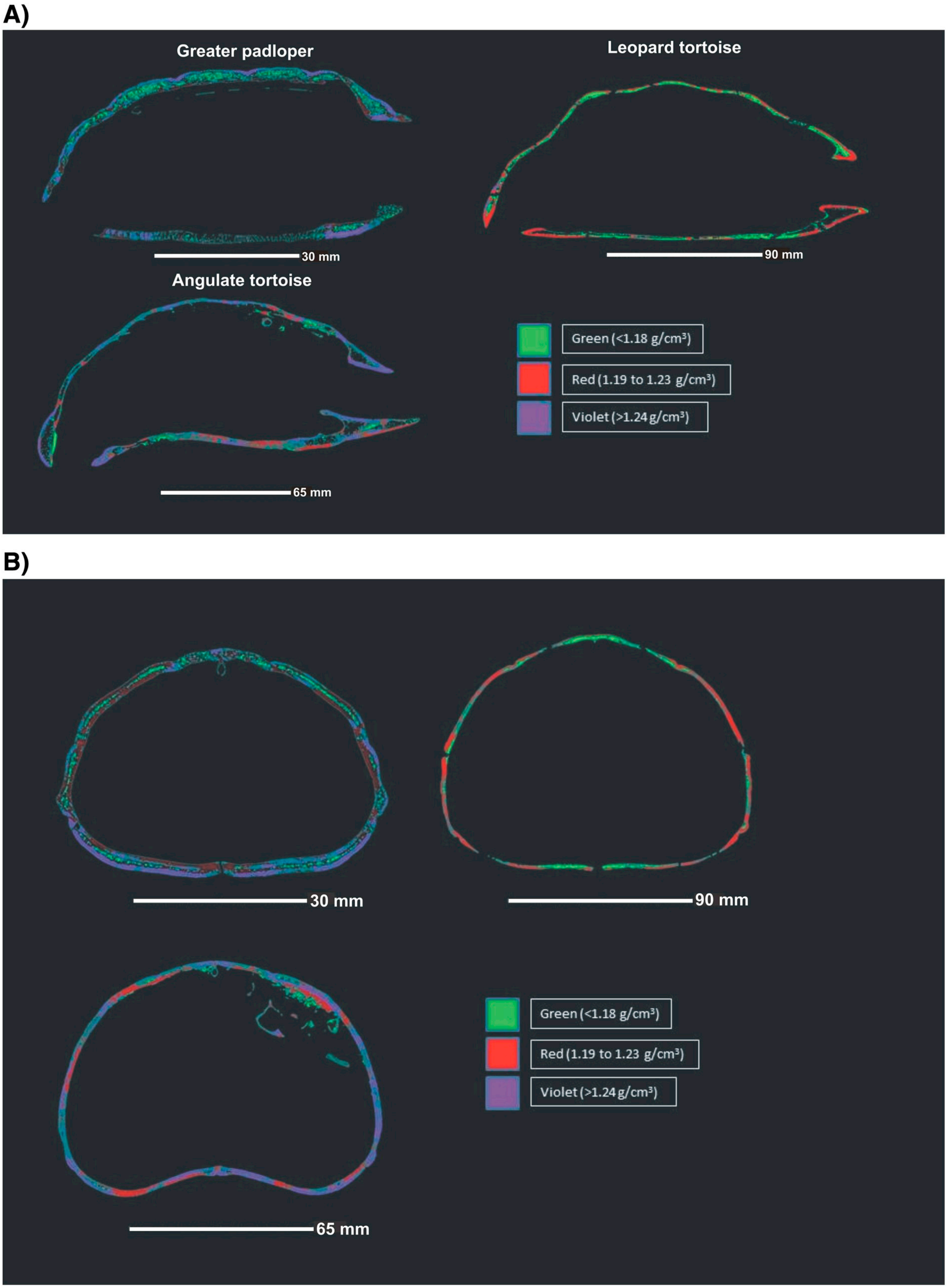

Fig. 4. Mid-point cross-section CT density profile maps of the three tortoise species. (a) Side view, anterio-posterior section. (b) Medio-lateral section. Note inter-specific differences in carapace and plastron shape. For density calibration procedures, refer to the Materials and methods section.

3.2. Computed tomography (CT) scans

CT scans of shells of three different South African tortoise species were undertaken. Species were selected that differ in size and/or shape (Fig. 4):

- The leopard tortoise (specimen NMBF 2439 ♂), is the largest tortoise species found in South Africa, and is also the most widespread in its biogeography - from South Africa to Ethiopia and the Sudan (Boycott and Bourquin, 2000; Branch, 2008; Hofmeyr et al., 2014). Females are usually larger than males, but adults of both sexes attain average weights of 15–20 kg, and even weights of up to 40 kg, and lengths of up to 700 mm (Boycott and Bourquin, 2000; Branch, 2008). The leopard tortoise shell can vary in shape but usually has a convex carapace with quite steep sides, while in males the plastron is concave (Fig. 4, Boycott and Bourquin, 2000; Branch, 2008).
- The angulate tortoise, (specimen NMBF 2338 ♂), is a medium-sized tortoise with males having a straight carapace length (SCL) of up to 272 mm and a mass of 2.1 kg, while females have a SCL of up to 216 mm and a mass of up to 1.8 kg (Boycott and Bourquin, 2000). Males are larger than females. This species is endemic to South Africa and Namibia and inhabits dry areas and coastal scrub vegetation (Hofmeyr et al., 2014). The carapace is convex like the leopard tortoise, with a concave plastron in males and prominent protrusion of the gulars (Fig. 4; Boycott and Bourquin, 2000).
- The greater padloper, (specimen MMK/F/1101 ♀), is the largest of the padlopers but is still a small-sized tortoise, with an average weight of 200–300 g (females are larger than males), and length of 100–130 mm, although females can reach 168 mm (Branch, 2008). It is endemic to South Africa and restricted to the southern and south-central part of the country including southern Lesotho (Boycott and Bourquin, 2000; Branch, 2008). The padloper shell is dorso-ventrally flat, and males lack a plastral concavity (Fig. 4; Boycott and Bourquin, 2000).
- The scanned angulate and padloper specimens were adults with ossifying bone plates, while the leopard tortoise was a sub-adult with patent sutures (adult leopard tortoise specimens were too large to fit inside the CT chamber used in this study). The ages of the specimens was not considered a limiting factor, as the purpose of this study was to assess the intra-specimen ranking of shell density, hence only the relative and not the absolute values obtained were considered important.

The scans were acquired using a Nikon XTH 225ST micro-focus X-ray computerized tomography (CT) unit located at the MIXRAD laboratory at the South African Nuclear Energy Corporation (Necsa), Pelindaba. Scanning parameters were standardized at 100 kV and 100 µA for all samples. Specimens were securely mounted in a polystyrene mould, with the body of the shell vertically oriented. In addition, three small tracers (comprising 1.1 g/cm^3, 1.5 g/cm^3 and 1.9 g/cm^3) of known density were included next to the specimens to calibrate the different scans. These tracers are plastic cubes dosed with an exact amount of heavy metal salts to give each a specific density. The mounted specimens were then placed on a rotating sample manipulator, which facilitated scanning through a full 360° rotation. One-thousand projection images were obtained in the 360° rotation and resulted in good-quality scans with optimised time. The scanning setup was optimised for highest spatial resolution by setting the sample with maximum magnification (magnification is a property of a cone beam). Consequently, a resolution of between 0.044 and 0.117 µm was obtained. The scans were then reconstructed using Nikon CTPro software (Nikon Metrology).

Following three-dimensional reconstruction, all the scans were imported into VGStudio Max V3 (http://www.volumegraphics.com/en/) as volume files for further analysis. All imported volume files were then subjected to a surface determination analysis to allow for clear and automatic determination of surface boundaries and to limit user defined errors. The orientation of the micro-CT slices of the shell was then standardized by orienting the sample vertically by aligning the sample to a plane specified on the underside of the sample (see below). Each voxel element in the volume files represents the density through a grey value, which ranged from 0 to 65,535 based on a 16 bit grey scale. The calibration procedure consisted of quantifying the average grey value of each density tracer and obtaining a density grey value relationship. The resulting parameterized linear equation was then used to model the specific densities at very specific grey values. Fig. 4 illustrates cross-sectional reconstructed images obtained from the CT scans for the three species.

The plane was fitted for all three specimens using four points on the plastron at the axillary notches. This allowed for measurements to be taken on a vertical or horizontal axis. For each element, density of the trabecular bone was measured at a specific point as well as the thickness (the maximum distance between the outer and inner surface of the element excluding the cortical voids) at the same point. On each element, the measurement points matched the scan sites used in the densitometry study insofar as possible (albeit over a smaller area). Due to time constraints, on the carapace only the right pygal, suprapygal, neurals #'s 1, 4 and 8; nuchal, costals #'s 1, 3 and 7 and peripherals #'s 1, 3, 5, 7, 9 and 11, were measured. On the plastron, the epiplastron, right entoplastron, hyoplastron, hypoplastron and xiphiplastron were measured. All measurements taken are given in Supplementary Table S2.

3.3. Data analysis

In order to determine how density varies across different elements, and at various scan sites on each element, for data derived from densitometry on the leopard tortoise we used a Mixed Effects Linear Model (MELM), with “Element” included as a random effect (see also Holt et al., 2018). Element was treated as a random effect because (i) multiple measures were taken from each element, and so the random term ensures that the correct error terms are compared in the model, and (ii) we make no a priori predictions about which elements should be more, or less, dense. Actually, with respect to point (ii), we were more interested in whether variance in density occurred among elements (i.e. if density is a function of the type and position of a particular bone in the shell), or within each element. For this we used a Variance Components Analysis (VCA) to differentiate variance explained by inter-element (the random effect) and intra-element (residual error) variance, respectively.

The second hypothesis we tested is related to other physical properties of the shell, in particular whether density is related to bone thickness. This hypothesis has both functional and practical implications: functional because we predict that thicker regions of the shell would be under selective pressure to become less dense and avoid ‘overloading’, whereas thinner regions would compensate for their lowered resistance to breakage by evolving higher densities; and practical because the prevalence of bones in archaeozoological assemblages are expected, in part, to reflect their relative density and hence likelihood of breakage and so survivorship (e.g. Lyman, 1984; Lyman et al., 1992; Elkin, 1995; Pavao and Stahl, 1999; see Wonderwerk Cave Case Study below). To test this hypothesis, we included median thickness as a covariate in the MELMs described above. It must be noted, however, that this measure of thickness also appears as part of the dependent variable in the case of DV ($=\frac{BMC}{Area * Thickness}$), and so the results of this particular model are, perhaps, spurious. In all cases, the relationships with thickness were non-linear, and so thickness values were $\log_{10}$-transformed. This also ensured that residuals of the models had a normal distribution (Shapiro Wilk's test). In addition, we investigated whether thickness effects differed between the carapace and plastron, using a second MELM in which model terms were nested within the term "Carapace" (a binary variable where 1 = carapace and 0 = plastron). The two models for each density measure were compared using the Akaike's Information Criterion adjusted for small samples (AIC_c), and selected for goodness-of-fit using the ΔAIC_c (AIC_c – minimum AIC_c). We omitted models with a $\Delta AIC_c > 2$ (see Burnham and Anderson, 2001, 2002).

Unlike densitometry, measures of density from CT scans (hereafter DCT) are independent of other linear measurements we made. Hence, any relationships to bone thickness are not spurious but reflect a true functional relationship. We used similar MELMs as described above to evaluate (i) relationships between DCT with each of the three densitometry-based measures (for the leopard tortoise only), (ii) relationships between DCT with thickness (measured as the distance from the centre of the scanned field perpendicularly to the distal surface of the relevant bone), and (iii) differences in thickness effects between the carapace and plastron. Again, thickness data were $\log_{10}$-transformed. Models (ii) and (iii) were repeated for each of the three tortoise species for which we obtained DCT data. We also used MELMs to evaluate relationships between species pairs, to determine whether inter- and intra-element patterns of variation were similar across taxa.

All analyses described above were carried out in R 3.4.3 (R Core Team, 2015), using the package lmerTest to implement linear MELMs (Kuznetsova et al., 2017).

4. Results and discussion

4.1. Densitometry

Density estimates for each element and scan site are represented by three measures: the Bone Mineral Content (BMC, in g), BMC relative to surface area scanned (Bone Mineral Density, or BMD, in g mm^{-2}), and BMC relative to volume of the scanned region (Density Volume, or DV, in g mm^{-3}). We evaluated variation in all three measures independently.

BMC values varied from 0.58 to 15.24 g (neural 1- scan site 4 and pygal - scan site 2, respectively), BMD values varied from 0.0067 to 0.1169 g mm^{-2} (hyoplastron - scan site 1 and peripheral 3 - scan site 2, respectively), and DV values varied from 0.0017 to 0.0171 g mm^{-2} (hyoplastron - scan site 1 and neural 1 - scan site 3, respectively). In the best-supported models (where $\Delta AIC_c = 0$), differences between the shell elements were significant ($p < 0.05$) for BMD and DV, but not for BMC (Table 1). However, when plotting density measures for each element, we detected no obvious consistent patterns among elements, but instead observed a 'messy' distribution due to the immense variation between individual scan sites within each element (see online Supplementary material, Fig. S1). This observation is reflected in the Variance Components Analysis (VCA), which revealed that most of the variance in all three density measures (> 70% of total variance) is explained by variation within, rather than between, elements (Table 1).

When we included thickness as a covariate in our analyses, strongly significant relationships to density were found (Fig. 5; Table 1 – peripheral r^2 from 0.356 to 0.752; $p < 0.0001$ to < 0.001). This relationship was positive for BMC and BMD, a counter-intuitive result given that we expected thinner portions of the shell to compensate by having higher density. However, the relationship was negative for DV. Although the relationship between DV and thickness is potentially spurious (since thickness is also included in our calculations of DV), we believe the observed pattern to be real since (i) a truly spurious effect on a geometric measure like volume would result in a slope not different from 0, and (ii) the same pattern was found in density measures based on CT scans (see below).

Whether elements were located on the carapace or plastron had no influence on patterns observed for BMD and DV ($\Delta AIC_c = 10.30$ and 9.19, respectively). By contrast, for BMC, the model including the term "Carapace" had a $\Delta AIC_c = 0$, whereas the ΔAIC_c of the alternate model was poorly-supported at 7.95. Support for the former model is mainly because of a significant interaction with thickness: whereas the carapace-thickness relationship was positive, the slope of the plastron-thickness relationship was not different from zero (Table 1).

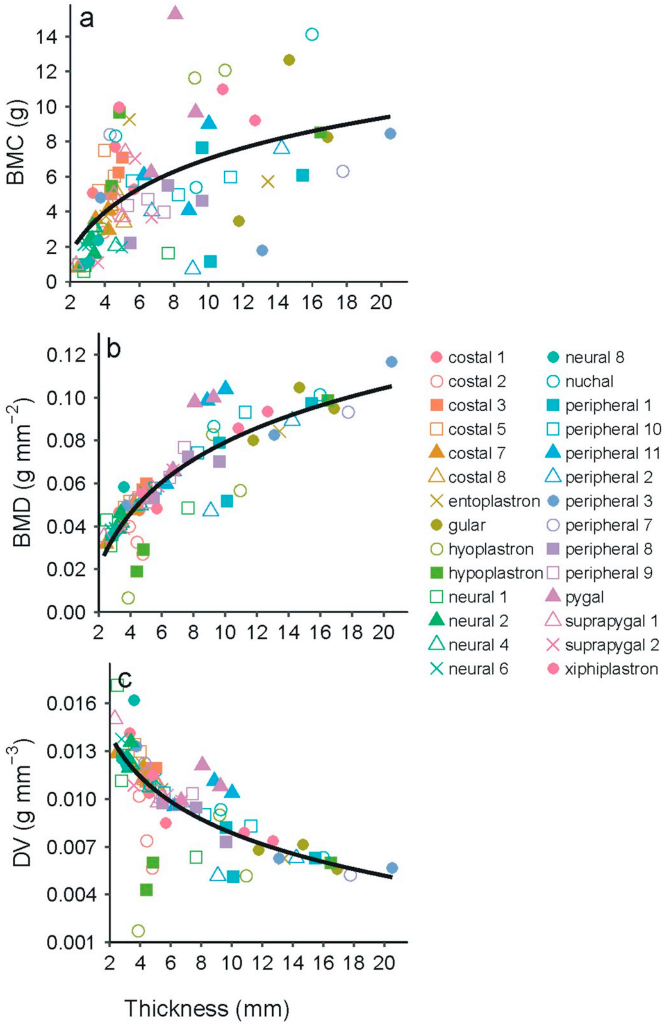

Fig. 5. Relationships between median density and thickness of the scanned region of different elements of the leopard tortoise carapace and plastron. Fit lines are least squares logarithmic regressions. Note that median thickness is part of the calculation of density volume (DV) as well as appearing on the *x*-axis.

4.2. CT scans

Leopard tortoise bone density measured from CT scans (DCT) ranged from 0.1112 to 0.1212 g mm^{-3} (peripheral #3 - scan sites 1 and 2, respectively). These values were not correlated to any of the three densitometry-based measures ($p = 0.433$ to 0.966; see Supplementary Material, Table S3), even accounting for the fact that multiple measurements were taken on the same element (inclusion of the random effect in the MELMs). This is probably due to the fact that the two methods measure different things. Densitometry values are taken over an area of each bone element and include measures of both cortical and trabecular bone, while the CT scan measures were 'spot measures', with these components measured independently (Bonnick, 2006). Moreover, as we were only interested in a general picture of intra-specific variation, for each scan site we only measured bone density for the trabecular bone and overall shell thickness i.e. dorsal, ventral and trabecular layers combined. The density of each cortical layer was not measured.

Nonetheless, in all three species, a significant, negative, relationship

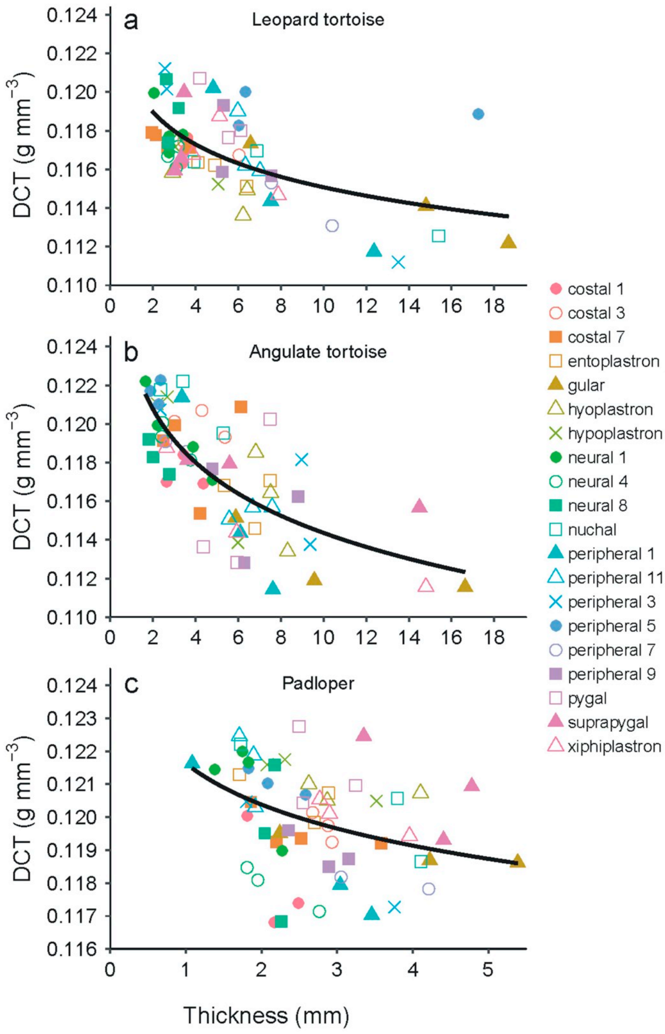

Fig. 6. Relationships between CT-scanned density (DCT) and thickness of the scanned region of different elements of the carapace and plastron in the three tortoise species. Fit lines are least squares logarithmic regressions.

between DCT and bone thickness was found (Fig. 6; Table 2; $p < 0.0001$ in all cases), resembling results obtained from estimates of DV described above for densitometry. Similarly, as found using densitometry, most of the variance in leopard tortoise DCT was explained by within-element rather than between-element differences (VCA, proportion of variance explained = 63.6%). This pattern was even more prominent in the angulate tortoise (94.0% of variance explained by

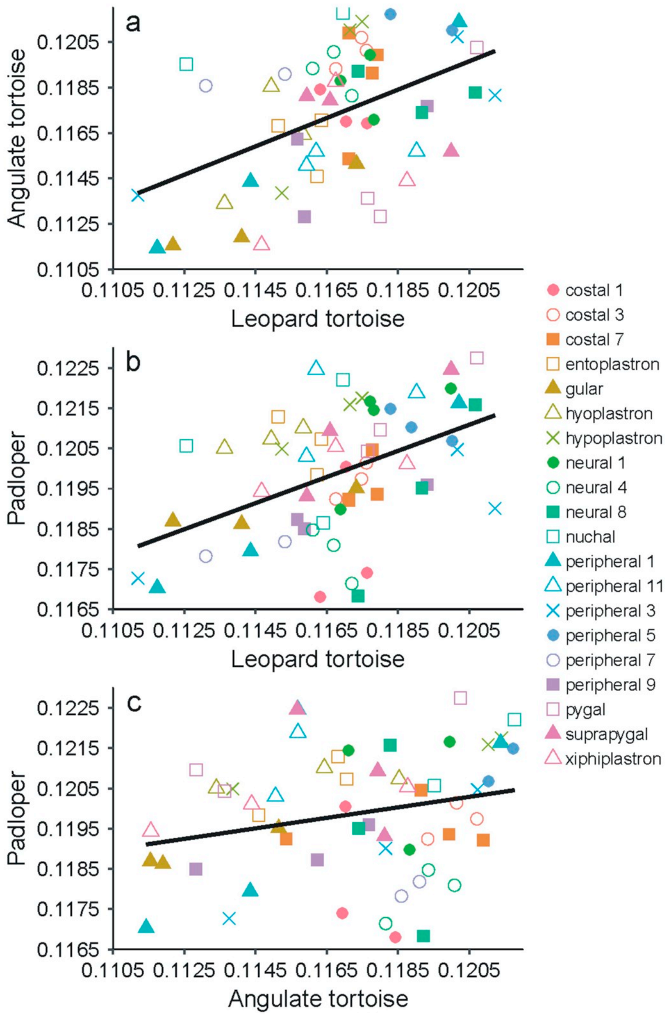

Fig. 7. Inter-species correlations of CT-scanned density of different elements of the plastron and carapace. Fit lines are least squares linear regressions.

within-element differences). However, the pattern was reversed for the padloper, in which only 43.4% of variance was explained by within-element differences. Coupled with the fact that the effect of thickness on DCT was lower in the padloper (peripheral $r^2 = 0.228$) than in the other two species ($r^2 = 0.454$ and 0.529, respectively), our results clearly indicate a fundamental difference in how density is distributed across differently-designed shells; the relatively flat padloper compared with the convex, steep-sided leopard and angulate tortoises shells. Actually, in the padloper, total variation in DCT was much lower (only

Table 2

Best-supported models ($\Delta AIC_c = 0$) of factors describing variation in CT-measured shell density (in g mm^{-3}) of three tortoise species across and within elements. Effect slopes are shown as means with 95% CI in parentheses.

Species	Model	n	K	r^2m	Effect	F or X^2	p	Slope	VCA (% explained)
Leopard tortoise	Thickness + Element	61	4	0.454	Thickness	45.730	< 0.0001	−0.007 (−0.009 to −0.005))	
					Element	4.930	0.026		36.4
					Within elements				63.6
Angulate tortoise	Thickness + Element	61	4	0.529	Thickness	64.856	< 0.0001	−0.009 (−0.011 to −0.007)	
					Element	0.190	0.663		6.0
					Within elements				94.0
Padloper	Thickness + Element	61	4	0.228	Thickness	25.574	< 0.0001	−0.005 (−0.007 to −0.003)	
					Element	16.371	< 0.001		26.6
					Within elements				73.4

n = number of observations; K = number of parameters in model; r^2m = marginal r^2 value; Element = bone element (random effect); CP = carapace or plastron; Thickness = width of element at density scan site, in mm ($\log_{10}$-transformed); F or X^2 = relevant statistic for fixed (CP, Thickness) or random (Element) effects, respectively; VCA = variance components analysis differentiating variance explained by between-element from within-element (residual) differences.

about 40% of the total range) than in the leopard and angulate tortoises (note differences in y-axis scales between Fig. 6a–b compared to Fig. 6c), probably because the dorso-ventrally flatter design of the padloper shell inherently results in a more homogeneous density across and within bone elements. Therefore, we included another hypothesis in our investigations: that DCT is also related to the angle of orientation of each point on the shell where density was measured, relative to the horizontal plane. However, we found no consistent effect of this angle on DCT, even after accounting for variations in thickness (see Supplementary Material, Table S4).

Models including the term "Carapace" were poorly supported in all three species ($\Delta AIC_c > 24$), indicating that DCT did not differ between carapace and plastron, nor did the effect of thickness differ between these two 'halves' of the shell.

Despite the differences in results for the padloper compared with the other two species, DCT variations were significantly correlated between all species (Fig. 7; peripheral $r^2 = 0.118$ to 0.281, $p < 0.0001$ to < 0.01), indicating that density is similarly distributed across the shell of all three species, even if the total absolute variation in the padloper is much lower.

5. Case study of Wonderwerk Cave

We applied our knowledge of inter and intra-element bone density variation in a modern leopard tortoise shell to explore the extent to which it may have influenced survivorship of elements in an archaeozoological tortoise assemblage. To this end we examined leopard tortoise remains from the Later Stone Age (LSA) layers in Excavation 1 at Wonderwerk Cave, Northern Cape Province South Africa. Four main LSA layers (Strata 1 through 4) were recognised, with several sub-phases labelled a, b, c, etc., spanning 12,200 BP to the last 100 years (see Holt et al., 2018 for further details on the excavation and sample).

We analysed a total of 3244 carapace and plastron elements, weighing a total of 1.6 kg (Supplementary Table S5). Previously, for his doctoral research, J.F. Thackeray had counted all the LSA tortoise remains from the site, but did not identify them to specific element (Thackeray, 1984, 2015). For the current study, all tortoise material from Strata 1–4 was re-sorted and identified to skeletal element including parts of the carapace and plastron. Often the fragments were too small or broken to determine to which part of the shell they belonged, and were placed in a joint carapace/plastron category (Supplementary Table S5). Similarly, the specific costals and peripherals (numbering 16 and 22 elements respectively in a complete leopard tortoise) are problematic to identify if they are not whole. The epiplastron, pygals and nuchals were used for species identification, and all corresponded to leopard tortoise morphology.

The number of identified specimens (NISP) refers to the counts of bones that could be identified to skeletal element or general skeletal category, such as indeterminable carapace or plastron. Sample sizes differed between the strata with the largest collection amounting to 1579 elements from Stratum 4c, and the smallest comprising only 11 elements from Stratum 4aLH. In the LSA assemblage as a whole, no articulated specimens were found and the material was highly fragmented. Moreover, across the strata examined there were few elements of the appendicular skeleton (limbs, vertebrae, pelvis NISP = 357; 11%) compared to remains of the shell (carapace and plastron NISP = 3244; 89% of combined identified and unidentified tortoise remains). There were far more identified carapace elements (NISP = 326; 10%) than identified plastron elements (NISP = 231; 7.1%), but this doubtless relates to the larger number of individual bones in the carapace. No marked differences were found in survival rate of anterior (NISP = 363; 48.5%) (epiplastron, entoplastron, hyoplastron, nuchal, peripherals #1–6, neurals #1–4, costals #1–4) versus posterior shell elements (NISP = 386; 51.5% = hypoplastron, xiphiplastron, pygal, suprapygals, peripherals #7–11, neurals #5–8, costals #5–8). For the assemblage as a whole, the most frequently preserved element was the carapace hyoplastron (NISP = 96; 12.8%) followed by the plastron xiphiplastron (NISP = 80; 10.7%). The least represented element in the assemblage was the carapace suprapygal 1 (NISP = 4; 0.5%) (Table S5).

It should be noted that only 18.4% of all the LSA tortoise shell evidenced signs of burning, a factor that is known to influence bone survivorship and completeness (e.g. Stiner et al., 1995; Villa et al., 2004; Kalsbeek and Richter, 2006). Among burned elements, the majority were brown in colour ($n = 333$, representing 10.2% of the total sample), indicative of low intensity burning, while grey-white coloured bones, indicating exposure to high temperatures, only comprised 1.1% of the total shell sample ($n = 34$). Thus, burning does not appear to have played a major role in determining shell fragmentation and element survivorship in this assemblage.

Surface trampling may have played a part in damaging, and especially facilitating disarticulation of tortoise shells, but no surface damage that could be exclusively attributed to this factor was observed (e.g. Fernandez-Jalvo and Andrews, 2016; Rozada et al., 2018). However, the cave sediment is quartz-rich and so has resulted in extensive abrasion and surface scoring to the bones, such that trampling damage may be masked (e.g. Shipman and Rose, 1983; Fernandez-Jalvo and Andrews, 2016). Only 0.2% of tortoise shell in the entire Wonderwerk LSA assemblage showed signs of butchery (scrape and cut marks) while a similar low frequency of bone plates exhibited percussion damage, again emphasizing that anthropogenic activities were not the main drivers of skeletal element survivorship in this assemblage. This is a significantly lower frequency of anthropogenic damage evident on tortoise shell than reported in other publications dealing with tortoise bone taphonomy (e.g. Blasco, 2008 [9.43%]; Thompson and Henshilwood, 2014a [2.76%]; Biton et al., 2017 [2.11%]), but the Wonderwerk data may be biased by the extreme fragmentation of the remains.

For the statistical analyses, we used NISP counts of the different parts of each element (i.e. skeletal element abundance) from each sub-phase, to estimate relative abundances of each ($\frac{NISP}{\text{number of elements in assemblage}}$). The resultant proportions were correlated with corresponding estimates of density in the extant leopard tortoise based on the densitometry values. Using relative abundance as the dependent variable, and each of the four density measures in turn, as covariates (with Element again included as a random effect), we evaluated the effect of density on differential preservation (see Section 3.3 above). These MELMs were repeated for each of the eight sub-phases separately.

5.1. Results

In general, for the Wonderwerk Cave assemblage there was a significant positive relationship between BMC and BMD, and frequency of occurrence (relative abundance of each element and scan site, per stratum; Fig. 8), indicating that denser shell elements are more likely to be recovered in archaeozoological assemblages. The positive relationship was significant ($p < 0.05$) for most layers, except for Strata 1–2 and 4aLH (and 4b in the case of BMC, but for BMD $p < 0.01$ even in Stratum 4b; Table 3). The lack of significant values for these strata is likely due to their very small sample sizes, and hence low statistical power in each (NISP = 8 and 12, respectively, compared with NISP = 43 to 59 in the other strata). For DV and DCT, however, no significant effect on frequency occurrence was found for any of the strata ($p = 0.153$ to 0.966), except for DV in Stratum 4d ($p = 0.015$), implying that while surface-based measures of density can be used to predict taphonomic effects on tortoise shell remains, volumetric-based measures cannot.

6. Discussion

This study constitutes the first investigation of bone density values

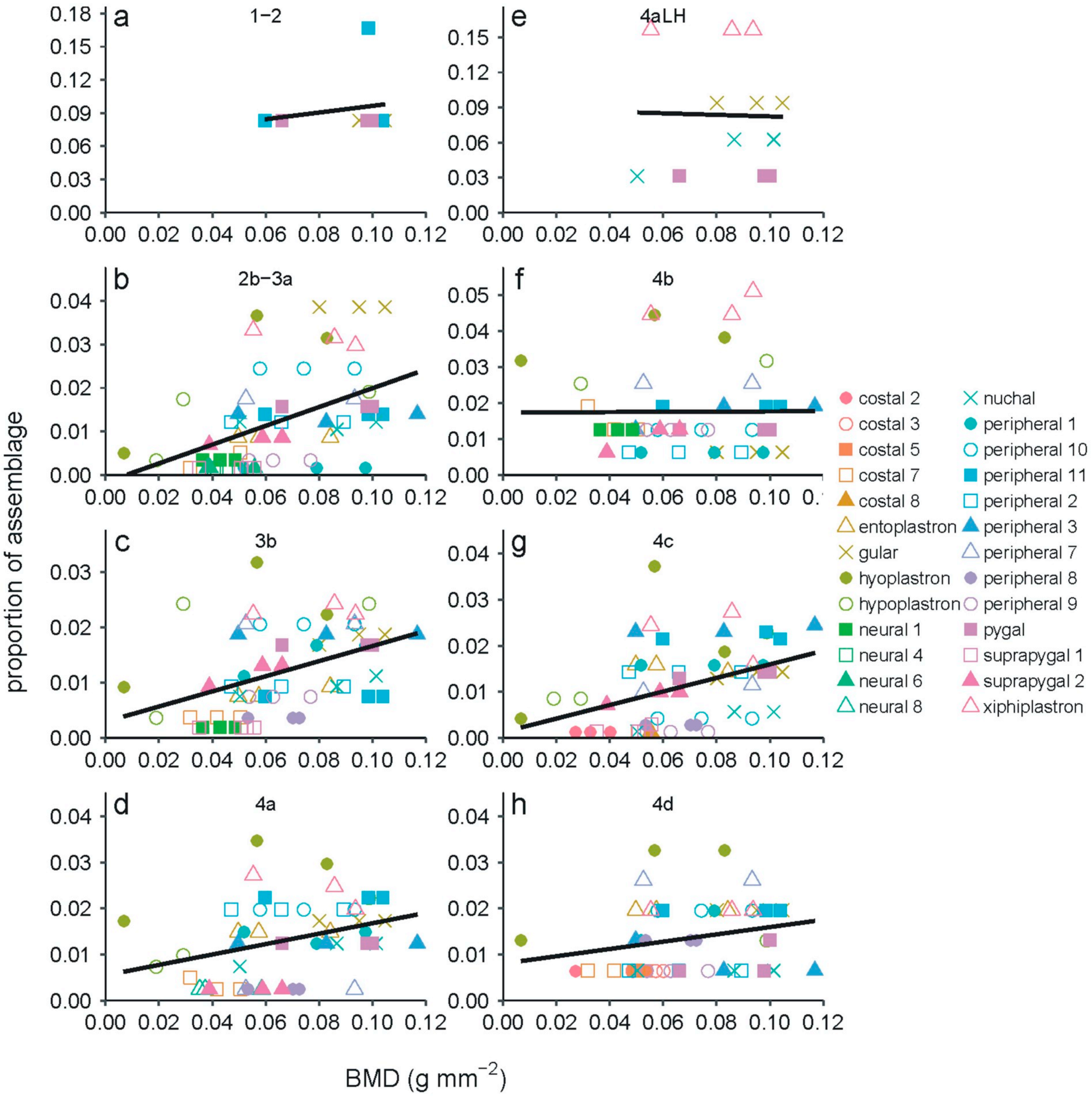

Fig. 8. Relationships between frequency occurrences of tortoise shell elements from Later Stone Age strata at Wonderwerk Cave and density of shell elements measured by densitometry on a modern leopard tortoise. Fit lines are least squares linear regressions.

for terrestrial tortoise shells. It complements our previous research on tortoise limb bones (Holt et al., 2018) and expands the spectrum of taxa covered by studies of bone density which have focused on terrestrial mammals (e.g. Binford and Bertram, 1977; Ioannidou, 2003; Symmons, 2005; Lam et al., 1999; Boaz and Behrensmeyer, 1976; Stahl, 1999; Carlson and Pickering, 2004), birds (e.g. Dirrigl, 2001; Cruz and Elkin, 2003; Broughton et al., 2007) and fish (e.g. Nicholson, 1992; Butler and Chatters, 1994; Butler, 1996). Taphonomy is an important aspect of the study of faunal remains in archaeology and paleontology and BMD plays an especially important part in bone element survivorship, which in turn shapes the composition of faunal assemblages (e.g. Brain, 1969; Elkin, 1995; Lyman, 1984; Kreutzer, 1992; Pavao and Stahl, 1999; Pickering and Carlson, 2002).

Using two different methods to quantify bone density in modern terrestrial tortoise shell, our research has shown that there is a significant association between bone mineral density and bone thickness.

Both densitometry and CT scans showed that most of the variance in bone mineral density values was due to within-element rather than between element differences. As such, it is not possible to state that a specific bone element class (e.g. costals, peripherals etc.) is more or less dense than another. However, within each of the bone plates of the carapace and plastron, there is marked variation in density with the “thinner” skeletal elements, or parts thereof, being more dense. This patterning may be explained with reference to studies on the tensile strength and composition of a tortoise shell. Achrai et al. (2014) demonstrated that for the red-eared terrapin, although trabecular bone occupies about half the total volume of a bone plate, the overall Youngs modulus for the spongy component is only slightly lower than for the rigid outer cortices. Moreover, the interior trabecular bone contains less mineral content (hydroxyapatite 50 wt%) than the two outer cortices (hydroxyapatite 60 wt%) (Achrai and Wagner, 2013). Since hydroxyapatite is denser than collagen, both the porous structure of the trabecular bone as well as its lighter composition, reduce the overall weight of the carapace. Thus, thinner bones in a tortoise shell have relatively more hydroxyapatite, and so will have relatively higher bone mineral density values, than thicker bones which have more trabecular

Table 3
Relationships between frequency occurrences of shell elements, recovered from eight sub-stratum of the Wonderwerk Cave sequence, with measures of leopard tortoise bone density. Intercepts and slopes for each layer are shown as means, with 95% confidence intervals in parentheses.

Density measure	Layer	*n*	*K*	r^2m	*F*	*p*	Intercept	Slope
BMC	1–2	8	4	0.254	2.379	0.174	13.197 (7.991 to 18.403)	−0.429 (−0.975 to 0.116)
	2b–3a	59	4	0.092	16.703	< 0.001	0.766 (0.306 to 1.227)	0.085 (0.044 to 0.126)
	3b	57	4	0.144	17.898	< 0.001	0.777 (0.436 to 1.119)	0.077 (0.041 to 0.112)
	4a	50	4	0.030	5.291	0.027	1.058 (0.638 to 1.478)	0.039 (0.006 to 0.073)
	4aLH	12	4	0.000	0.076	0.791	8.114 (2.480 to 13.748)	0.024 (−0.144 to 0.192)
	4b	43	4	0.008	2.876	0.101	1.625 (1.009 to 2.241)	0.029 (−0.005 to 0.062)
	4c	56	4	0.077	8.995	< 0.01	0.665 (0.248 to 1.082)	0.069 (0.024 to 0.114)
	4d	52	4	0.050	8.862	< 0.01	1.032 (0.660 to 1.404)	0.050 (0.017 to 0.083)
BMD	1–2	8	4	0.028	0.201	0.670	6.630 (−5.569 to 18.829)	30.227 (−102.065 to 162.519)
	2b–3a	59	4	0.055	12.493	< 0.01	0.606 (0.051 to 1.161)	9.946 (4.430 to 15.461)
	3b	57	4	0.091	14.389	< 0.001	0.616 (0.179 to 1.053)	9.262 (4.476 to 14.047)
	4a	50	4	0.045	11.488	< 0.01	0.825 (0.362 to 1.289)	6.967 (2.938 to 10.995)
	4aLH	12	4	0.008	4.495	0.072	5.971 (0.080 to 11.863)	27.917 (2.110 to 53.724)
	4b	43	4	0.014	8.736	< 0.01	1.403 (0.737 to 2.068)	5.792 (1.951 to 9.633)
	4c	56	4	0.088	11.405	< 0.01	0.408 (−0.096 to 0.911)	10.084 (4.232 to 15.937)
	4d	52	4	0.037	6.481	0.015	0.927 (0.473 to 1.380)	6.159 (1.417 to 10.901)
DV	1–2	8	4	0.086	0.592	0.509	5.124 (−5.896 to 16.143)	444.705 (−688.571 to 1577.982)
	2b–3a	59	4	0.007	1.451	0.235	0.950 (0.259 to 1.641)	32.514 (−20.393 to 85.421)
	3b	57	4	0.000	0.013	0.911	1.214 (0.671 to 1.757)	2.769 (−45.689 to 51.228)
	4a	50	4	0.003	0.559	0.460	1.145 (0.569 to 1.721)	17.846 (−28.943 to 64.634)
	4aLH	12	4	0.012	2.562	0.153	10.700 (4.726 to 16.675)	−267.930 (−595.998 to 60.138)
	4b	43	4	0.001	0.385	0.540	1.915 (1.218 to 2.613)	−12.681 (−52.737 to 27.375)
	4c	56	4	0.000	0.032	0.859	1.031 (0.367 to 1.696)	5.828 (−58.228 to 69.884)
	4d	52	4	0.036	6.500	0.015	0.852 (0.334 to 1.370)	56.559 (13.079 to 100.039)
DCT	1–2	8	4	0.072	0.545	0.488	58.918 (−72.677 to 190.513)	−422.133 (−1543.198 to 698.931)
	2b–3a	43	4	0.006	0.895	0.352	5.699 (−3.323 to 14.722)	−37.332 (−114.676 to 40.013)
	3b	41	4	0.004	0.293	0.592	3.565 (−4.484 to 11.614)	−19.072 (−88.144 to 50.000)
	4a	38	4	0.008	0.993	0.328	4.732 (−1.908 to 11.373)	−28.935 (−85.852 to 27.982)
	4aLH	12	4	0.002	0.391	0.551	19.251 (−15.358 to 53.861)	−93.812 (−387.710 to 200.086)
	4b	34	4	0.000	0.157	0.696	0.912 (−4.555 to 6.379)	9.396 (−37.134 to 55.926)
	4c	36	4	0.000	0.002	0.966	1.629 (−8.663 to 11.920)	−1.946 (−90.394 to 86.501)
	4d	39	4	0.016	1.950	0.174	6.161 (−0.448 to 12.771)	−40.444 (−97.206 to 16.319)

n = number of observations; *K* = number of parameters in model; r^2m = marginal r^2 value; BMC = bone mineral content (g); BMD = bone mineral density (g mm^{-2}); DV = density volume (g mm-3); DCT = density determined by CT scan (g mm^{-3}); Results for the random effect ‘Element’ not shown.

bone. As Achrai et al. (2014: 230) state: “This structural and compositional combination enables a sufficiently light carapace, to allow free movement of the animal while bearing its weight.”

Another interesting point is that for the densitometry results, when bone mineral density was assessed as a raw measure without taking area or volume into account, there appears to be a difference between the carapace and plastron in this parameter, with only the carapace statistically related to thickness. We suggest that this may be due to the more homogenous shape and overall flatter structure of the bones that comprise the plastron. Moreover, bones of the plastron have a relatively higher mineral content (median value ~68% dry weight - Magwene and Socha, 2013) compared to the dorsal and ventral cortices of the carapace (~60 ± 3 and 60 ± 4 wt% respectively - Achrai and Wagner, 2013). In the plastron, mineral content is negatively correlated with maximum ultimate bending strain, but positively correlated with Youngs modulus (elasticity), a configuration that favours stiffness, strength and toughness in order to withstand bending and compression.

Inter-species differences in bone mineral density (DCT) and bone thickness were observed. The padloper showed the least variation within and between different elements of the shell, a finding that we ascribe to the more homogenous, low-domed and overall flatter morphology of its shell relative to the morphology of the high-domed angulate and leopard tortoises carapaces. However, we did find that in all three species, variations in density are similarly distributed across shell elements and scan sites.

When comparing the densitometry results of the modern leopard tortoise to those of the archaeozoological assemblage from Wonderwerk Cave, it was found that overall, there was a significant positive relationship between BMD and the frequency occurrence of skeletal elements, indicating that bone mineral density has played a significant role in shaping the composition of this tortoise assemblage with denser elements more likely to be recovered. This pattern echoes results obtained for tortoise limb bones recovered from the same assemblage (Holt et al., 2018).

Given the abundance of tortoise shell elements in archaeological contexts, this study illustrates the value of examining bone density of shells which can clearly play a critical role in reconstructing and interpreting taphonomic histories. Moreover, our research has demonstrated that bone mineral density can elucidate inter-specific differences in form, function and biomechanics of Testudines.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jasrep.2019.04.008.

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Chapter 4

Holt, S., Codron, D., Birkenfeld, M., Horwitz, L.K. 2019. Early Pleistocene Tortoise Exploitation at Wonderwerk Cave, South Africa. In preparation for submission.

Early Pleistocene Tortoise Exploitation at Wonderwerk Cave, South Africa

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Abstract

Here we present findings on species identification, spatial distribution and taphonomy of an assemblage of tortoise remains from the Oldowan and Earlier Stone Age (ESA) layers at Wonderwerk Cave spanning the period ca. 2.0 - 0.781 Mya. Biometric analysis has enabled us to confidently attribute the ESA remains to the leopard tortoise (*Stigmochelys pardalis*), providing the earliest identification of this species in southern Africa. GIS analysis shows spatial concentrations of bones, probably representing individual tortoises, while taphonomic investigation has revealed evidence of extensive burning and clear evidence of percussion fractures in ESA remains, both indicative of anthropogenic action. Together these data demonstrate that land tortoises were exploited by early hominids in the interior of South Africa as early as ~2 million years ago.

Keywords: Leopard tortoise (*Stigmochelys pardalis*), Chelonians, Testudinidae, Oldowan, Earlier Stone Age, Acheulean, GIS

1. Introduction

Remains of land tortoises (Testudinidae) are ubiquitous in archaeological sites worldwide, reflecting their attraction as a resource for past peoples (e.g. Connolly and Eckert, 1969; Schneider and Everson, 1989; Sampson, 1998; Klein et al., 1999, 2004; Lapparent de Broin, 2000; Speth and Tchernov, 2002; Avery et al., 2004; Stiner, 2005; Blasco, 2008; Blasco et al., 2011; Del Papa, 2016; Hawkins et al., 2016). They are also a common dietary item for modern traditional communities (Lee, 1968, 1978:101; Kitanishi, 1995; Klemens and Thorbjarnarson, 1995; Roulon-Doko, 2004; Marlowe, 2010). Tortoise meat is considered very palatable and provides protein, fat and micronutrients (Balée, 1985; Chambers, 2006). For example, Thompson and Henshilwood (2014a, 2014b) calculated that the edible tissues of a single angulate tortoise (*Chersina angulata*) (with an average adult weight of 860g) provides an estimated 3332 kJ (796 kcal), when the average estimated caloric requirements for a hunter-gatherer is 12552 kJ (3000 kcal) calories per day (Thompson and Henshilwood, 2014b). They also calculated that fat content in five South African tortoise species (*Testudo hermanni, Testudo horsfieldii, Stigmochelys pardalis* [previously *Geochelone pardalis*] and *Testudo graeca*) ranged between 2-13% (Thompson and Henshilwood, 2014a). Low average values for body fat content (2.7 ± 2.2% dry matter) were reported by Kienzle et al. (2006) for four different species of land tortoises in a sample that included all age classes (29 *Testudo hermanni*, 12 *Testudo horsfieldii*, 11 *Geochelone pardalis*, 3 *Testudo graeca*), while average protein content of the body (minus the shell) was 74.6 ± 3.8% dry matter in the same sample. The percentages for fat content are similar to those for wild African ungulates which range from 5-10% of body mass (Owen-Smith, 2002).

In addition to meat and fat, tortoises provide non-dietary resources. In the past the shell was used as a container, for the manufacture of ornaments and household utensils, as a musical instrument, as a ritual object, and – presumably, given its use today - in traditional medicines (Roberts, 1981; Schneider and Everson, 1989; Sampson, 1998; Speth and Tchernov, 2002; Avery et al., 2004; Da Nóbrega Alves et al., 2008; Grosman et al., 2008; Orton, 2012; Setlalekgomo, 2013; Gillreath-Brown and Peres, 2018). Live tortoises also served as pets (e.g. Thomas, 2010) and in the southern African ethnographic literature (Selous, 1907) it is described how a tortoise was given to San children to track over rocky terrain and so learn animal tracking skills.

In addition to the broad spectrum of products they provide, further advantages in exploiting Testudinidae include:

(1) Their year-round availability, with the exception of a short seasonal dip in the winter when species in the wild may hibernate to avoid cold temperatures (e.g. Diaz-Paniagua et al., 1995; Boycott and Bourquin, 2000; Nussear et al., 2007). This may result in a reduction in their availability in the archaeofaunal record (e.g. Del Papa, 2016) although given that most archaeological assemblages time-averaged, this may be difficult to detect.

(2) They are quite sessile, slow moving and docile, making them vulnerable and relatively easy prey. Indeed, archaeozoologists have categorized tortoises as ‘slow game’ versus fast moving small mammals such as hares (e.g. Stiner et al., 1999; Luppo and Schmitt, 2002; Speth and Tchernov, 2002; Stiner, 2005).

(3) Tortoise predation involves little technology. Most commonly they are accidentally encountered in the field and as such may be considered as an opportunistic resource that is foraged rather than trapped or hunted (Marshall, 1960). Bank (2006:191) cites the 19th century records of Bleek and Llyod who wrote that the /Xam Bushmen place collected tortoises in a bag. Bleeks ‘Bushman teacher’ (Old Jantje Tooren), put the tortoises on a stick when he didn’t have his collecting bag available.

(4) Given their small size and low weight (relative to most ungulates and carnivores), whole tortoises can easily be transported back to a settlement and even kept alive in captivity

until the need arises to consume them (Thompson and Henshilwood, 2014a; Blasco et al., 2016; Del Papa, 2016). Relating to this point, Paul Chambers (2006) noted that giant tortoises, such as those of the Galapagos, could live on ships in an age prior to refrigerators which meant that in addition to their palatability, they served as excellent sources of fresh food for sailors. He observes that in the 18th century, over 4,000 tortoises per annum were taken by ships from the Rodrigues Island alone (Indian Ocean, east of Mauritius).

However, these amenable traits have, in the long term, led to a negative outcome, namely human over-exploitation, which has undoubtedly contributed to the near extinction of many tortoise species globally, especially the giant forms (e.g. O'Brien et al., 2003; Morcatty and Valsecchi, 2015; Hawkins et al., 2016; Rhodin et al., 2018). This trend is exacerbated by the slow growth rates, late sexual maturation and high hatchling mortality of tortoises. Their susceptibility to over-exploitation is best expressed in a significant size reduction since the Mid-Pleistocene, as documented in archaeological sites in South Africa and the Levant (e.g. Klein and Cruz-Uribe, 1983, 1987; Klein, 1999; Speth and Tchernov, 2002; Stiner and Tchernov, 2002; Stiner, 2005; Thompson and Henshilwood, 2014b).

Worldwide, most data on past land tortoise exploitation derives from archaeological assemblages dating to the late Mid-Pleistocene through Holocene. These assemblages are characterised by anthropogenic damage - percussion fractures, tooth and cut marks as well as burning (e.g. Speth and Tchernov, 2002; Stiner, 2005; Blasco, 2008; Stiner and Munro, 2011; Biton et al., 2017). In contrast, although tortoise remains have been found in many Early Pleistocene and early Middle Pleistocene sites (defined here as ending ca. 300,000 BP) in Europe, Asia and Africa (see site lists in Lapparent de Broin, 2000 and Rhodin et al., 2015), examples of intentional anthropogenic damage to their remains, are few. Notable exceptions are Sterkfontein in South Africa (Broadley, 1997) and Sima del Elefante in Spain (Blasco et al., 2011) where cut marks - either incisions or scrapes - were noted. To this short list, one may add hominin damage, in the form of percussion notches, on freshwater turtles from sites such as Uraha in Malawi (Karl, 2012) and FwJJ20 in Kenya (Braun et al., 2010; Archer et al., 2014). The lack of more examples may be attributed to the fact that the taphonomy of many assemblages has not been investigated, or alternately, that in these early time periods anthropogenic damage was less common. Consequently, despite their close spatial association with archaeological material, many of these early tortoise bone assemblages cannot be unequivocally attributed to hominin activity and may represent natural mortalities.

In this paper we discuss this issue with reference to a diachronic sequence of terrestrial tortoise remains from Excavation 1, Strata 12 to 6, from Wonderwerk Cave (Northern Cape Province, South Africa), spanning the Early through early Middle Pleistocene. Notably, there is evidence in the cave for activities of a mixture of abiotic as well as biotic agents, including hominins (Horwitz and Chazan, 2015; Goldberg et al., 2015; Brink et al., 2016), such that several potential agents may have played a role in the introduction, consumption and modification of tortoises. In addition, the palaeoecology of Testudinids recovered at this site is discussed. In this regard, the Wonderwerk Cave finds are especially valuable as they provide an almost complete 1 million year record from the same locality (Beaumont and Vogel, 2006; Chazan et al., 2012; Horwitz and Chazan, 2015).

2. Materials

Wonderwerk Cave (27º50’44.7”S; 23º33’12.3”E) is a large dolomitic cavity about 140m long, situated in a low foothill of the Kuruman hills, Northern Cape Province (Beaumont and Morris, 1990; Horwitz and Chazan, 2015; Ecker et al., 2017). The cave currently falls within the summer rainfall region while the vegetation is attributed to the Savanna Biome (Figure 1) (Rutherford et al., 2006; Scott and Thackeray, 2015).

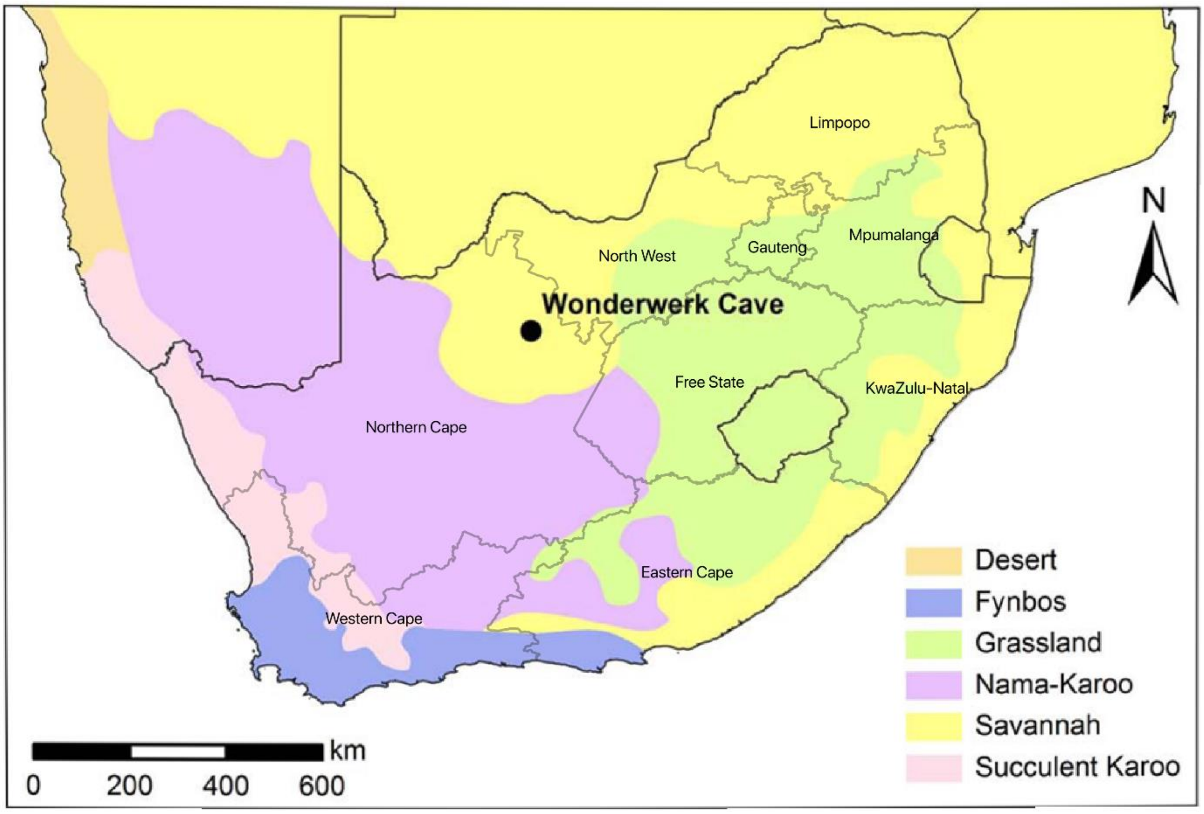


Figure 1 - Map of South Africa showing the location of Wonderwerk Cave within the Savanna Biome (taken from Ecker et al. 2017).

The first archaeological excavations in the cave were undertaken in 1943 by Malan and Wells (Thackeray, 1983; Beaumont and Morris, 1990), with several subsequent investigations by other researchers. The most extensive excavations were undertaken between 1978 to 1982 by the late Peter Beaumont. He identified Earlier, Middle and Later Stone Age layers in seven different excavation areas throughout the cave (Beaumont and Morris, 1990; Beaumont and Vogel, 2006). Recent research has indicated the presence of an Oldowan industry, such that the archaeological sequence spans ca. 2.0 Ma years (Chazan et al., 2012).

In the deep sounding in Excavation 1 (5m deep), that lies adjacent to the cave entrance, an Oldowan stratum (Str. 12) and several ESA layers were excavated by Beaumont (Strata 11 through 6). All layers yielded rich assemblages of lithics, macro-botanical as well as macroand micro-faunal remains. According to Beaumont and Vogel (2006:218) a dry sieve with a 1 mm or smaller mesh was used to sift all the deposit removed from the cave, which has resulted in good recovery of even very small skeletal elements. The tortoise assemblage studied here derives from these strata.

3. Methods

3.1 Bone Counts and Skeletal Element Representation

For the current study, all tortoise material collected during the Beaumont excavations was sorted and all specimens identified to anatomical element (a specific bony plate or appendicular element) and side. Nomenclature for skeletal elements followed Zangerl (1969). All identified remains were counted as Number of Identified Specimens (NISP's) while estimates of the Minimum Number of Individuals (MNI's) were made based on the abundance of a specific skeletal part within a stratum, taking side and size into account. The Minimum Number of Elements (MNE) was not calculated given that few bones could be identified to skeletal element due to extreme fragmentation, and almost no appendicular skeleton elements were found. Most remains comprised shell fragments that were too small or too broken to determine whether they belonged to the carapace or plastron, and also could not be sided. They were placed in a combined carapace/plastron category (Table 1). Those fragments that could be identified to plastron or carapace but not to a specific bone type, were placed in a general plastron or carapace category. A special effort was made to distinguish elements such as the gulars and pygals since these were used for species identification. Chi-square tests were used to compare frequency distributions of elements across strata. Since most sample sizes are too small, only plastron and carapace values could be compared, and then only between Strata 8, 9 and 10.

Table 1 – Tortoise skeletal elements of Strata 6-12 at Wonderwerk Cave.

		Stratum 6		Stratum 7		Stratum 8		Stratum 9		Stratum 10		Stratum 11		Stratum 12	
Skeletal Element	**Total NISP**	**NISP**	**Side**	**NISP**	**Side**	**NISP**	**side**	**NISP**	**Side**	**NISP**	**Side**	**NISP**	**Side**	**NISP**	**Side**
Humerus	1													1	1L
Tibia	1									1	1R				
Fibula	1	1													
Ilium	2					2	2L								
Phalanx 3	1									1					
Total Appendicular	***6***	***1***				***2***	***2L***			***2***	***1R***			***1***	***1L***
Vertebrae	4					1		1		2					
Neurals	11					6				5					
Costals	22	1				4				17					
Peripherals	21	1				4		3		12		1			
Peripheral 1	1					1	1R								
Peripheral 3	1									1	1R				
Peripheral 6	2							1		1					
Peripheral 7	1							1	1L						
Peripheral 9	1					1	1R								
Peripheral 10	2					1	1L			1	1L				
Peripheral 11	2					2	1R+1L								
Suprapygal	2					1				1					
Pygal	2									2					
Undet. Carapace	62			1		7		15		39					
Total Carapace	***134***	***2***		***1***		***28***	***3R+2L***	***21***	***1L***	***81***	***1R+1L***	***1***			
Gular	4					1	1R			3	2R+1L				
Entoplastron	1									1					
Hyoplastron	1							1	1R						
Xiphiplastron	8					3		2	1R+1L	3	2R				
Undet. Plastron	59					27		4		15		13			
Total Plastron	***73***					***31***	***1R***	***7***	***2R+1L***	***22***	***4R+1L***	***13***			
carapace/ plastron	198	2		1		85		16		44		46		4	
Total NISP	**411**	**5**		**2**		**146**	**4R+4L**	**44**	**2R+2L**	**149**	**5R+2L**	**60**		**5**	**1L**
MNI/Stratum	**9**	**1**		**1**		**2**		**1**		**2**		**1**		**1**	

3.2 Species Identification

As noted by other researchers, (e.g. Baker and Shaffer, 1999; Biton et al., 2017), species identification, though often problematic, is an integral and important aspect of zooarchaeological research on tortoises. In this study, species identification was based on present-day species distribution and the size and shape of indicative skeletal elements.

3.2.1 Biogeography

Today, Wonderwerk Cave falls within the biogeographic distribution of three species of tortoise; the leopard tortoise (*Stigmochelys pardalis*), greater padloper (*Homopus femoralis*) and the Kalahari tent tortoise (*Psammobates oculifer*) (Boycott and Bourquin, 2000; Branch, 2008; Hofmeyr et al., 2014). Our approach using biogeography was to first examine the traits of these species and exclude them, before looking for other candidate species.

Leopard tortoise: This is the largest Chelonian species found in South Africa and is also the most widespread in its biogeography. The distribution of the leopard tortoise covers northeast to southwest Africa (Sudan to South Africa) where it inhabits a range of habitats: Savanna, plain, dry woodland, thorn scrub and grassland (Ernst and Barbour, 1989; Branch, 2008; Hofmeyr et al., 2016). Their limited occurrence or absence from the eastern parts of South Africa (e.g. former Transkei, adjacent Kwa-Zulu Natal and Lesotho) could be as a result of the sour grasses that dominate this region (Branch, 2008; Hofmeyr et al., 2014). Their size varies according to localities within their natural range, but adult males and females can weigh 15-20 kg and lengths that average 300-400 mm in East Africa, with the largest specimen recorded in South Africa having a carapace length of 650 cm and an estimated weight >40 kg (Boycott and Bourquin, 2000; Branch, 2008).

Greater padloper: This is the largest of the padlopers but is still a medium-sized tortoise, with an average weight of 200-300 grams (females are larger than males), and a shell length of 100-130 mm, although females can reach 168 mm (Branch, 2008). They are endemic to South Africa and inhabit the mountain plateaus of the Karoo, the south-west Free State, mountains of the Eastern Cape and south-west Lesotho, at altitudes of over 900 m (Boycott and Bourquin, 2000; Branch, 2008; Hofmeyr et al., 2014).

Kalahari tent tortoise: This small-sized tortoise (females are larger than males) is endemic to southern Africa and occurs in the Northern Cape, adjacent regions of the Free State and the Northern Province, but has never been recorded south of the Orange River (Hofmeyr et al., 2014). They have an average shell length of 80-120 mm (Branch, 2008) and females can weigh up to 489 grams and males up to 319 grams (Boycott and Bourquin, 2000).

To date, only the leopard tortoise has been positively identified in the Holocene levels at Wonderwerk Cave (Holt et al., 2018, 2019). Consequently, one of the aims of this study was to identify the tortoise species present in the earlier levels at the site taking into account that during the ESA, palaeoclimatic conditions differed from those of today (Ecker et al., 2018b). As such, we could not exclude *a priori*, the possibility of other extant or extinct tortoise species having inhabited the region.

3.2.2. Morphology

In the absence of articulated shell bony plates or complete limb bones in the Wonderwerk Cave assemblage, we based our species identification on the morphology of gular and pygal elements (no complete nuchals were preserved) aided by examination of the morphology of the bony plates - angulation, thickness and location and shape of ridges - compared to modern museum specimens from which the keratin scutes had been removed. For the former bones we used criteria published by Loveridge and Williams (1957), Auffenberg (1974, 1981), Broadley (1997), Lapparent de Broin (2003) and Lapparent de Broin et al. (2006).

The leopard tortoise has two paired gulars that are rectangular in shape and at least as long as they are broad (Figure 2). In the adult, the anterior edge of the gulars has a tip that dips back to form a slightly rounded front edge. On the sides the gulars slope backwards and have a slightly rounded edge. On the inner aspect of the leopard tortoise gulars is an elongated deep hollow. In shape they differ significantly from those of the Kalahari tent tortoise (*P. oculifer*) in which the gulars form a point on their anterior end and create a u-shape where they connect to the hypoplastron. In the greater padloper (*H. femoralis*) the gulars form almost a straight line on their anterior end with a point at each end such that they seem almost square (Figure 2).

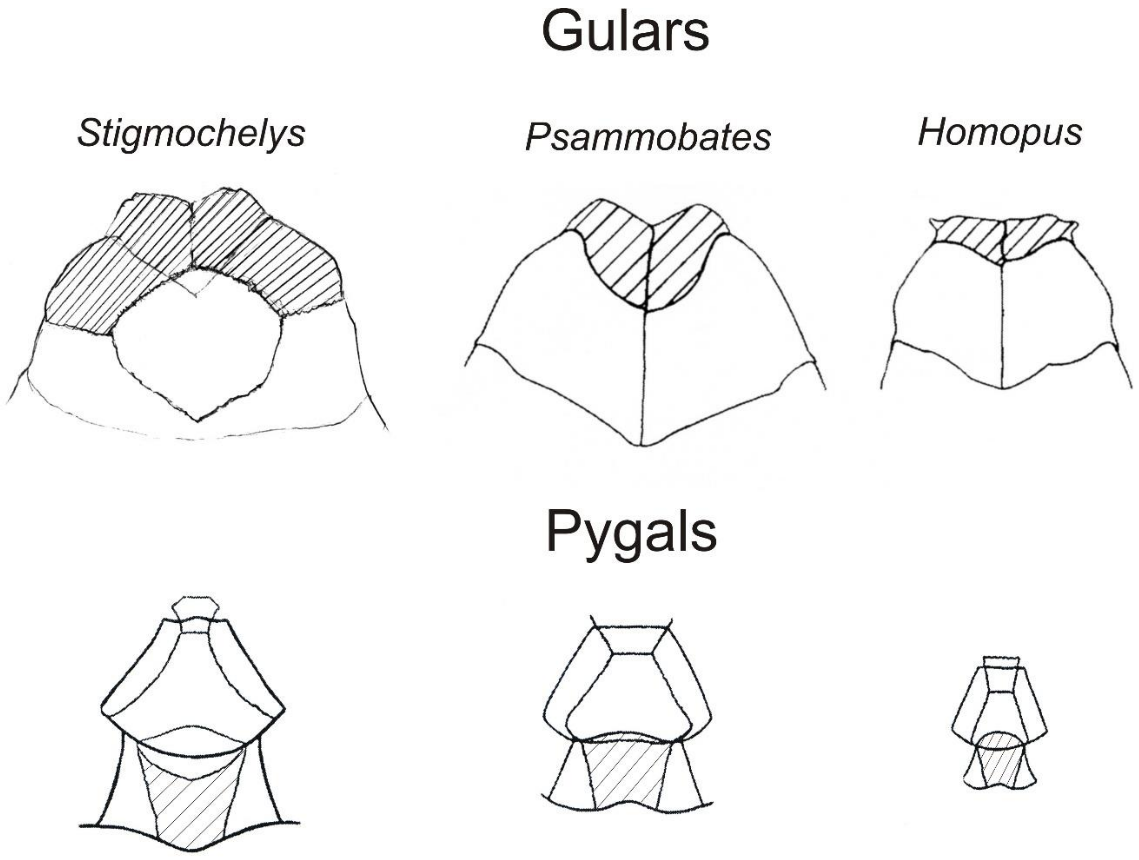


Figure 2 - Morphology of the gulars of adult tortoises of the three genera potentially found in the region of Wonderwerk Cave today. (*Homopus* and *Psammobates* after Loveridge & Williams 1957; *Stigmochelys* gular drawn by L. Wheeler)

The pygals of the three species also differ in shape. The leopard tortoise has a concave anterior section and a convex posterior section on the pygal, whereas the Karoo padloper and the Kalahari tent tortoise have a convex anterior section and a concave posterior section as illustrated in Figure 2.

3.2.3 Biometry

The leopard tortoise is considerably larger than the other two species, thus measurements were made of all complete bones in the hope that these could be used to separate species. However, few limb bones could be measured. Thus, gulars were also measured and the Wonderwerk Cave specimens compared to those of the modern tortoise species that currently inhabit the region (Figure 3). For a large series of modern leopard tortoises from the arid interior of South Africa, changes in the shape of the gular were analyzed by evaluating the relationship between length (L) and width (W). For allometric considerations, power relationships were evaluated using ln-transformed data in linear regression models, with $\ln(W)$ as the dependent variable. Three models were considered: a simple log-linear relationship, a model including Sex as a main effect, and a model including the interaction between Sex and $\ln(L)$. These tests were carried out using general linear models in R v 3.5.2 (R Core Team 2015). Models were compared for goodness of fit using the AIC adjusted for small sample sizes, AIC_c (Burnham and Anderson, 2001, 2002).

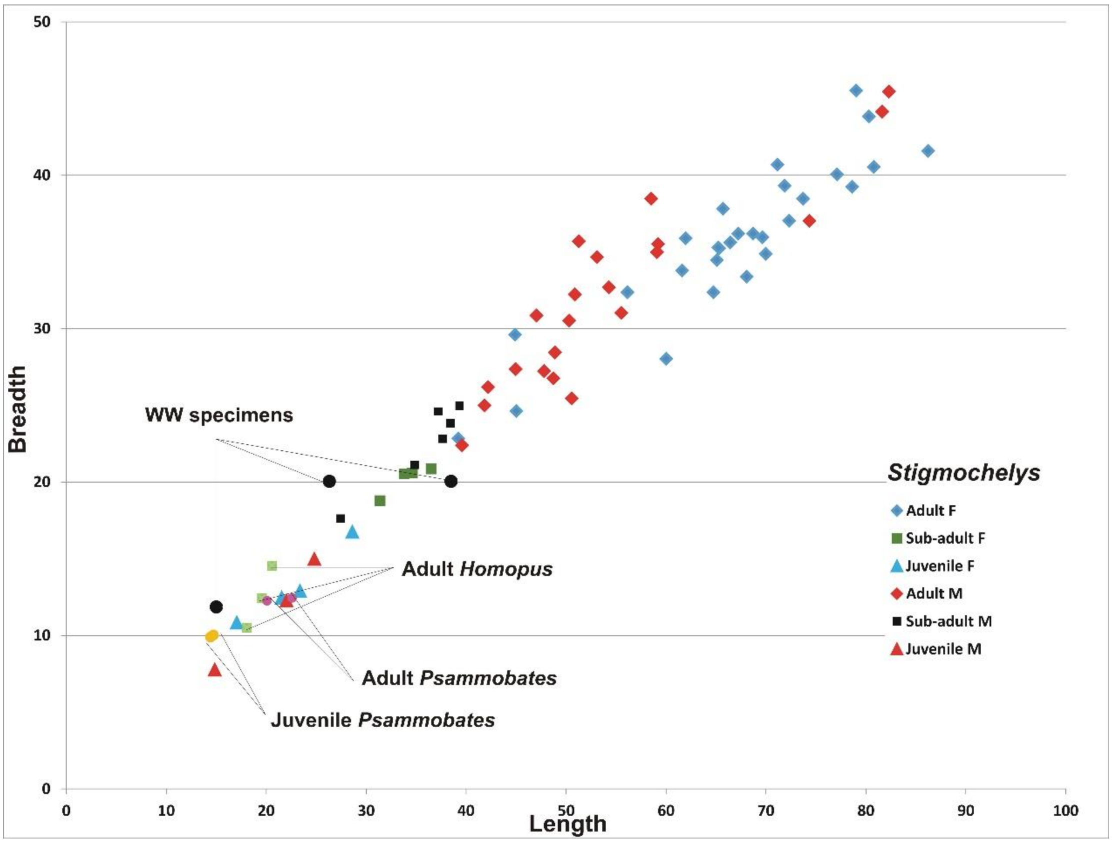


Figure 3 - Plot of length and breadth measurements (in mm) of the right gulars of modern leopard tortoises in the Florisbad collection plotted against the ESA gulars from Wonderwerk Cave (WW), three adult *Homopus femoralis* and two adult and two juvenile *Psammobates oculifer* specimens. The Wonderwerk specimens represent a juvenile and two sub-adults. Note that the *Homopus* and *Psammobates* adults are significantly smaller than the *Stigmochelys* sub-adults and adults.

3.3 Taphonomy

3.3.1 Discolouration

All bones were scored for burning using six colour categories: brown, red, black, grey, white (totally calcined) and unburnt. In addition, the location of burning on the shell was documented (on the inner side only, on the outer side only, on both sides). Scoring the colour and location of the burning on the shell is an indication of intensity and duration of exposure to heat, as well as position of the shell, and so may enable us to determine whether the bones were burnt intentionally i.e. due to human activities such as cooking – with the tortoise cooked directly in its shell and placed in the fire, on either its dorsal or ventral aspect, or on both (Avery et al., 2004; Thompson, 2010; Blasco et al., 2016) or else burnt accidentally (i.e. discarded in hearth refuse). As burning is known to make bones brittle and so more susceptible to fragmentation (Kalsbeek and Richter, 2006; Stiner, 2005: 59-79), its effect on tortoise shell elements was studied by comparing L and W (maximum measures) of burnt with unburnt bones. We used a linear mixed effects model (MELM) with Burnt (0 or 1) as a fixed effect, and included Element as a random effect to account for variation in size of different elements. These analyses were carried out using the lmerTest package for R (Kuznetsova et al., 2017).

Manganese staining on the bone surface can be confused with burning as it can present itself as black or black/greenish patches in the shape of a flower, as lots of little round spots or, as a stain that can cover a part or even most of the bone (Shahack-Gross et al., 1997; Fernandez-Jalvo and Avery, 2015). We documented what appeared to be manganese staining as present or absent but did not undertake any elemental analyses to test it.

3.3.2 Butchery

All 411 skeletal elements were first examined with a magnifying glass and then under higher magnification using an Olympus SZX10 microscope (magnification up to x1.25). This was intended to identify cut or chop marks, especially on the inner (visceral) surface of carapace elements where they may indicate meat removal (e.g., Blasco et al., 2011, 2016; Thompson and Henshilwood, 2014a, 2014b), as well as to identify impact fractures (percussion or cone fractures) which has been documented primarily on the peripherals and near the bridge area, following attempts by hominins to smash open the shell (e.g., Stiner, 2005; Thompson and Henshilwood, 2014a, 2014b; Biton et al., 2017). All elements were also examined for chew marks and stripping characteristic of human gnawing (Stiner, 2005; Fernández-Jalvo and Andrews, 2011).

3.4 Spatial Analysis

The distribution of all skeletal elements was examined to discern whether any spatial patterning existed within the assemblage. Two methodological difficulties had to be addressed: first, as the tortoise assemblage originates from the excavation conducted by Beaumont between 1978-1982 (Beaumont and Morris, 1990; Beaumont and Vogel, 2006; and see discussion above), it had limited contextual information (i.e no detailed x-y-z coordinates, and see discussion in Birkenfeld et al., 2015). Thus, all elements had to be plotted by excavation square. To do so, a polygonal layer was created using ESRI's *ArcMap* 10.5.1., recreating the excavation grid of Area 1. Following Chazan (2015: Fig 1), six other polygonal layers were created, delineating the area exposed per stratum. These were used as mask layers to select the required number and layout of excavated squares per stratum (and see Birkenfeld et al., 2015 for the complete procedure). The second difficulty encountered was the relatively small sample sizes per stratum. This significantly hindered the use of robust statistical methods, restricting the evaluation of the distribution of finds within each stratum to visual observation.

Using an *Excel* datasheet, the assemblage catalogue was digitized and imported into *ArcMap* and joined with the grid layers (attribute join, based on square number) to create a stratum-based digital representation of the finds distribution. Three maps were created for each stratum: first, a general distribution map, showing the total number of elements found within each excavation square (Figure 4); second, a map showing the distribution of elements by body part groupings (i.e. limb, carapace, plastron and carapace/plastron) (Figure 5); and third, a map showing the distribution of burnt versus unburnt material (Figure 6). A unified

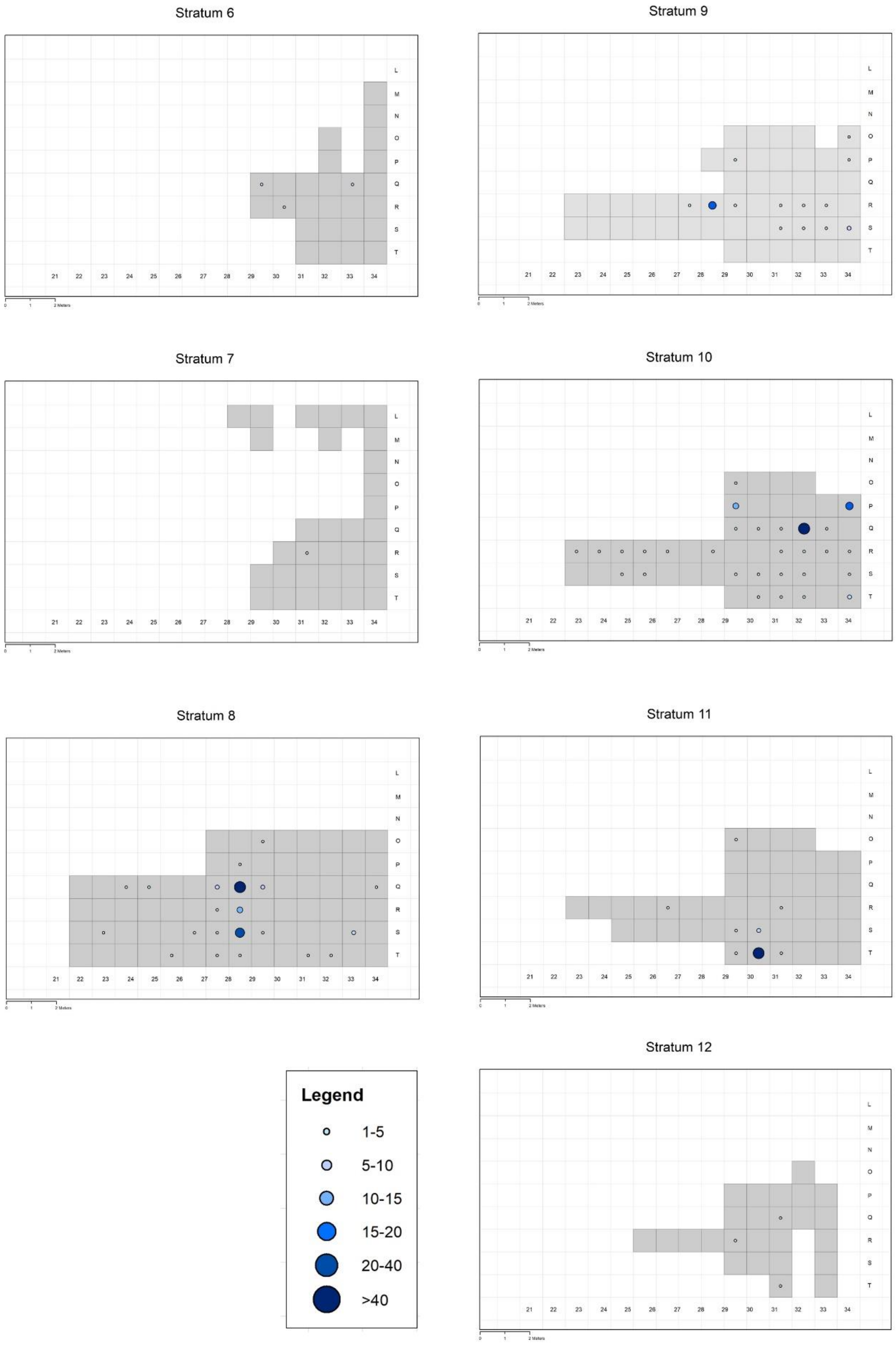


Figure 4 - General distribution maps, showing the counts of the total number of elements found within each excavation square.

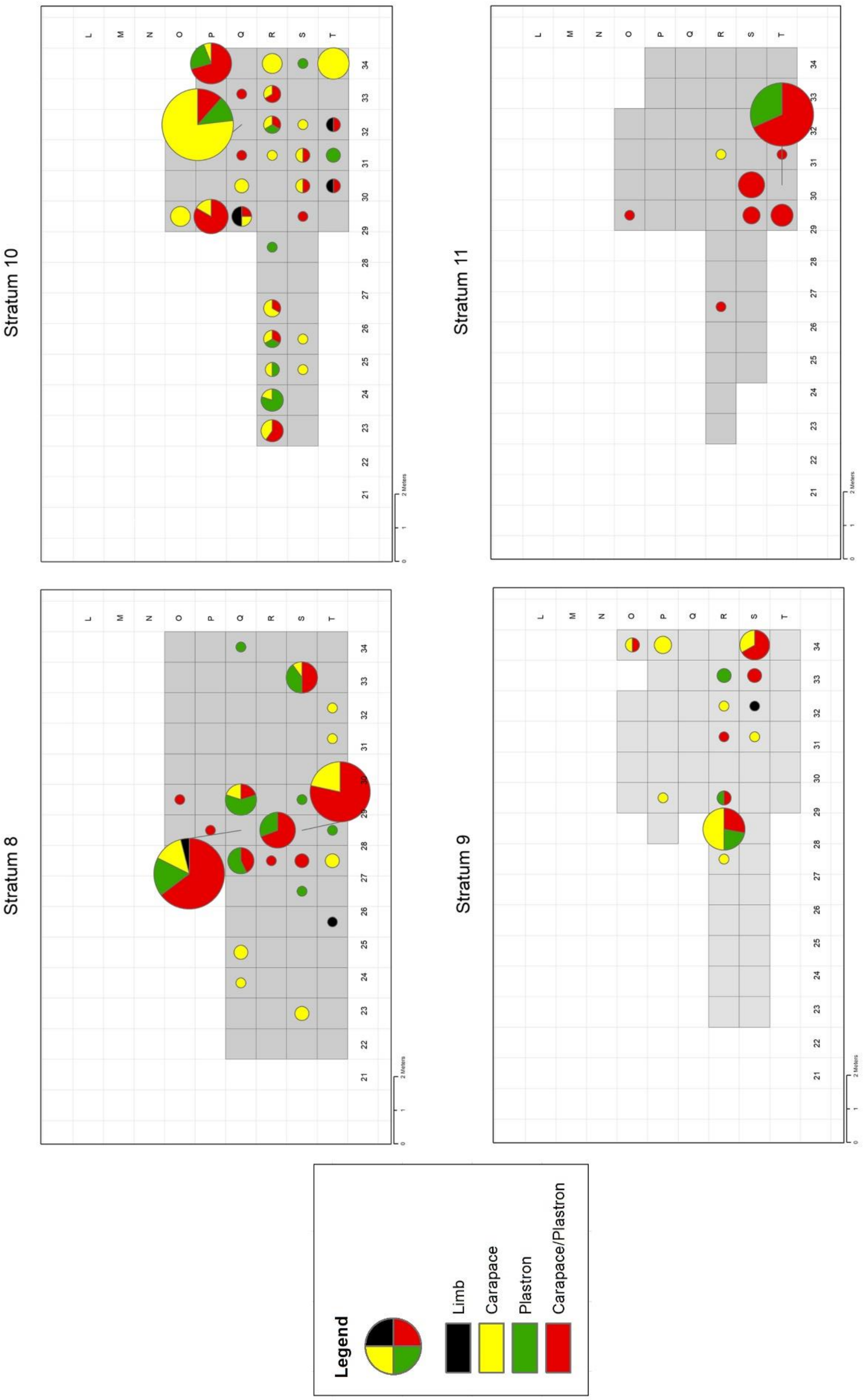


Figure 5 - Distribution maps showing the relative frequencies of skeletal elements by body part groupings (i.e. limb, carapace, plastron and carapace/plastron).

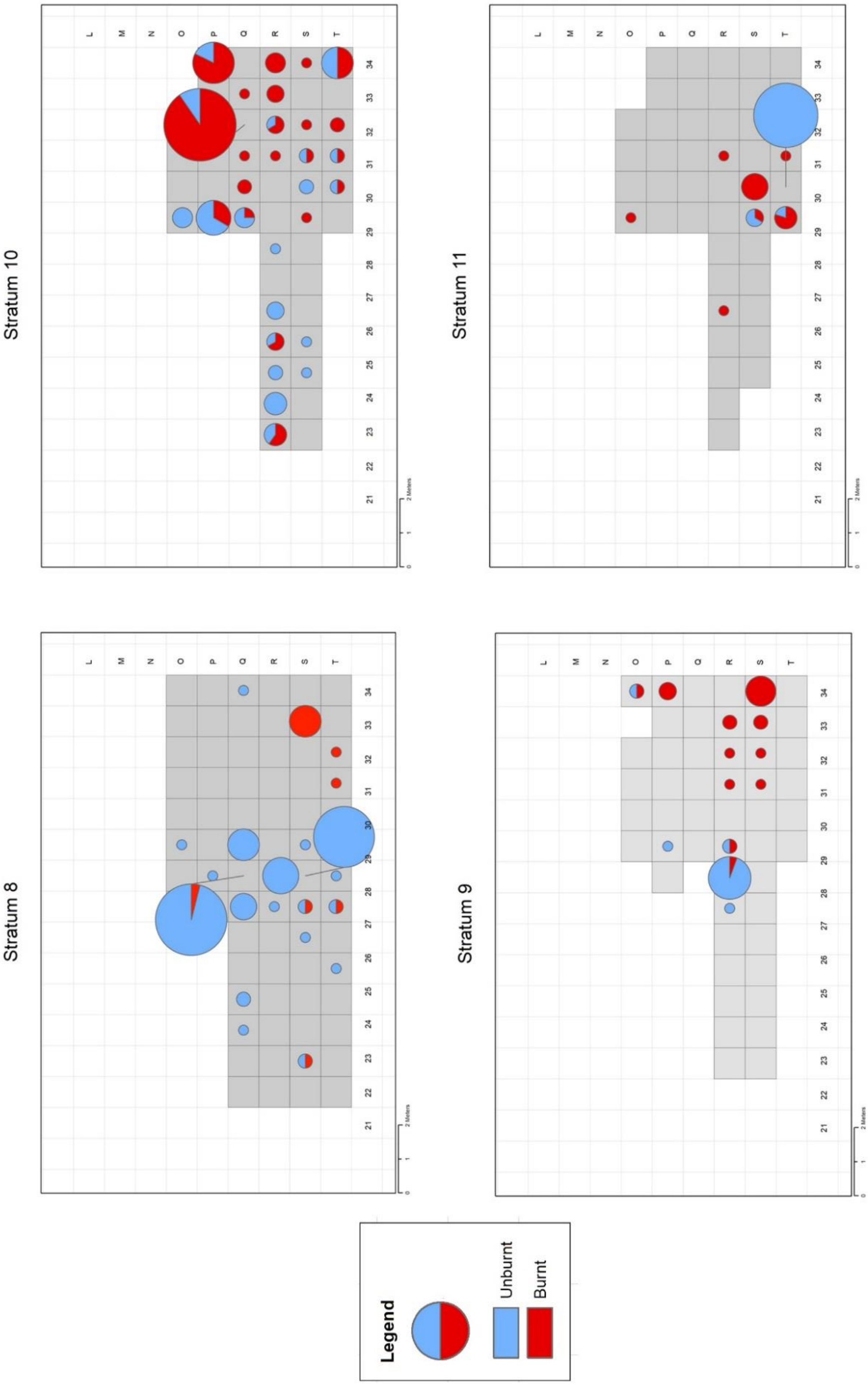


Figure 6 - Distribution maps showing the relative frequencies of burnt versus unburnt material.

symbology was used for all strata, to enable a straightforward evaluation of each map and the comparison between them.

4. Results

4.1 NISP and MNI counts

The ESA levels at Wonderwerk Cave yielded a total of 411 skeletal elements (NISP counts) with a total weight of 501.75 grams that includes limb bones, trunk elements (vertebrae) and shell remains (carapace and plastron). The stratum with the most bones was Stratum 10 (NISP = 149) and the one with the least bones was Stratum 7 (NISP = 2). This pattern is proportional to the volume of sediment excavated per stratum and does not reflect the intensity of tortoise exploitation in each layer. Table 1 illustrates the skeletal elements present by stratum. The MNI counts are low for all levels which may be attributed to the high degree of fragmentation which has limited the identification of most bones to element. MNI counts for Strata 8 and 10, are two each, while all other strata are one each, giving a total of only nine tortoises for the entire Early Pleistocene sequence at Wonderwerk Cave. This is corroborated by the GIS analysis, which shows that clusters of elements can be identified in single or adjacent squares within a layer. The distribution of body parts also implies the presence of a small number of individuals (and see discussion below).

4.2 Skeletal Element Representation

Few limb bones are represented in the assemblage and comprise an isolated humerus, tibia, fibula, phalanx and two ilium fragments that together make up only 1.4% of the entire assemblage. Likewise trunk elements, consisting of only four cervical vertebrae (excluding 11 neural plates with attached vertebrae), amounted to 1%. No cranial elements were identified in the assemblage. The carapace elements make up 31.6% and the plastron elements 17.8% of the entire tortoise bone assemblage. The combined carapace/plastron group comprising unidentified fragments consists of 48.2% of the whole assemblage, such that together with the separated carapace and plastron elements, the shell comprises 97.6% of all the tortoise finds.

There was no significant difference in the numbers of limb and trunk bones that are embedded in the shell (NISP = 13; 11 neural plates with vertebrae attached; 2 ilium) and limb elements that protrude from the shell (NISP = 8; 1 each of humerus, tibia, fibula, phalanx, 4 vertebrae). When specific elements were examined for the assemblage as a whole (excluding non-identified bony plates from the shell), peripherals were the most frequent element present while the humerus, tibia, fibula, phalanx, entoplastron and hyoplastron were the least represented, each by only one element.

Using Chi-square tests of carapace versus plastron elements in the largest sized samples (Strata 8, 9 and 10), we found a significant difference in frequency distributions across strata ($\chi^2=17.54$, $p<0.001$ for 2 df). Comparing pairs of strata shows no significant difference between Strata 10 and 9 ($\chi^2=0.169$, df=1, $p=0.681$), while both levels differ significantly from Stratum 8 ($\chi^2=5.855$ and 16.571, $p = 0.016$ and <0.0001, respectively). The difference in results is due to the relatively high proportion of plastron elements in Stratum 8, whereas in Strata 9 and 10 carapace/plastron ratios are more even.

4.3 Morphology and Biometry

Based on morphological criteria described above, the gulars and pygals from the ESA levels at Wonderwerk Cave were morphologically congruent with the osteological characters of the leopard tortoise (*Stigmochelys pardalis* Bell, 1828). The earliest gular and pygal bones that could be attributed to this species derive from Stratum 10, dated to ca. 1.0 Mya. No suitable bones were recovered in Strata 11 and 12 so we are unable to corroborate the identity of the species found in these earlier layers.

In terms of size, in the modern leopard tortoise sample, the relationship between gular length (*L*) and width (*W*) was strong (r^2 ranged between 0.955 and 0.964, $p < 0.0001$, across the three models evaluated), but differed between the sexes, with both the interaction term and main effect Sex being significant ($F_{1,62} = 13.901$ and 5.250, $p < 0.001$ and 0.025, respectively). The model including both the interaction term and main effect Sex had the best fit ($\Delta AIC_c = 0$) compared to both the model with Sex but with no interaction term ($\Delta AIC_c = 3.02$) and the model without Sex ($\Delta AIC_c = 13.153$). The interaction effect arises because the scaling exponent for females was lower (0.882, 95%CI: 0.834 to 0.930) than in males (0.980, 95%CI: 0.906 to 1.070; Figure 7). The scaling factor (anti-logged) for females was higher (0.877, 95%CI: 0.724 to 0.930) than that of males (0.622, 95%CI: 0.455 to 0.852), accounting for the significant main effect in the best-fit model. The near-isometric scaling in males means that, although their gulars are relatively narrower at small sizes than females, the length-width proportions of this element remain more-or-less constant, whereas the female gular becoming increasingly elongated through growth.

As illustrated in Figure 3, measurements of the three right sided gulars from Wonderwerk Cave (greatest gular length and breadth (L/B): 15.01/11.85 mm, 26.32/14.00 mm, 38.51/20.04 mm) fall within the juvenile and sub-adult range of our modern leopard tortoise sample from the Northern Cape and outside that of adults of the two smaller tortoise species found in the region today.

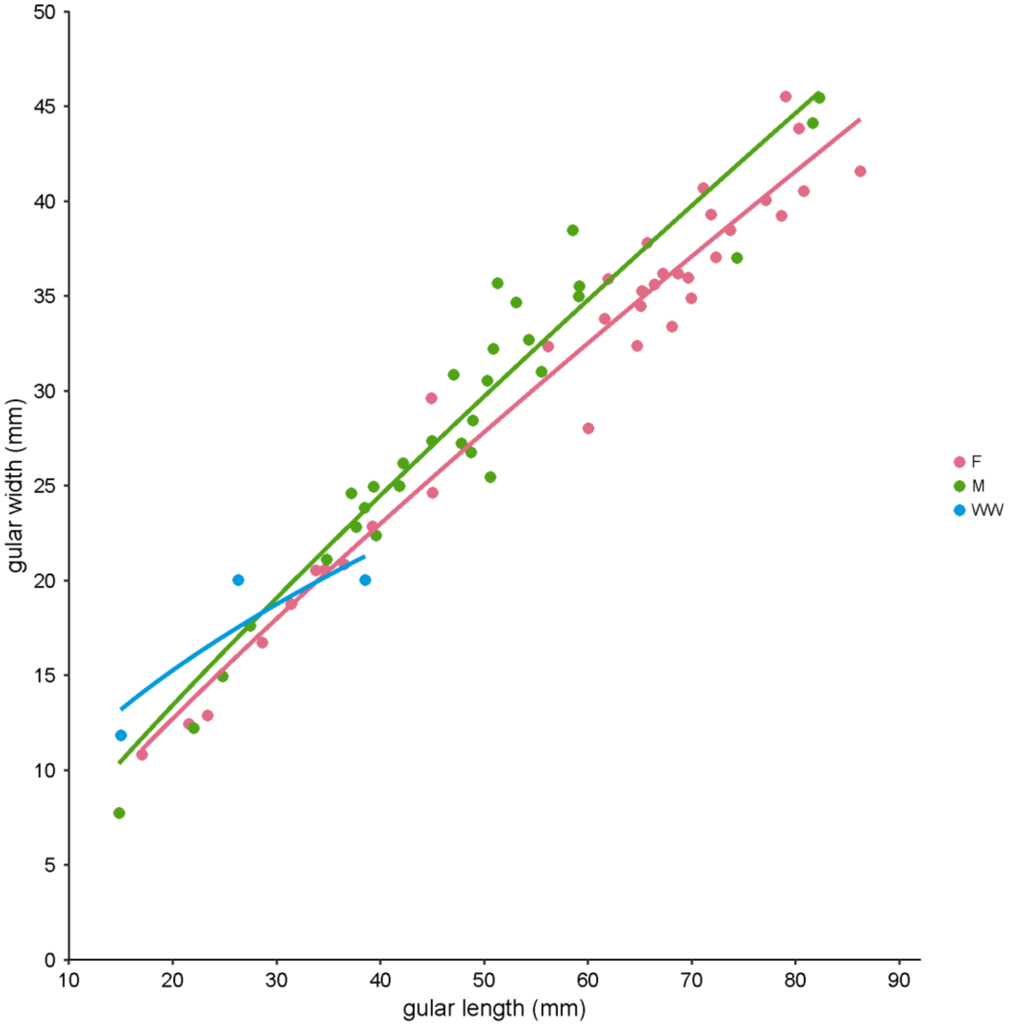


Figure 7 - Differences in gular length (L) – width (W) relationships between male (M) and female (F) leopard tortoises. Fit lines are power regressions of the form $W = 0.622(0.160)L^{0.988(0.042)}$ in males, and $W = 0.877(0.098)L^{0.882(0.024)}$ in females (numbers in parentheses are standard errors of parameter estimates). WW are data for three individuals from Wonderwerk.

4.4 Taphonomy

Of the 411 elements present, 38.4% (NISP = 158) showed discolouration (stages 1 to 5) that we associated with burning. Of these, only two derive from the appendicular skeleton; a vertebra and a tibia while the remainder are shell elements. As illustrated in Figure 6, of the bones that exhibited signs of burning, the majority (73.4%; NISP = 116) were calcined (white in colour), indicating burning at high temperatures. The calcined bones are concentrated in Strata 11, 10 and 9. Only one element from Stratum 12 was burnt and its colour was black.

A total of 43% (NISP = 68) of the 158 burnt remains were carapace fragments and only 10.1% (NISP = 16) plastron elements. Examination of the location of burning indicated that the vast majority (94.9%; NISP = 150) of both plastron and carapace elements were burnt on both the inner and outer aspects of the shell (Table 2). Of the remaining eight shell fragments, four were carapace fragments that were burnt solely on the inner surface, one carapace fragment was burnt only on the outer surface, two elements from the combined carapace/plastron group, were burnt only on the outer surface and one only on the inner surface. Figure 8 illustrates the percentage of burning by colour and by stratum.

Table 2 - Elements burnt on the inside, outside and on both sides and the damage, given in percentage.

Stratum	Element	Carnivore	Precussion Fracture
Stratum 6	pleural	1	
Stratum 8	peripheral		3
	car/plas		1
	xiphiplastron		1
Stratum 9			
Stratum 10	hyoplastron		1
	pleural		1
	car/plas		1
Stratum 11	plastron	13	
Total		**14**	**8**

Although lengths (*L*) of elements were generally higher for unburnt (mean = 20.8 ± 12.54 sd) than burnt bones (17.2 ± 8.28), the difference in *L* was not significant (MELM $F_{1,208} = 2.149$, $p = 0.144$). This may be due to the fact that many of the bones not identified to specific skeletal element but labelled “carapace” or “carapace/plastron” did not differ in *L*. Repeating the analysis while omitting these two element categories revealed a significant

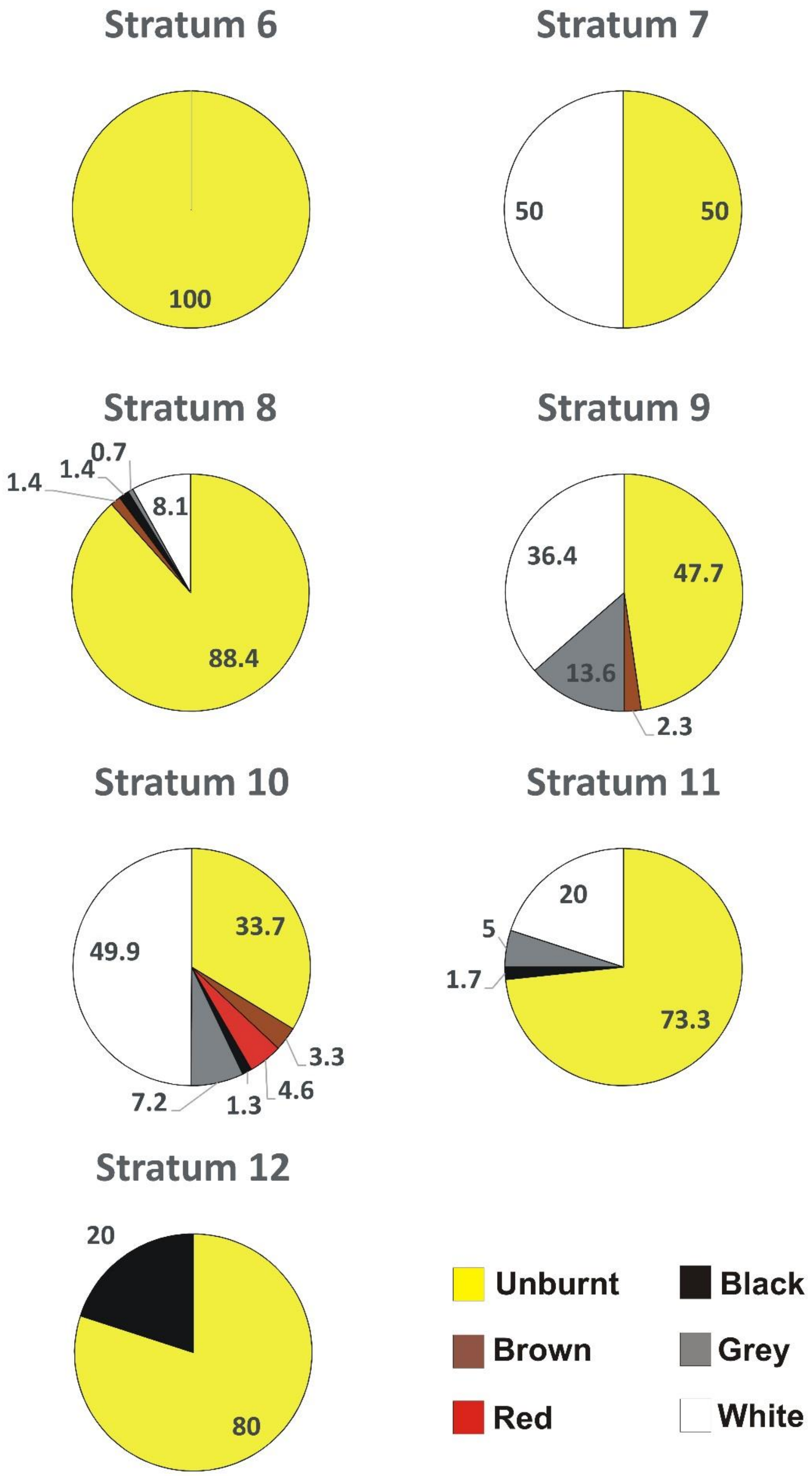


Figure 8 - Pie chart of showing frequency of different colours associated with burning by stratum in percentage.

effect of burning on bone *L* ($F_{1,33} = 11.953$, $p < 0.01$). The most significant effect of burning was found for bone width (*W*), in which the lower values for burnt bones (11.9 ± 5.68) was significantly different to that of unburnt bones (14.96 ± 8.43), even with the unidentifiable "carapace" or "carapace/plastron" specimens included ($F_{1,206} = 5.083$, $p = 0.025$).

In addition to burning, over half the tortoise assemblage (51.3%; NISP = 211) exhibited manganese staining on both the inner and outer bone surface. This number may have been higher as in some cases the staining may have been obscured by burning. Manganese stained bones occur in all the strata.

A total of 14 elements exhibited carnivore puncture holes (Figure 9, Table 3). One is from Stratum 6 and is a fragment of a pleural. The rest derive from Stratum 11 and comprise 13 fragments of plastron that may have belonged to the same tortoise. No cut marks were observed on any elements in the assemblage as a whole. There were, however, 8 elements

Figure 9 - Carnivore puncture holes in tortoise remains from Wonderwerk Cave.

Table 3 - Measurements of limb bones from Wonderwerk Cave and the average measurements for modern specimens (in mm). The *Homopus* measurements are for *H. areolatus*.

Level	Element	GL	Bp	Bd	SD depth	SD width
Wonderwerk Str 6	Fibula			4.12		
Stigmochelys (n=96)	Fibula ♂			7.25		
(n=91)	Fibula ♀			8.43		
Homopus (n=2)	Fibula			1.37		
Psammobates (n=2)	Fibula ♂			1.82		
(n=2)	Fibula ♀			2.33		
Wonderwerk Str 10	Tibia	30.45	9.60	6.21	3.52	3.33
Stigmochelys (n=116)	Tibia ♂	45.44	15.04	10.18	5.14	5.50
(n=91)	Tibia ♀	59.31	18.95	12.87	6.44	6.86
Homopus (n=3)	Tibia	14.87	4.14	2.83	1.43	1.55
Psammobates (n=2)	Tibia ♂	17.09	4.47	3.28	1.15	1.74
(n=2)	Tibia ♀	19.67	5.75	4.15	1.72	2.75

with percussion fractures. They originate in Strata 8, 9 and 10. Of these, 2 were on unidentified carapace/plastron elements, 3 were on peripherals and one each on a pleural, hyoplastron and xiphiplastron, respectively. Five had stepped percussion fractures and three others had cone fractures (Figure 10).

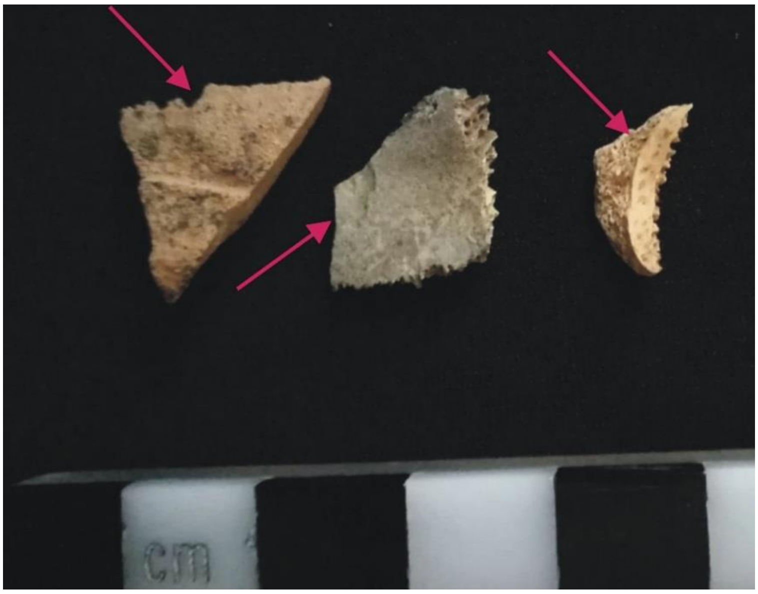


Figure 10 - Photograph showing examples of percussion fractures on tortoise remains from Wonderwerk Cave (indicated by red arrows).

4.5 GIS spatial location

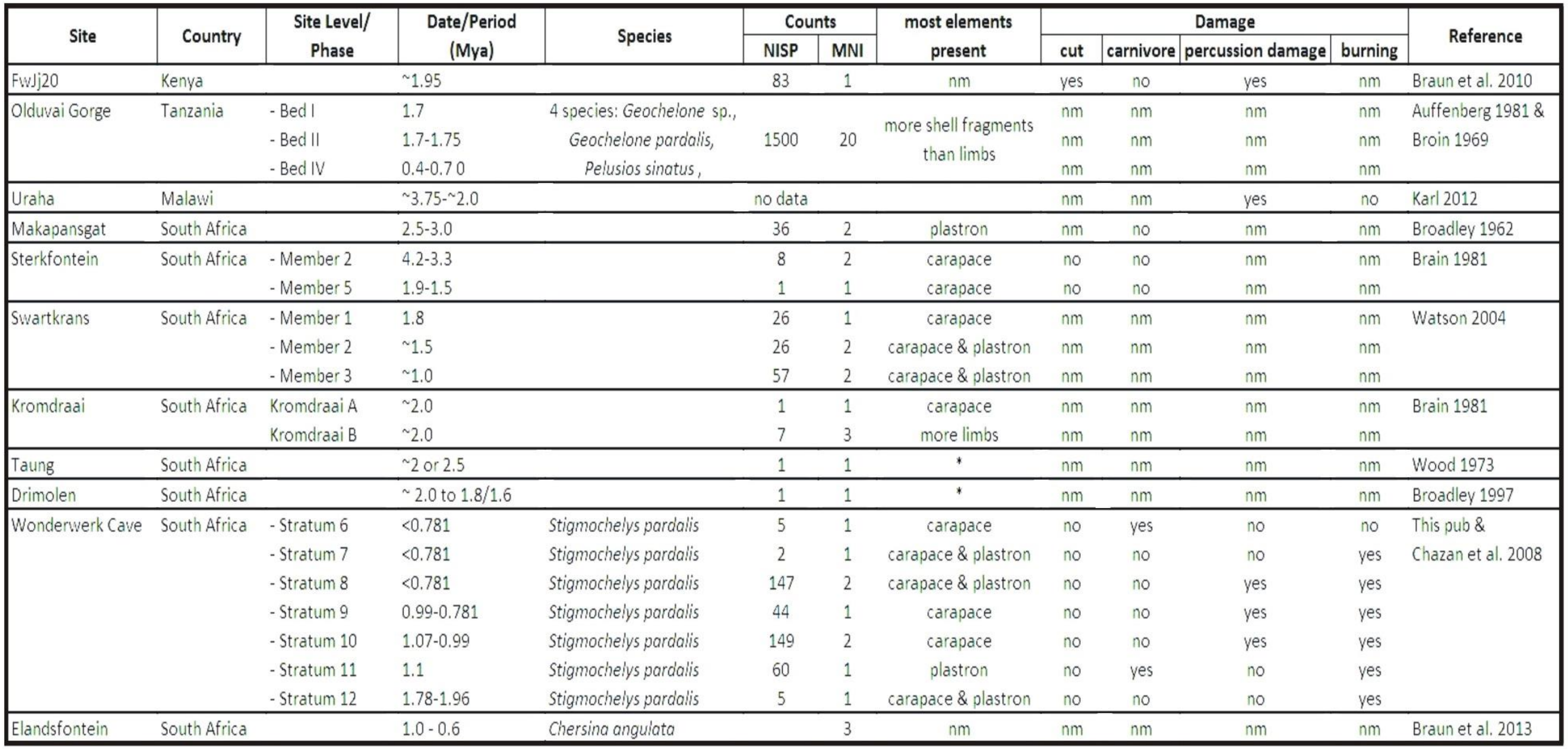
Although limited to visual evaluation, the distribution of elements showed several interesting patterns, especially within the strata with larger sample sizes (i.e. Strata 8-11). Firstly, it is important to note that each stratum exhibits a different distribution pattern, as the location of squares with high numbers of tortoise remains shifts between them, demonstrating that activities in each layer follows a unique spatial pattern. Secondly, in all strata, clear concentrations of elements can be discerned. These are usually restricted to one or two adjoining squares, even though isolated remains may be found throughout the excavated area. This is clearly demonstrated in Strata 8-11 (Figure 5): Stratum 11 shows a clear concentration of remains in and around Square T30; in Stratum 10, three focal areas can be identified, mainly in Square Q32, but also in Squares P34 and P29; Stratum 9 shows a possible concentration focused on Square R28 and in Stratum 8 a defined area of high density for tortoise remains is centred along a row of Squares Q28-R28-S28 and their adjacent squares. This clustered pattern supports the notion that the tortoise assemblage represents a relatively small number of individuals. As illustrated in Figure 4, the distribution of elements by body part lends some support for this contention with the most abundant body part type in a concentration of tortoise remains, also occurring in adjacent squares. However, no conjoins between bones could be made between adjacent squares or within a stratum, probably due to the high degree of fragmentation.

The quantities of burnt versus unburnt material differs between strata, implying differences in the types of activities or processes that took place within each layer (Figure 6). For example, Stratum 8 has far more burnt material than Stratum 10. However, most strata do not exhibit any clear spatial patterning with regard to burnt material, which seems to be spread quite evenly throughout the excavated area. Stratum 9 is somewhat different, with a possible concentration of burnt material in squares R-S/31-34, although this may be the result of the relatively small numbers of bones in this sample. All tortoise remains were found in squares together with archaeological material – macro-faunal remains, lithic artefacts and in some cases botanical remains.

5. Discussion

Table 4 summarises the data for Early to late Mid-Pleistocene Testudinae remains found in archaeological contexts in East and Southern Africa. Although they occur in several sites, few species attributions have been made. Exceptions are a fossil tortoise from Sterkfontein, from a layer dated to ca. 2.0 to 1.8/1.6 Mya, that was attributed by Broadley (1997) to *Psammobates oculifer*. However, Lapparent de Broin (2000), notes that the depressed carapace is closer to *Homopus femoralis* than *P. oculifer*. At Elandsfontein, Braun et al. (2013) identified the remains as those of angulate tortoises. In addition, Broadley (1997) attributed remains from the Pliocene site of Langebaanweg, and Early Pleistocene sites of Kromdraai B and Makapansgat Limeworks site to a large form of the genus *Geochelone*, but no species attribution was given. In the past, the leopard tortoise (*Stigmochelys pardalis*) was placed under the genus *Geochelone* (e.g. Loveridge and Williams, 1957), but more recently has been recognised as the only member of the genus *Stigmochelys* (Gerlach, 2001; IUCN Red List http://oldredlist.iucnredlist.org/details/163449/0). Consequently, it is possible that the Kromdraai B and the Makapansgat Limeworks tortoise remains belong to the same genus, and even species, as those from Wonderwerk Cave. The earliest finds of leopard tortoise are from BK2 and DK1 in Olduvai Gorge dating to ca. 1.70/1.75 Mya (Auffenberg, 1981; Lapparent de Broin, 2000). The Wonderwerk Cave remains from Stratum 10 (dated to ca. 1.0 Mya), although younger, document the earliest definite identification of this species in southern Africa.

Table 4 – A summary of the data for Early to late Mid-Pleistocene Testudinae remains found in archaeological contexts in East and Southern Africa.



Site	Country	Site Level/ Phase	Date/Period (Mya)	Species	Counts		most elements present	Damage				Reference
					NISP	MNI		cut	carnivore	percussion damage	burning	
FwJj20	Kenya		~1.95		83	1	nm	yes	no	yes	nm	Braun et al. 2010
Olduvai Gorge	Tanzania	- Bed I	1.7	4 species: *Geochelone* sp.,	1500	20	more shell fragments than limbs	nm	nm	nm	nm	Auffenberg 1981 &
		- Bed II	1.7-1.75	*Geochelone pardalis,*				nm	nm	nm	nm	Broin 1969
		- Bed IV	0.4-0.7 0	*Pelusios sinatus ,*				nm	nm	nm	nm	
Uraha	Malawi		~3.75-~2.0		no data			nm	nm	yes	no	Karl 2012
Makapansgat	South Africa		2.5-3.0		36	2	plastron	nm	no	nm	nm	Broadley 1962
Sterkfontein	South Africa	- Member 2	4.2-3.3		8	2	carapace	no	no	nm	nm	Brain 1981
		- Member 5	1.9-1.5		1	1	carapace	no	no	nm	nm	
Swartkrans	South Africa	- Member 1	1.8		26	1	carapace	nm	nm	nm	nm	Watson 2004
		- Member 2	~1.5		26	2	carapace & plastron	nm	nm	nm	nm	
		- Member 3	~1.0		57	2	carapace & plastron	nm	nm	nm	nm	
Kromdraai	South Africa	Kromdraai A	~2.0		1	1	carapace	nm	nm	nm	nm	Brain 1981
		Kromdraai B	~2.0		7	3	more limbs	nm	nm	nm	nm	
Taung	South Africa		~2 or 2.5		1	1	*	nm	nm	nm	nm	Wood 1973
Drimolen	South Africa		~ 2.0 to 1.8/1.6		1	1	*	nm	nm	nm	nm	Broadley 1997
Wonderwerk Cave	South Africa	- Stratum 6	<0.781	*Stigmochelys pardalis*	5	1	carapace	no	yes	no	no	This pub &
		- Stratum 7	<0.781	*Stigmochelys pardalis*	2	1	carapace & plastron	no	no	no	yes	Chazan et al. 2008
		- Stratum 8	<0.781	*Stigmochelys pardalis*	147	2	carapace & plastron	no	no	yes	yes	
		- Stratum 9	0.99-0.781	*Stigmochelys pardalis*	44	1	carapace	no	no	yes	yes	
		- Stratum 10	1.07-0.99	*Stigmochelys pardalis*	149	2	carapace	no	no	yes	yes	
		- Stratum 11	1.1	*Stigmochelys pardalis*	60	1	plastron	no	yes	no	yes	
		- Stratum 12	1.78-1.96	*Stigmochelys pardalis*	5	1	carapace & plastron	no	no	no	yes	
Elandsfontein	South Africa		1.0 - 0.6	*Chersina angulata*		3	nm	nm	nm	nm	nm	Braun et al. 2013

The fact that only remains of *S. pardalis* have been positively identified in Wonderwerk Cave is of special interest given that the site currently falls within the biogeographic range of two other tortoise species. Aside from size, gulars and pygals were used for species identification, skeletal elements that are some of the densest bones in the tortoise shell (Holt et al., 2019), and so are expected to have been preserved, regardless of species. A possible explanation may relate to the palaeoclimatic conditions that prevailed in the region during the Early/Mid-Pleistocene.

Palaeoclimate reconstruction for Wonderwerk Cave has emphasized the presence of grasslands - beginning in the Oldowan with semi-arid and warm conditions associated with C_3 vegetation, followed by a shift to warm, arid C_4 Savanna grassland from ESA Stratum 9 (ca. mid-way through the Jaramillo sub-chron to its end ca. 0.90 Mya) through to Stratum 6 (Ecker et al., 2015, 2018a, 2018b; Horwitz et al., in press). Unstable and fluctuating conditions characterised the underlying Stratum 10 (dated to ca. 1.07/06 Mya), from very moist (C_3 environment) to very xeric conditions, (C_4 environment).

Although all three tortoise species presently found in the area of the cave are sympatric in part of their ranges, *Stigmochelys* inhabits a far wider range of habitats and climatic conditions with the Savanna regions than the other two. It is considered a generalist herbivore, feeding extensively on grass (Milton, 1992; Rall and Fairall, 1993), but depending on seasonal availability, also feeds on a wider variety of plants forbs, succulents, fruit, legumes, compared to other African tortoises (Broadly, 1989). Based on these findings, it is tentatively suggested that the leopard tortoise was perhaps better adapted than the other two tortoise species to the changing palaeoenvironmental conditions prevailing in the environs of Wonderwerk in the Early and Mid-Pleistocene. As such, it may have been the sole Testudinid species in the region at this time.

An additional factor may relate to visibility of tortoises and the fact that in arid environments they generally occur in low densities (Freilich et al., 2000; Berry et al., 2006; McMaster and Downs, 2006; Keswick and Hofmeyr, 2013). Notably, all sites listed in Table 4, including Wonderwerk Cave, have relatively low NISP/MNI counts, implying that tortoises were only an occasional food source. At Wonderwerk Cave, the spatial concentrations of tortoise remains supports the notion that a relatively small number of individuals are represented.

In the context of species choice, it is suggested that the leopard tortoise, which is by far the region's largest species and also the one that travels the furthest (especially in more mesic conditions - McMaster and Downs, 2009), may have been more visible and due to its size, was also more attractive to hominins in the palaeolandscape. An interesting observation relating to visibility was recently made by researchers reporting chimpanzee exploitation of tortoises. Pika et al. (2019) noted that the noise made by tortoises moving through the desiccated leaf litter in the dry season may alert chimpanzees to the presence of a tortoise and so lead to their being discovered and preyed on.

A critical question relating to the Wonderwerk Cave tortoise bone assemblage and those from other coeval sites, is identification of the agent/s responsible for their introduction. Resolving this issue is hampered by the fact that detailed taphonomic studies have not been undertaken on most assemblages.

Sampson (2000) states that an over-abundance of carapace and plastron fragments in an assemblage indicates human intervention. This is because limb elements protrude from the shell and are selectively removed by carnivores and other non-human predators (e.g. Branch and Els, 1990; Lloyd, 1998; Hill, 1999). This fits the pattern of skeletal element representation observed at Wonderwerk Cave (Table 1). However, Schneider and Everson (1989) notes that First Nations communities in North America often disarticulated the limbs before cooking, an act which may explain the paucity of limb elements at Wonderwerk Cave and explain the evidence for limbs having been ripped off or torn away from the body as reported for the Middle Palaeolithic tortoise assemblage from Hayonim Cave, Israel (Stiner, 2005).

Methods used by First Nations communities in North America to prepare turtles for cooking include stewing or placing them in direct contact with a hearth. Preparation procedures varied greatly and entailed removal or retention of the shell, prying open the shell before or after baking, placing heated pebbles in the carapace, or else by removing all the meat and then cooking it within the shell (Schneider and Everson, 1989). It is expected that such actions are likely to leave butchery marks or percussion fractures on the bones.

In the Wonderwerk Cave tortoise assemblage, there is no evidence for anthropogenic damage in the form of cut and chop marks, but fracture damage is present on 8 bones (1.9% of all tortoise remains). This is lower than frequencies reported for other Early and Middle Pleistocene tortoise bone assemblages. For example, Braun et al. (2010) indicated that 5.9% of the modified tortoise bones at the site of FwJj20 showed evidence of hominin modification either in the form of cut marks (incisions or scrapes that are located on the ventral surface of the carapace - mostly pleural and neural bones), or percussion marks. Blasco et al. (2011) found a total of eight (10.7%) tortoise remains with cut marks in the Early Pleistocene assemblage from Sima del Elefante, Spain, while in Mid-Pleistocene Bolomor Cave, she documented high frequencies of cut marks (9.32%; NISP = 49), percussion damage (2.47%; NISP = 13) and human tooth marks (3%; NISP = 16) (Blasco, 2008). Cut marks on both shell and limb bones (13.2%; NISP = 7) were also identified at Late Acheulean Qesem Cave (Israel), in addition to impact flakes on two carapace elements (Blasco et al., 2016). On a total of 4343 tortoise remains from Blombos Cave (South Africa), Thompson and Henshilwood (2014a) identified tooth marks on 5.1 % (NISP = 223) of the tortoise remains (the agent responsible is not specified), in addition to percussion marks on 1.6% (NISP = 71) and cut marks on 1% (NISP = 44). Low frequencies of cut marks (2.1%; NISP = 7) were reported at the Middle Palaeolithic site of Nahal Mahanayeem Outlet (Biton et al., 2017), while peeling from human gnawing was also reported on 1.5% (NISP = 5) limb bones. Stiner (2005) found that in the Middle Palaeolithic levels at Hayonim Cave (Israel), 14% of marginal plates had impact fractures on their edges indicating that the shells were often set on their edge and struck on the opposite rim to break the shell open. Cone fractures, impact depressions, dents and localised crushing on the shell parts are present.

This brief summary clearly indicates that there is a lot of inter-site variability in the frequencies of the different types of anthropogenic damage to the shell (and limbs). Regardless of time period, cuts/chops and human gnawing marks are less common in all assemblages than impact fractures on the bony plates of the shell. Using percussion to pry open the shell is evidently the simplest and most effective method to process a tortoise. This may entail smashing the tortoise against a rock, as documented by Gifford (1932) for the western Yavapai of North America, or by smashing it against an anvil as recently documented for chimpanzees in Loango National Park (Gabon), who successfully used a tree (Pika et al., 2019).

Another common signature of anthropogenic processing is burning. In the Wonderwerk Cave assemblage, 38.4% of the tortoise remains are burnt, the majority being carapace and plastron plates (Figure 6). Most of the burnt elements were coloured white (calcined), indicating they were burnt at a high temperature or exposed for a long time to heat. Temperatures between 300-400ºC (for black) and 500-900ºC (for white) are needed to reach these colours (Asmusen, 2009). Bushfires in African Savanna environments can reach similar temperatures (Trollope, 1983; Shea et al., 1996; N'Dri et al., 2018) and tortoise remains collected after wildfires (Royer et al., 2011) were found to have bony plates charred on both their inner and outer aspects. It seems most likely that the observed burning is the result of an intentional fire within the cave rather than a bush fire. This, since at present the tortoise remains are ca. 20 - 30 m in from the cave entrance and this distance was even greater in the past as the cave mouth has retreated since the Early Pleistocene (Matmon et al., 2012). Indeed, Stratum 10 at the Wonderwerk Cave contains the earliest known evidence worldwide for the intentional use of fire, but to date lacks any evidence for a hearth structure or concentrated burnt area (Berna et al., 2012).

Studies have shown that bones may be accidentally burnt and altered in colour and texture, such as those lying underneath or adjacent to hearths or on cooled ashes. However, they tend to be burnt to a lesser degree than bones that were in direct contact with a fire (e.g. Stiner et al., 1995; Bennett, 1999; Cain, 2005; Pérez et al., 2017). Moreover, the distribution of burning on the bone is more random than in the case of burning resulting from cooking (Stiner et al., 1995). Some researchers have proposed that burning will primarily occur on the outer surface of the tortoise carapace with less burning on the plastron, since tortoises were primarily cooked, upside-down in their carapace (Flannery, 1986; Sampson, 1998; Stahl and Oyuela-Caycedo, 2007). This pattern of burning is evident in the Mousterian site of Kebara Cave, with a higher incidence of burning on the carapace (10.2%) than the plastron, and negligible burning on limb bones (0.9%; Speth and Tchernov, 2002). Moreover, on the carapace, burning was localized ranging from the lateral to the medial edge. In the M1 phase at Blombos Cave, 76.2% carapace fragments were burnt compared to only 59.2% plastron, and 59% of all tortoise shell remains were burnt only on the outside and only 1.8% on the inside (Thompson and Henshilwood, 2014a). Similarly, in the Mousterian deposit at Bolomor Cave, there was a higher incidence of burnt carapace (NISP = 190; 65.97% of all carapace fragments) than plastron remains (NISP = 72; 62.61% of all plastron fragments) with a similar pattern of localization interpreted by Blasco (2008) as typical of cooking of the shell on its dorsal aspect. In all ESA strata at Wonderwerk Cave, the majority of burnt remains were indeed those of the carapace, although there was a preponderance of plates burnt entirely on both their inner and outer aspects. This differs from the general pattern reported by Speth and Tchernov (2002) where mainly the outer and peripheral aspect of the carapace plates were burnt. This, plus the fact that many of the Wonderwerk Cave bones were calcined suggests that they were accidentally burnt within the deposit, or exposed again to fire after cooking/consumption. This is borne out by the results of a burning experiment undertaken on six North American terrapins (*Trachemys scripta*) (Royer et al., 2011). They found that cooking of an entire individual on embers led to differential burning according to the anatomical part considered: the bones protected by the shell remained unburnt while those of the carapace are systematically damaged on their peripherals. Moreover, a difference in burning intensity was also found between the inside and the outside of the shell. The terrapin burnt with the plastron face-down exhibited strong signs of burning on this bone (Royer et al., 2011). At Qesem Cave (Israel), more burning was found on the outer surface of the plastron (NISP = 9; 32%) than carapace (NISP = 6; 14%; Stiner et al., 2011) similar to the picture at some Upper Paleolithic-Mesolithic sites in Italy (Fiore et al., 2004), suggesting that at these sites the tortoise was placed on the plastron in a hearth.

The data on burning summarised above suggests that there is a great deal of variability in the degree, extent and patterning of this type of damage on tortoise shell. However, a high proportion of bony plates with both the inner and outer surfaces burnt, as well as calcined shell - as found at Wonderwerk Cave, imply direct exposure to fire rather than cooking in a hearth. Even in the absence of cut marks, the presence of burnt tortoise remains in many of the Early to early Mid-Pleistocene sites lends support to their association with hominid activities, especially in cave sites where incineration due to natural fires can be excluded.

Regarding the relatively high frequency of manganese staining on the tortoise bones at Wonderwerk Cave, the manganese flowers are not surprising as both iron and manganese occur in the cave sediment (Goldberg et al., 2015).

In the Wonderwerk Cave assemblage, carnivore damage is evident on 14 tortoise remains (3.4% of all remains) and solely in the form of puncture holes from canines (Table 3). Moreover, with one exception, all are associated with tortoise shell from Stratum 11. In the published literature on tortoise taphonomy, there are few reports of carnivore damage on their remains, even from cave sites. For example, no evidence of carnivore damage was observed on finds from Bolomor Cave or Sima del Elefante in Spain (Blasco, 2008; Blasco et al., 2011), Hayonim Cave in Israel (Stiner and Tchernov, 2002), Qesem Cave, Israel (Blasco et al., 2016) or at Blombos Cave, South Africa (Thompson and Henshilwood, 2014a). Neither was any carnivore damage reported from the open-air site of Nahal Mahanayeem Outlet, Israel (Biton et al., 2017). One exception is Kebara Cave (Israel), where Speth and Tchernov (2002) reported carnivore gnawed and punctured bones, although no numbers were given. Although Kebara Cave exhibits evidence for hyaena activity, due to the modest number of damaged bones they attributed the formation of the tortoise bone accumulations primarily to human action. Another example is the site of FwJj20 where carnivore tooth marks were found on limb bone fragments (Braun et al., 2010). The authors further noted that this comprised 1.9% of the overall observed surface damage to tortoise bones and is well below the experimentally determined thresholds (~67%) for damage associated with carnivore-only accumulations. Using this as a standard, we may conclude then that the carnivore damage on the Wonderwerk Cave tortoise bone assemblage, which is also concentrated in Stratum 11, is negligible and does not point to carnivores as the primary agents responsible for introducing their remains into the site.

In conclusion, the Wonderwerk Cave Early Pleistocene Testudinidae remains provide insights into early hominid activities in the interior of South Africa. Leopard tortoises were encountered in the bush and whole animals were brought back to the cave where they were processed for consumption. Processing seems to have taken place in defined areas within each layer and appears to have entailed removal of the limbs followed by fracturing of the shell with an implement to get it open. It is not possible to reconstruct whether the tortoises were then cooked in the shell but certainly, either during or after consumption, many of the tortoise bones were exposed to fire.

These remains join a growing corpus of data from Europe (e.g. Bailon et al., 2011; Blasco et al., 2011; Pérez-García et al., 2017), South West Asia (e.g. Hartman and Horwitz, 2007; Alperson-Afil et al., 2009; Güleç et al., 2009; Blain et al., 2014) and Africa (e.g. Auffenberg, 1981; Braun et al., 2010; Blasco et al., 2011; Karl, 2012; Rook et al., 2013), on the exploitation of reptiles in general, and tortoises and turtles in particular, by early homininds. This is borne out by (i) the close association between Testunid and archaeological remains, (ii) the presence of percussion fractures and burning on their remains, (ii) though less common, the presence of cut marks. It reflects but one facet of the broad spectrum of resources that were recognised and used by a range of different hominids, often on a seasonal basis, in very different ecosystems throughout the world.

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Conclusion

This dissertation comprises four papers relating to the subject of land tortoises (Testudinidae) that inhabit the arid interior of South Africa. An attempt was made to link their present-day ecology with their palaeoecology, which can be defined as the investigation of individuals, populations, and communities of organisms which lived in the past, and their interactions with, and dynamic responses to, changing environments (Rull, 2010). Palaeoecology can thus contribute to our understanding of ecology and conservation biology as it provides insights into past ecosystems, covers long periods of time, and represents systems unaffected by present-day anthropogenic disturbances (Meffe and Carroll, 1997).

This dissertation also contributes to our understanding of the effects of human activities on species, communities, and ecosystems; and enables us to develop practical interdisciplinary approaches to protecting and restoring biological diversity. This is achieved by firstly examining the mortality rate caused by electrified fences to present-day leopard tortoises (*Stigmochelys pardalis*) in the central interior of South Africa, and then secondly, by examining the pattern of tortoise exploitation in a diachronic record spanning over 2.0 Mya, from Wonderwerk Cave located in the Northern Cape Province.

There are numerous factors that affect the survivorship of tortoises in South Africa. Their eggs are destroyed during incubation by ants, dug up and consumed by carnivores, while hatchlings are eaten by various bird species (e.g. Pied Crow, Pale Chanting Goshawk, Verreaux's Eagle), mammalian carnivores such as the black-backed jackal, honey badger, mongooses and monitor lizards (Broadley, 1989; Malan and Branch, 1992; Lloyd and Stadler, 1998; Ramsay, 2002; Branch 2008; Branch et al., 2015). Veld fires also contribute to their demise or cause serious injuries (Broadley, 1989). Humans are an additional negative factor, as tortoises are a common dietary item for many populations worldwide and their products are used for the manufacture of ornaments, musical instruments and traditional medicines, while they are also used as trade items and kept as pets (Schneider and Everson, 1989; Swingland and Klemens, 1989; O'Brien et al., 2003; Kiester and Olson, 2011; Del Papa, 2016).

In South Africa, an additional recent threat that are investigated in this dissertation, are electrified fences. Our results show that large, breeding age adult leopard tortoises experience elevated mortality rates due to electrified fencing. This affects their populations negatively, and may even accelerate extinction rates. This trend should be of great concern for conservationists, and this is confirmed by results of this dissertation. Although, not yet considered as a threatened or vulnerable species, the leopard tortoise's status could change in the near future as the erection of electrified fences grows in popularity around the country (Beck, 2010; Macray, 2017). Should such a change occur, especially if population growth enters a negative phase, it will be very difficult to rectify later on given that tortoises are slow-growing and late-maturing. Sanctuaries, like Grant's Hill in Bloemfontein (described in the introduction), may become a necessity all around the country, to protect tortoises in the long run. Other studies undertaken on the electrocution of leopard tortoises (Burger and Branch, 1994; Beck, 2010; Arnot and Molteno, 2017; Macray, 2017) have only reported on the deaths of the tortoises but did not explore the long term demographic impact of electrified fences on tortoise populations, which is addressed here. The other researchers did however offer some guidelines as to what can be done to prevent these mortalities, such as raising the height of the lowest strand to at least 250 mm so that some of the large leopard tortoise can easily pass by these fences without being electrocuted. Given the clear demographic impact shown here, conservationists need to pressure the authorities responsible for natural heritage to implement a plan of action before it is too late. This should entail putting legislation in place to help regulate electrified fences.

Human consumption of leopard tortoises was a second focus of research in this dissertation, based on examination of the Wonderwerk Cave archaeozoological assemblage. Although South Africa is a hotspot for land tortoises (Hofmeyr et al., 2014), to date relatively little in depth research has been done on their past distributions and pattern of exploitation, especially of Pleistocene or earlier tortoise species that inhabited the interior of South Africa. This dissertation has attempted to fill the gap. It has also led to the creation of a modern osteological tortoise collection that will be accessible to future researchers.

This study has shown that exploitation of leopard tortoise (*Stigmochelys pardalis*) in this area dates back at least ~1 million years, although given the small numbers of remains in archaeological sites dating to this early time period, they may only have served as an occasional food source for early hominids. Most archaeozoological studies of faunal remains from South Africa have tended to focus on the larger mammals as they are seen as supplying the most meat to hunter-gatherer communities, or, as in the case of tortoises, only on remains dating to the late mid-Pleistocene/Holocene. Remains of smaller animals, such as the tortoise, have largely been ignored in palaeoecological studies (exceptions are, for example, Klein and Cruz-Uribe, 1983, 2000, 2016; Klein et al., 1999, 2004; Avery et al., 2004, 2008; Sampson, 1998, 2000; Thompson and Henshilwood, 2014a, 2014b), although abundant amounts of their remains are found at these sites. This dissertation should make researchers aware of the value of analysing all the faunal remains recovered in an archaeological site, including the reptiles, as well as the application and/or development of criteria with which to identify species. In addition to the exploration of the manner in which tortoises were exploited, this dissertation is also the first detailed report on tortoise remains from a South African site that deals in some detail with species identification.

Given that only leopard tortoise was identified at Wonderwerk Cave, we have tentatively suggested that the biogeographic distribution of *Homopus oculifer* and *Psammobates* *femoralis*, species that are currently sympatric with *Stigmochelys pardalis* in the region, may have been more limited in the Pleistocene. If this interpretation is correct, it is a good example of the role of climate in determining the spatial dispersion of tortoise species.

This study required the creation of a comparative osteology collection of modern tortoise specimens comprising of hatchlings, juveniles, sub-adults, adults and even very old individuals (males and females), which has subsequently been accessioned as part of the collections of the Florisbad Quaternary Research Department of the National Museum in Bloemfontein. Currently there are 197 leopard tortoises accessioned into the collection, which is probably the largest collection of complete and partially complete skeletons of this species in the country. This collection served as the baseline for comparison with archaeological remains from the same region and enabled us to CT-scan the limb bones and the shell of a leopard tortoise, the first data set of bone mineral density (BMD) values for a reptile. Therefore, this dissertation has contributed to the dataset of BMD values that can be used by other archaeozoologists and palaeontologists. The results showed that bone density is a key taphonomic agent as can be clearly seen when the obtained data was applied to the Wonderwerk Cave material in this study. Bones differ in size and shape and are uneven in their robusticity. Results of this study confirmed the hypothesis that this unevenness is related to the mineral component of the bone. Bone density mediated attrition means that the less dense (fragile) parts of the bones will break and fracture before the more dense (robust) parts of the bone.

Despite the publication of several guides, atlases (Loveridge and Williams, 1957; Olsen, 1968; Sobolik and Steele, 1996; Plug, 2014) and numerous scientific articles on South African tortoises, there remain gaps in our knowledge concerning the ecology, demography and adaptations of many of the 13 living species, of which three are near-endemic and five are classified as endemic to the region. There is also a need for studies on phylogeography to promote our understanding of past species distributions and present-day trends. In addition, although we report here on mortalities caused by electric fences, the models are used to infer population dynamics based on many assumptions about population parameters from elsewhere. To verify our results, and more importantly to ensure continued survival of the animals, there is an urgent need to conduct demographic studies of populations (including of populations affected by electric fences) to quantify actual extinction risks. Finally, the generation of data on past tortoise populations is of great value as noted by Rhodin et al. (2015) since it "informs our understanding of the impacts of the history of human exploitation of turtles and the effects of climate change, and their relevance to current and future patterns."

The year 2011 was designated the "Year of the turtle" by Partners in Amphibian and Reptile Conservation (PARC), an organization that focuses on groups conserving turtles and tortoises, to help make the public, nature enthusiasts, biologists and managers aware of the dangers facing these reptiles (Kiester and Olson, 2011). More such campaigns are needed worldwide, and in South Africa in particular. Moreover, in South Africa more focus should be put on informing and educating the general public, farmers and even people working in Nature Reserves regarding the dangers to tortoises and this can only be done by researchers pointing out the threats, such as has been done in this dissertation.

It is remarkable how long tortoises have been around and one can only think that they are the most wonderful examples of the "fittest" life forms. It would really be a shame if we undercut millions of years of persistence of a species (or multiple species) that are so well-adapted to their environments through ignorance and lack of suitable legislation.

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Appendix

Appendix 1

List of measurements taken of all the electrified fence mortality specimens. Measurements are in mm.

Appendix 2

University of the Free State Ethics Committee Approval letter.

NMBF No	Location	Sex	Age	SCL/SCL2	CB/CB2	PL/PL2	PB/PB2
2266	Jacobsdal	F	A	380	245	315	245
2267	Jacobsdal	F	A	335	240	290	220
2268	Jacobsdal	F	A	355	260	310	260
2271	Jacobsdal	F	A	330	210	290	195
2277	Jacobsdal	F	A	385	275	335	270
2279	Jacobsdal	F	A	375	245	320	260
2280	Jacobsdal	F	A		220	285	210
2281	Jacobsdal	F	A	375	245	335	240
2282	Jacobsdal	M	A	255	165	230	160
2283	Jacobsdal	M	A			240	140
2284	Jacobsdal	M	A	355	230	320	225
2286	Jacobsdal	M	A	250	180	230	170
2288	Jacobsdal	F	A	365	250	320	240
2289	Jacobsdal	M	A	380	240	345	240
2290	Jacobsdal	F	A	380	255	325	250
2291	Jacobsdal	F	A	315	200	295	200
2292	Jacobsdal	M	A	380	220	320	210
2293	Jacobsdal	M	A	345			
2294	Jacobsdal	F	A	415	325	375	310
2296	Jacobsdal	F	A	510	300	455	280
2297	Jacobsdal	M	A	350	210	305	190
2298	Jacobsdal	F	A	400	260	330	220
2301	Jacobsdal	F	A	385	260	340	245
2302	Jacobsdal	M	A	400	270	330	270
2304	Jacobsdal	M	A	340	220	310	210
2305	Jacobsdal	M	A	340	215	285	190
2306	Jacobsdal	F	A	385	230	350	215
2328	Jacobsdal	M	A	235		215	
2331	Jacobsdal	M	A	335	230	305	230
2340	Strydenburg	F	A	425	275	380	270
2341	Strydenburg	F	A			330	215
2342	Jacobsdal	F	A	390	290	330	260
2343	Strydenburg	M	A			265	175
2344	Strydenburg	M	A			285	190
2346	Strydenburg	M	A	320	205	290	200
2347	Jacobsdal	F	S-A		130	170	120
2352	Jacobsdal	F	A	370	250	330	250
2353	Jacobsdal	F	A	380	250	335	250
2354	Jacobsdal	M	A	310	190	270	185
2355	Jacobsdal	M	A	280	165	240	160
2356	Jacobsdal	M	A	250	165	225	160
2357	Strydenburg	M	A	245	165	225	160
2358	Jacobsdal	F	A	400	255	345	250

NMBF No	Location	Sex	Age	SCL/SCL2	CB/CB2	PL/PL2	PB/PB2
2361	Strydenburg	M	A			240	150
2362	Strydenburg	M	A			230	145
2363	Strydenburg	M	S-A			170	110
2364	Jacobsdal	M	A			360	225
2365	Jacobsdal	M	A	250	160	220	160
2368	Jacobsdal	M	A	330	210	300	200
2372	Jacobsdal	F	A			385	260
2375	Jacobsdal	F	A			260	170
2377	Strydenburg	M	A			290	200
2379	Jacobsdal	F	A			340	240
2380	Strydenburg	M	A			230	150
2381	Jacobsdal	F	A			290	210
2384	Jacobsdal	M	A			305	180
2386	Jacobsdal	M	A		190	265	180
2389	Strydenburg	F	A			305	210
2390	Jacobsdal	M	A			260	170
2395	Strydenburg	F	A			340	230
2400	Jacobsdal	F	A			220	
2401	Jacobsdal	M	A	290	180	260	170
2403	Jacobsdal	M	A	250	175	240	165
2404	Jacobsdal	F	J	135	90	115	80
2406	Jacobsdal	F	S-A	175	120	160	110
2407	Jacobsdal	F	A			330	210
2408	Jacobsdal	M	A	350	250	330	240
2409	Jacobsdal	M	A	320	200	290	200
2410	Jacobsdal	F	A	345	240	315	230
2411	Jacobsdal	M	A	325	230	300	220
2412	Jacobsdal	M	S-A	230	130	205	230
2433	Jacobsdal	M	A	315	200	290	185
2434	Jacobsdal	M	A	380	240	325	240
2436	Jacobsdal	M	A	345	190	300	190
2437	Jacobsdal	M	A	320	200	270	180
2438	Jacobsdal	F	J	180	110	150	110
2439	Jacobsdal	M	S-A	220	14	200	135
2440	Jacobsdal	M	A	300	200	280	190
2441	Jacobsdal	F	A			325	250
2442	Jacobsdal	F	S-A	200	125	175	110
2443	Jacobsdal	F	A		260	330	250
2445	Jacobsdal	M	A	340	210	295	210
2446	Jacobsdal	F	S-A	235	160	220	150
2447	Jacobsdal	M	A	340	215	310	200
2448	Jacobsdal	F	A	400	265	355	265
2449	Jacobsdal	F	A	390	230	370	220

NMBF No	Location	Sex	Age	SCL/SCL2	CB/CB2	PL/PL2	PB/PB2
2518	Jacobsdal	F	A	355		310	
2519	Jacobsdal	M	S-A			200	
2521	Jacobsdal	M	A	300		260	
2522	Jacobsdal	M	A	340		295	
2523	Jacobsdal	F	A	410		360	
2524	Jacobsdal	F	A			345	
2525	Jacobsdal	M	A			275	
2526	Jacobsdal	M	A			410	
2532	Jacobsdal	M	A			320	
2533	Jacobsdal	M	A	300		255	
2534	Jacobsdal	F	A	380		350	
2536	Jacobsdal	M	S-A			180	
2537	Jacobsdal	F	A	330		310	
2538	Jacobsdal	M	S-A	215		195	
2539	Jacobsdal	M	A	375		330	
2540	Jacobsdal	M	A			310	
2541	Jacobsdal	M	A	355		310	
2542	Jacobsdal	M	A			220	
2543	Jacobsdal	M	A			315	
2544	Strydenburg	F	A	390			
2545	Strydenburg	F	A	410		350	
2546	Strydenburg	F	A	375		330	

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2014-11-10

MS SHARON HOLT
COLLECTIONS MANAGER
FLORISBAD QUATERNARY RESEARCH DEPARTMENT
NATIONAL MUSEUM
PO BOX 266
BLOEMFONTEIN
9300

Dear Ms Holt

ANIMAL EXPERIMENT NR: 21/2014 (LETTER OF NOTIFICATION)
RESEARCHER: SHARON HOLT
PROJECT TITLE: BIOMETRY AND MORPHOLOGY OF FOUR MODERN TERRESTRIAL TORTOISE SPECIES CHELONIA, TESTUDINIDAE) SOUTH AFRICA IN COLLABORATION WITH DR LIORA HORWITZ OF THE HEBREW UNIVERSITY, JERUSALEM, ISRAEL

You are hereby kindly informed that the Interfaculty Animal Ethics Committee approved the above at the meeting on 30 October 2014.

ANIMAL	*NUMBER*	*EXPIRY DATE*
Tortoise		

Kindly take note of the following:

1. ***Fully completed and signed applications have to be submitted electronically to viljoenjj@ufs.ac.za and a hard copy has to be submitted too.***
2. ***A signed progress report with regard to the above study has to be submitted electronically to viljoenjj@ufs.ac.za while a hard copy has to be submitted to Ms H Viljoen, Room D115, Francois Retief building, Faculty of Health Sciences. A report has to be submitted when animals are physically involved and after completion of the study. Guidelines with regard to progress reports are available from the secretary and on the Faculty Intranet.***
3. ***Researchers that plan to make use of the Animal Experimentation Unit must ensure to request and receive a quotation from the Head, Mr Seb Lamprecht. A copy of the quotation has to be submitted with the application before the application will be considered for approval.***
4. ***Fifty (50%) of the quoted amount is payable when you receive the letter of approval.***

Regards

....

CHAIR:
INTERFACULTY ANIMAL ETHICS COMMITTEE

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