PHYSIOLOGICAL FLEXIBILITY OF FREE-LIVING AARDVARKS (*ORYCTEROPUS AFER*) IN RESPONSE TO ENVIRONMENTAL FLUCTUATIONS

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DECLARATION

I, Nora Marie Weyer, declare that this thesis was solely composed by myself, that the work contained herein is my own, and that any assistance has been acknowledged and all sources duly referenced. This thesis is being submitted for the degree of Doctor of Philosophy at the University of the Witwatersrand, Johannesburg. It has not previously been submitted for any degree or examination at any other University.

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Signed on **04 June 2018**

CONFERENCE PRESENTATIONS

International conferences

1. **Weyer NM, Hetem RS, Mitchell D, Picker MD, Rey B, Fuller A.** *Aardvark ecophysiology revealed by biologging: Body temperature and activity of an elusive mammal responding to drought events*. Talk presented at the 6th International Bio-Logging Science Symposium, Lake Constance, Germany, 25 - 29 September 2017.

2. **Weyer NM, Hetem RS, Mitchell D, Picker MD, Rey B, Fuller A.** *Kalahari aardvarks on the edge: Drought-induced resource deficiency may compromise aardvark survival under climate change.* Talk presented at the 12th International Mammalogical Congress (IMC-12), Perth, Australia, 9 - 14 July 2017.

3. **Weyer, NM, Hetem, RS, Picker, MD, Fuller, A.** *Heterothermy in aardvarks - a physiological response to environmental stress?* Poster presented at the 5th International Meeting on the Physiology and Pharmacology of Temperature Regulation (PPTR), Kruger National Park, South Africa, 7 - 12 September 2014.

Local conferences

1. **Weyer NM, Hetem RS, Mitchell D, Picker MD, Rey B, Fuller A.** *Kalahari aardvarks on the edge: Drought-induced resource deficiency may compromise aardvark survival under climate change*. Talk presented at the Combined Congress of the Entomological Society of Southern Africa and the Zoological Society of Southern Africa (ESSA & ZSSA), Pretoria, 3 - 7 July 2017.

2. **Weyer NM, Hetem RS, Fuller A, Picker MD.** *Diet and prey abundance of aardvarks in a semi-desert environment - the importance of termites*. Talk presented at the 7th Diamond Route Research Conference, Johannesburg, 18 - 19 October 2016.

3. **Weyer NM, Hetem RS, Picker MD, Fuller A.** *Physiological responses of aardvarks to seasonal fluctuations in the Kalahari.* Poster presented at the Faculty of Health Sciences Research Day, University of the Witwatersrand, Johannesburg, 1 September 2016.

4. **Weyer NM, Hetem RS, Picker MD, Fuller A.** *Physiological responses of aardvarks to seasonal fluctuations in the Kalahari*. Poster presented at the 6th Diamond Route Research Conference, Johannesburg, 20 - 21 October 2015.

5. **Weyer NM, Hetem RS, Picker MD, Fuller A.** *Heterothermy in aardvark - a physiological response to environmental stress?* Poster presented at the 5th Diamond Route Research Conference, Johannesburg, 21 - 22 October 2014.

6. **Weyer NM, Fuller A, Hetem RS, Picker MD.** *How do seasonal fluctuations in prey availability affect the aardvark?* Talk presented at the 4th Diamond Route Research Conference, Johannesburg, 29 - 30 October 2013.

ABSTRACT

Aardvarks (*Orycteropus afer*) are ecological engineers because they dig the burrows that provide shelter for numerous sympatric animals and, as such, are keystone mammals in sub-Saharan Africa. They are nocturnally-active, solitary and elusive. As a result, aardvark ecophysiology is poorly understood, despite their ecological significance. Much of their range is becoming hotter and drier with global climate change, with potential impacts on the aardvarks. A recent drought in the Kalahari in the summer of 2012-13 coincided with high aardvark mortality. The Kalahari semi-desert at the south-western edge of aardvark distribution is the hottest and driest environment currently inhabited by aardvarks. Climate change will likely exacerbate the Kalahari's harsh conditions through increased aridification and higher environmental temperatures. Whether the physiological plasticity of aardvarks will allow them to buffer such changes is unknown.

I therefore studied wild, free-living aardvarks for ~3.5 years (July 2012 to September 2015) at Tswalu Kalahari Reserve, South Africa. Aardvarks were implanted with VHF-tracking units and data loggers to record body temperature and locomotor activity. Camera traps at burrows recorded the aardvarks' times of emergence. I scored aardvark body condition and collected fresh scats for dietary analysis. Aardvarks typically feed exclusively on ants and termites, which depend largely on vegetation productivity. Thus, I assessed prey abundance and availability monthly using pitfall traps and signs of termite surface activity, and assessed vegetation productivity using field-based transect methods and remote-sensing data (MODIS-EVI). I subsequently measured energy and water content of the aardvarks' main prey items.

Harvester termites (*Hodotermes mossambicus*) were the most important dietary item for aardvarks throughout the study period, accounting for ~75 % of prey ingested, and providing ~90 % of water and energy needs. By contrast, research in less arid southern African regions found ants to be the dominant dietary item. Although the aardvarks' regional flexibility in feeding on the most abundant social insects likely improves survival under normal conditions, aardvark well-being in the Kalahari might depend on fluctuations in harvester termite populations. I found that harvester termite abundance correlated with grass availability, which in turn depended on rainfall.

During my study, inter-annual variability in rainfall was high; two good rainfall years occurred which had large amounts of rainfall early in the wet season, resulting in high vegetation productivity. During these years, ant (largely in summer) and termite abundances were high, thus aardvarks obtained sufficient prey to cover their minimum daily energy and water requirements, and were in good body condition. Irrespective of the season, aardvarks in good condition remained nocturnal, and were homeothermic, with a low 24-h amplitude of body temperature rhythm (~2.5 °C; varying from 35 to 37.5 °C). Their body temperature rhythm over 24-h closely tracked that of activity, with body temperature increasing at the beginning of the active phase, and declining at the end of the active phase.

A drought during summer 2012-13 likely resulted in local declines of termite populations, such that aardvarks were no longer able to meet their energetic requirements. A mass mortality of aardvarks occurred at the end of the summer drought, and surviving aardvarks were in poor condition. Nutritionally-compromised aardvarks relaxed the precision of body temperature regulation, resulting in heterothermy with a high 24-h amplitude of body temperature rhythm, primarily because of low minimum 24-h body temperature (~25 °C). These nutritionally-compromised aardvarks became partly diurnal, some shifting activity entirely to the daytime in the weeks leading up to their deaths. In moribund aardvarks, a dissociation of the 24-h rhythm of body temperature and activity occurred, with minimum 24-h body temperatures occurring during daytime activity, and maximum 24-h body temperature while resting at night. By the winter that followed the summer drought, the late and poor summer rains had not sufficed to ensure a complete recovery of the termite and ant populations at Tswalu. The aardvarks displayed exaggerated heterothermy with 24-h amplitude of body temperature rhythm as high as 11.7 °C, the greatest amplitude ever recorded in a large mammal. During this winter, many aardvarks were in poor body condition and started foraging unusually early, during midday, presumably to compensate for their energetic needs. Some individuals basked in the sun outside their burrows for lengthy periods, thereby passively increasing their body temperature and potentially allowing for savings of up to 7 % of daily energy requirements. However, these energy-saving strategies were not sufficient in all aardvarks to prevent death by starvation, and many more individuals died.

This study was the first long-term, and the most comprehensive, study of aardvark diet, behaviour, and thermoregulation in response to prey availability to date. To my knowledge, it was also one of the first studies to record physiological variables in a free-ranging large mammal over a period of more than one year, thereby allowing the assessment of physiological flexibility of aardvarks in response to seasonal and annual changes in the environment. Moreover, it was the first study identifying termites as the aardvark's key prey item, and the first to estimate the aardvark's energetic needs in relation to fluctuating food resources as a result of drought.

Records of body temperature and activity patterns provided useful direct indicators of physiological well-being in aardvarks. Vegetation cover was a useful index of termite abundance, and thus aardvark resource availability. Understanding the physiological and behavioural limitations of animals in arid ecosystems is vital for assessing responses to increased environmental stress resulting from current and ongoing climate change. The anticipated increase in the frequency and intensity of droughts will likely result in a decline in grass biomass throughout Africa, impacting on termites and other herbivores. Termite declines were likely the main cause of the Kalahari aardvark mass mortality following the drought in the summer of 2012-13. I advocate that future environmental stressors such as drought-induced lack of resources, brought about by climate change, pose a greater threat to aardvarks than previously thought. Aardvark extirpation in the Kalahari will likely have severe cascading effects on other animals co-using aardvark burrows.

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Global climate change is occurring at an unprecedented rate and is associated with an increase in the frequency and intensity of extreme weather events such as droughts, floods and storms. Global biodiversity has already been impacted by global climate change, and the demise of many more organisms has been predicted. However, little is known about the capacity of mammalian species to buffer the effects of climate change. In particular, knowledge is lacking on the responses of keystone species to changing environments; their demise may disrupt entire ecosystems through ecological cascade effects. Furthermore, despite the vulnerability of the African continent to global climate change, a dearth of studies on ecosystem responses to the predicted increasing heat and aridity prevails. Within this introductory chapter, I provide an overview of likely responses of large mammals to the challenging environmental conditions expected from climate change. I will focus on adaptations of large mammals to hot, arid regions that are likely to become more prevalent under future climate change, to provide backdrop for the likely impact of climate change on aardvarks (*Orycteropus afer* Pallas 1766), a key ecosystem engineer species in sub-Saharan Africa.

1.1 Climate change

1.1.1 Global climate change

As a consequence of anthropogenic factors, such as elevated greenhouse gas emissions (Crowley 2000; Rosenzweig et al., 2008), mean global temperature has risen by approximately 1 °C since 1901, and it is expected to increase steeply at a rate of 0.1 °C per decade globally (Jones et al., 2012; Pachauri et al., 2014). Not only has mean global temperature risen, but the number of hot days and nights has increased globally, concomitant with a decline in the number of cold days and nights (Alexander et al., 2006). Along with temperature increases, extreme weather events such as droughts and floods have increased in frequency, intensity, and areas affected, and will likely become challenges for ecological responses to climatic changes (Coumou & Rahmstorf, 2012; Le Roux et al., 2016). The period 2011 to 2015 has been the warmest five-year-period on record globally, and numerous extreme weather events including heat waves were attributed directly to climate change by the World Meteorological Organisation (WMO, 2015). The world’s climate has changed in the past, and although the maximum magnitude of the current climate change event has not yet been reached, the rate of modern climate change is already unprecedented, exceeding that of previous climatic changes by orders of magnitude (Diffenbaugh & Field, 2013). Past climatic changes have been linked to extensive species extinctions, such as during the Permian-Triassic or the Cretaceous-Paleogene, and a species’ failure to respond adequately to rapid global climate change can lead to extinction. A global temperature increase of 2 °C by mid- to late 21st century has been proposed as an ecological tipping point above which major ecosystems will be severely and irreversibly compromised (Hoegh-Guldberg et al., 2007). The magnitude of climate change projections is substantially affected by ongoing emissions and is predicted to vary from a mean global temperature increase of 1 °C (range 0.3 to 1.7 °C) to 3.7 °C (range 2.6 to 4.8 °C) by the end of the 21st century (Pachauri et al., 2014). At this point, as a result of combined effects of human emissions, deforestation, inertia of climate processes in the global system, and other factors, the aim of limiting and stabilising the global temperature increase to within 2 °C of pre-industrial levels might have become unattainable unless gross negative emissions are achieved (Fuss et al., 2014). Even so, temperatures over Africa are predicted to increase faster than the global average, with potential severe consequences on ecosystems.

1.1.2 Climatic change in Africa

Temperature in Africa is predicted to increase, on average, twice as fast as in the rest of the world and, under a low mitigation or “business as usual” scenario, will reach the globally ratified temperature increase of the Earth’s mean temperature of 2 °C since pre-industrial times decades earlier (i.e., mid-21st century) than many other regions (Niang et al., 2014). The magnitude of temperature rise has been greater in northern and southern Africa than in other regions, with drier subtropics warming even faster than more humid regions (Engelbrecht et al., 2015; Hulme et al., 2001; Niang et al., 2014; Rosenzweig et al., 2008). Heat waves have become more prevalent in recent decades (Russo et al., 2016). Combined with the increasingly arid conditions over the continent (Engelbrecht et al., 2015; Le Roux et al., 2016), heat waves currently considered anomalous may become the rule by 2040 under the most severe climate change scenarios (Russo et al., 2016).

Rainfall over Africa has shown a decreasing trend and a progressively delayed onset of the rainy season since the mid-20th century, and although different climate prediction models show rather divergent patterns for the magnitude and direction of future rainfall changes, the general consensus is that a further decline in precipitation is anticipated over much of the continent (Alexander et al., 2006; Hulme et al., 2001; Kniveton et al., 2008; Niang et al., 2014). Predictions for rainfall patterns over southern Africa remain largely varied and uncertain (Hewitson & Crane, 2006; England et al., 2014; Maidment et al., 2015); however, with greater warming, rainfall is becoming less, and less frequent, in the western parts of southern Africa, notably the Kalahari semi-desert (Shongwe et al., 2009; James and Washington 2013; Niang et al., 2014).

1.1.3 Southern Africa

The southern African sub-region is predicted to experience particularly rapid rates of warming compared to the remainder of Africa, with strongest effects on the semi-arid south-western parts of Botswana and Namibia, and north-western South Africa, including the Kalahari (Niang et al., 2014). Pronounced temperature increases of up to 3.5 °C during the last four decades have already been recorded in north-western South Africa (Rosenzweig et al., 2008). An average temperature rise of twice the global rate has been occurring in southern Africa since the 1950s and is predicted to continue, resulting in a temperature rise of up to 4 to 6 °C by the end of the 21st century if climate change mitigation remains limited (Engelbrecht et al., 2015).

In addition to warming temperatures and changing rainfall patterns, southern Africa is strongly affected by the El Niño / Southern Oscillation (ENSO) phenomenon, with warm ENSO-events resulting in lower-than-average rainfall across the region, especially during the December-February wet season (Hulme et al., 2001). Warm ENSO-events are linked to drought conditions and decreased primary productivity in southern Africa, a relationship which has been strengthening since the 1970s (Anyamba et al., 2002; Richard et al., 2000; Rouault & Richard, 2005; Woodborne et al., 2015). With increasing anthropogenic emissions, ENSO-events are likely to become more frequent and intense (Timmermann et al., 1999). Southern Africa has experienced several intense, hot drought years recently (2013 to 2017; some of which were linked to ENSO-events), with years during the drought period sequentially breaking historical aridity records and resulting in the worst drought period in a century (Beraki, 2016; Rouault, 2017; Van Dam, 2017). This multi-year drought has resulted in large areas of South Africa recently having been declared a disaster area, and the recovery period is deemed to take several years (De Villiers, 2017; Ferreira, 2017; Reuters, 2017; SA-News, 2017).

Water availability is the main driver of ecosystem processes in hot, arid regions, particularly in the Southern Hemisphere (Chown et al., 2004), and timing and amount of rainfall are major determining factors for vegetation dynamics. Synergistic effects of drastic warming, amplified soil desiccation, and delayed rainfall onset will result in prolonged dry periods and shortened productive periods, effectively causing agricultural drought (Engelbrecht et al., 2015; Shongwe et al., 2009). Under future climate scenarios, hot arid zones of southern Africa are projected to expand, together with a prolonged dry period in southern Africa (May to December), effectively bringing about a shorter growing season (Engelbrecht et al., 2015; James & Washington, 2013; Shongwe et al., 2009). The combination of reduced growing time and increasing atmospheric CO_2-levels may lead to a replacement of grasslands in African savannahs with savannah trees in areas of sufficient rainfall (Engelbrecht & Engelbrecht, 2016; Higgins & Scheiter, 2012), resulting in bush encroachment or, in more arid regions, degradation and eventual desertification of grassy habitats. As another consequence of southern Africa's changing climate, dune fields in Namibia and western South Africa are expected to remobilise during this century (Thomas et al., 2005), and combined with increasing warming and aridification, may further accelerate desertification of the neighbouring Kalahari (Darkoh, 1998) or other grasslands in Namibia (Ward & Ngairorue, 2000). This process will result in degraded habitats with decreased carrying capacity for animal species, and ultimately loss of biodiversity. The precise impacts of chronic exposure of organisms and the environment to high temperatures and aridity are yet to be understood.

1.2 Biological impact of climate change

In dealing with environmental change, organisms may (1) perish, resulting in local or complete extinction, (2) track their bioclimatic envelope by migrating and shifting their geographic range, or (3) adapt to the changes either through alterations in the genetic composition of the population, or by employing phenotypic plasticity (Holt 1990; Davis et al., 2005; Hoffmann and Sgrò 2011). Organisms respond to environmental changes in many ways, including range shifts, changes in relative abundance within their geographic ranges, and on the level of the individual, changes in activity timing and microhabitat use (Williams et al., 2008). Individual species are likely to respond differently, thereby disrupting ecosystem structures. Species that remain in one location because they are able to adapt to climatic changes or are unable to move will face novel interactions with other, more-mobile species, or habitat disturbances (Walther et al., 2002; Jetz et al., 2007; Atkins & Travis, 2010; Hof et al., 2011). Some communities are already showing responses in the form of novel species assemblages that can be linked to climate change (Walther et al., 2002). Additionally, man-made degradation and fragmentation of habitats exacerbate the effects of climate change, and may act as barriers to migration of animals responding to altered climates (Walther et al., 2002). Land degradation, desertification, and climate change in semi-arid environments of southern Africa threaten the continued existence of animals adapted to life in these habitats (Walsberg 2000; Thuiller et al., 2006). The geographic range of a species is linked to its physiological tolerance to its abiotic environment, dispersal constraints, and biological interactions with other species (Peterson et al., 2011). Just 30 years of elevated temperatures at the end of the 20th century have already had both large-scale impacts on range and distribution of species, their relative abundance within their range, and composition and dynamics of communities, as well as more subtle effects on shifts in the phenology, behaviour or allelic selection of organisms (Walther et al., 2002; Williams et al., 2008).

Climate change can have direct (changing temperatures or water availability for thermoregulatory and osmoregulatory needs), and indirect (changing food availability or changing species interactions) impacts on vertebrates. These climate-related impacts can act in combination with other factors unrelated to climate, such as man-made habitat alterations (Tylianakis et al., 2008), and may exacerbate extinctions risk (Cahill et al., 2012). In addition, direct culling and hunting of large mammals is a key driver of large mammal extinction globally (Milner-Gulland & Bennett, 2003; Cardillo, 2005; Hoffmann et al., 2011; Ripple et al., 2017). Such peripheral effects can mask the direct impacts of climate change on species, such that the number of species threatened by climate change might be severely underestimated. Cahill et al. (2012) conducted an extensive review of the literature on species whose local or total extinctions had been attributed to current global climate change, and identified 136 relevant studies on climatic impacts on species. The authors raised the concern that in only seven instances was climate change named as the proximate cause of species' declines or extinctions, but that the actual numbers of species declines likely were greater than those estimated, because climate change-linked alterations in species interactions were another important cause of population declines (Cahill et al., 2013). A recent study on climate change impacts on endotherms estimated that nearly half of all mammal and a quarter of all bird species classified as 'Threatened' on the Red List of Threatened Species^{TM} of the International Union for Conservation of Nature (IUCN) have already been negatively affected by compounded effects of climate change in terms of population size, reproduction and survival, body size, or geographic range size, and that their life-history traits will have a strong influence on their future survival (Pacifici et al., 2017). Of the mammals included in this study, the groups most negatively affected were those in low rainfall regions, with a long life-span, slow reproduction, and a specialised diet (Pacifici et al., 2017).

1.2.1.1 Extirpations and extinctions

The first mammal reported to have gone extinct as a result of direct effects of anthropogenic climate change was the Bramble Cay melomys (*Melomys rubicola*) in Australia (Gynther et al., 2016). The recent extinction of this small rodent and only mammal endemic to the northernmost vegetated cays of the Great Barrier Reef was attributed to climate-change related sea-level rise eliminating its habitat. Extirpation of the mountain pika (*Ochotona princeps*), a small mammal in western North America, has also been attributed to climate change, with extirpation and upslope range retraction in much of its geographic distribution due to climate-change linked habitat warming (Beever et al., 2016). As much as 15 to 37 % of species are estimated to be committed to extinction by mid-21st century as a result of the current rapid climate change event (Thomas et al., 2004). With more intense changes yet to be anticipated, extinctions will likely become more prevalent in all habitats, clades, and regions as the impacts of ongoing global climate change unfold (Wiens, 2016). This recent study assessed the number of climate-related local extinctions reported among 976 plant and animal species worldwide (Wiens, 2016). The study reported that to date, nearly one-half of these species showed extirpations at the warm edge (low elevations and latitudes) of their distribution. Approximately half of all species had undergone extirpations in response to climate change despite the modest increase in global mean temperature of ~1 °C to date, with great potential for further extinctions under progressing warming (Wiens, 2016). Of the 40 mammal species surveyed, 35 % had suffered local extinctions (Wiens, 2016).

Knowledge on the extent of animals' adaptability to the projected changes in global climate via behavioural, physiological, range modification, and genetic options is limited and inconsistent across animal groups around the world (Erasmus et al., 2002, Thuiller et al., 2006). However, several studies have modelled likely consequences of climate change, such as extinction risk, on African mammals (Erasmus et al., 2002; Thomas et al., 2004; Thuiller et al., 2006). According to these models, southern Africa may experience not only drastic changes in species composition of communities, but also high local extinction rates of mammal species, as well as species distribution shifts, during the 21st century (Erasmus et al., 2002; Thomas et al., 2004; Thuiller et al., 2006). The number of southern African mammal species classified as critically endangered or extinct might increase by 15 % by 2050, and by up to 40 % by 2080 (Thuiller et al., 2006). Predictions for mammals in the arid Kalahari that are unable to move are even more extreme: up to 80 % of species might be lost from this region by 2050, and, under worst-case scenarios, up to 100 % of species might be extinct by 2080 (Thuiller et al., 2006). The reasons proposed for these local extinction predictions include (1) land degradation and habitat loss resulting from climatic changes, (2) inability of species to adapt fast enough to the rapidly progressing changes in their environment, (3) restricted possibilities for larger animals to migrate through migration corridors, and (4) limited ability of some species to change their location to a more suitable habitat as a result of their body size, lifestyle, or confinement to territories (Thuiller et al., 2006). In this study, transformed habitats and future climates were incorporated into models and animals were allowed to freely disperse or not; however, this study did not include mechanistic responses of animals to a changing environment. Thus, the predictions for species declines and extinctions may not hold if certain species are able to adapt rapidly to environmental change, for example through range shift or migration, phenotypic plasticity, and genetic adaptations.

1.2.1.2 Range shift and migration

Extinction risks of many animal species are higher if animals are unable to move - in turn, an option for species confronted with climate change is to track their bioclimatic niche or escape unsuitable conditions by shifting their geographic distribution. As climate change progresses, species are predicted to move upward in latitude (poleward) or in altitude (upward along mountain slopes). Extensive documentation of species changing their distribution in such directions exists for terrestrial and marine animals and plants (Parmesan, 2006; Parmesan et al., 2000; Pecl et al., 2017; Root et al., 2003). However, the success of relocation depends on a variety of factors. Firstly, to actively seek new and more suitable habitats, a species must have a high degree of vagility, but territorial animals may be less inclined to disperse to new areas. Also, the mobility of a species might determine the rate at which it can relocate. Large animals may be able to redistribute more easily than smaller species simply because of their size, while flying animals such as bats may be able to move more freely than other, non-volant terrestrial species. Indeed, shifts in the breeding range of certain Australian flying fox species have been attributed to recent climate change (Steffen et al., 2009).

The dispersal of species can be hampered by numerous external factors, such as habitat fragmentation (natural or anthropogenic), fencing, hunting, or poaching (Travis, 2003; Opdam & Wascher, 2004). In Africa, these factors have been cause for concern regarding large mammal species such as elephants and ungulates, which naturally migrate across long distances at regular intervals and whose numbers have been in decline in recent decades and may decline further with climate change (Galanti et al., 2006; Ogutu & Owen-Smith, 2003; Ogutu et al., 2011, 2014). If migration routes or corridors are disturbed or suitable habitats lack connectivity as a result of movement barriers such as fences or expanding infrastructure and agriculture, species may not be able to reach suitable, existing colonisation areas. For many species, even a successful migration does not guarantee survival and establishment of the population at a novel location, where various ecological factors such as availability of climatic refuges, resource availability, predator-prey interactions, competition, and disease come into play (Berg et al., 2010; Dobrowski, 2011; Lenoir et al., 2017). If a species' movement is only gradual or disrupted, it is likely to lag behind the effects of climate change, and might not reach suitable environments fast enough (Santini et al., 2016). Such lag patterns are likely to be found in habitat specialists and organisms with poor dispersal or colonisation ability (Travis 2003; Santini et al., 2016). A study of terrestrial mammals in the Western Hemisphere suggests that, on average, nearly 10 % of mammals at any given location will not be able to move their range fast enough to keep track with suitable climates while in some areas, up to nearly 40 % of mammals might be affected due to the rapidity of climate change in some regions, and low dispersal ability of some species (Schloss et al., 2012). The geographic ranges of the majority of mammal species might undergo contraction, and inability to keep pace with shifts of suitable climates will render mammals more vulnerable than previously thought (Schloss et al., 2012). Immigration of some species may affect the reproductive success of other, local species by changing predation risk, as was observed in African herbivores (Lee et al., 2016). A rare example of a mammal having potentially benefited from climate change-related desertification in Africa is the arid-adapted Cape fox (*Vulpes chama*), which has recently expanded its range into northern Botswana. This (potentially ongoing) range expansion most likely resulted from increasingly arid conditions causing a more open environment (Rich et al., 2016). However, the novel interactions that the Cape fox may face in the newly-acclaimed area of its range have not been assessed, but might have long-term impacts on the persistence of the Cape fox as well as resident species in this area.

1.2.1.3 Genetic responses

For organisms to genetically adapt to a changing environment, they need to incorporate minor evolutionary changes or adaptive modifications, generally defined as microevolution, such as a heritable shift of allele frequencies at the population level. Some evolutionary responses to climate change have already taken place in small animal species, such as invertebrates or short-lived vertebrates (Bradshaw and Holzapfel 2006; Skelly et al., 2007). However, until recently, very few studies had investigated the link between genetics and observed responses, instead, this link was simply assumed to exist. A classic study on red squirrels (*Tamiasciurus hudsonicus*) highlights that a single response (in this case, a change in phenology) can have both a genetic and phenotypic component (Réale et al., 2003). Nevertheless, evolutionary responses are likely limited to animals with fast reproduction rates, short generation time, and high numbers of offspring, because the rate of climate change is too rapid for species with long life history traits (Fuller et al., 2016). Recently, an unexpectedly fast change in genetic diversity was observed in a large mammal, the Canada lynx (*Lynx canadensis*), whose genetic variability was linked to a winter snow cover gradient (Row et al., 2014). However, in long-lived species and particularly in large mammals, predicted environmental changes will likely occur during their own lifetime (Mitchell et al., 2008), rendering genetic responses inadequately slow. The reproductive traits of large mammals such as long gestation times, delayed sexual maturity, low breeding frequency, and small litter sizes limit the potential for hereditable adaptive responses to the very rapid rates of current climate change (Fuller et al., 2016). Large mammals are therefore required to pursue alternative, faster routes of adaptation to allow their survival through climate change.

1.2.1.4 Phenotypic plasticity

Many species will be unable to adapt genetically at a rate fast enough keep up with the rapidity of environmental change under climate change, and numerous of these species will also not be able to shift their distribution in response to global climate change, largely because of human barriers to dispersal, and fragmented habitats. Phenotypic plasticity is the ability of an organism to cope with environmental variation by producing alternative phenotypes that are based on the same genotype in different environments (Garland Jr. & Kelly, 2006).

Phenotypic plasticity may be reversible, differ between individuals of a species or population, and occur in cycles (for example, seasonally), and can further be categorised as (1) developmental and (2) phenotypic (Piersma & Lindström, 1997; Piersma & Drent, 2003), although the term phenotypic flexibility might be considered more appropriate because of its reversibility. In large mammals, developmental plasticity includes processes that are controlled by maternal effects, such as plasticity in offspring birth mass in response to changing climate conditions. For example, antelope species in the Northern Hemisphere show plasticity in offspring birth mass in response to environmental change (Stenseth, 2002). Though this effect may enhance reproductive fitness of the mother and ensure the continuance of the population, long-term trade-offs for the offspring are likely. What is more, such plasticity in development usually only occurs once in the lifetime of an individual (namely during development) and thus only once per generation (Nussey et al., 2007). Hence, similar to genetic adaptation, developmental plasticity likely is too slow an option for many large mammals to allow for rapid adaptation to climate change.

Many published examples exist on how animals change the phenology, or timing of life-cycle events, such as reproduction, in response to environmental change. Phenological changes are often complex, and indeed, the direction and rate of such changes may not be adequate to counter climate change in mammals (Boutin & Lane, 2014). In addition, depending on the cues for life cycle events, a mismatch may result between resource availability and breeding periods. For example, most plants respond to changes in temperature, which changes with climate change, whereas many life cycle events of mammals respond to photoperiod, which does not change with climate change. Phenological changes might thus be insufficient to buffer effects of climate change. Phenotypic flexibility includes reversible variations in behaviour, physiology and morphology of an individual responding to irregularly varying environmental conditions (Piersma & Drent, 2003). Phenotypic flexibility will most likely be the primary option of long-lived, large mammals to cope with changes in their natural habitat, since they are likely to experience impacts of climate change during their own lifetime and do not have enough time to rely on slow processes of genetic adaptations to take action (Fuller et al., 2016). Another lifestyle trait that may impact the adaptive capacity of mammals to climate change is inflexibility of their daily activity patterns (McCain & King, 2014). Thus, a combination of behavioural and physiological adjustments will contribute to resilience and adaptive capacity of free-living large mammals, and ultimately determine their vulnerability to future changed climates (reviewed in Hetem et al., 2014; Fuller et al., 2016).

1.3 Effects of climate change on large mammals

Certain life-history traits of large mammals, such as slow reproduction and long life-span, are linked to high extinction risk (Johnson, 2002). Large mammals have in the past been disproportionately impacted by extinction events (Johnson, 2002; Morrison et al., 2007; Davidson et al., 2009; Ripple et al., 2015; Galetti et al., 2017). Large mammals play fundamental roles in many ecosystems, often generating trophic cascades (Ripple & Beschta, 2003, 2006; Côté et al., 2004; Owen-Smith & Mills, 2008). In the following sections, I will describe impacts of climate change on large mammals, and the adaptation options that might mitigate impacts of climate change.

1.3.1 Direct effects of increasing aridity as caused by climate change

Despite impending threats of extinction from climatic warming on populations at the warm edge of their distribution (i.e., low elevations and latitudes, Cahill et al., 2013) especially on large mammals in Africa, where temperatures are expected to rise particularly rapidly (Pachauri et al., 2014), little is known about the capacity of large mammals to cope with seasonal changes and climatic extremes. Phenotypic flexibility will likely include physiological and behavioural adaptations to reduce heat stress (thermoregulation) and conserve body water (osmoregulation). The flexibility of thermoregulatory and osmoregulatory responses will likely gain importance in the light of current and future climate change. In deserts and semi-deserts, animals may be expected to have evolved some degree of physiological capability to the natural environmental extremes in air temperature and rainfall. An unknown, however, is the extent to which animals in hot and arid zones will be able to cope with further increases of heat and aridity in their environment, at levels of intensity not apparent prior to current climate change.

Alterations in behavioural thermoregulation may buffer animals against a warming environment (Kearney et al., 2009), and generally come at a lower metabolic cost than autonomic adjustments (Bartholomew, 1964). While air temperature is lower than body temperature, endotherms commonly lose metabolic heat through non-evaporative or dry heat loss. However, when ambient temperature exceeds body temperature, endotherms must employ evaporative cooling to achieve heat loss. Large mammals commonly cope with such high heat loads through sweating, panting or skin-wetting, all of which are dependent on water availability (Fuller et al., 2016). Limited supply of surface water in hot and arid environments will impede evaporative cooling mechanisms in large mammals, forcing them to depend on water-efficient thermoregulation avenues and to reduce heat exposure.

Perhaps the most common behavioural response to heat is shade-seeking to avoid heat gain from solar radiation. In one of the world's hottest regions, the Arabian desert, Arabian oryx (*Oryx leucoryx*) retreated to shade from early morning onward to pass the hottest hours of the day, thereby reducing the need for evaporative cooling (Ostrowski et al., 2003). Arabian oryx further increased their water savings by preferring cooler microclimates in drier periods than in wetter periods when drinking water was available (Hetem et al., 2012a). In North America during summer, grizzly bears (*Ursus arctos horribilis*) preferred cooler tree stands during hotter parts of the day, thereby avoiding heat exposure (Pigeon et al., 2016). Some large mammals can create their own microclimates, such as wombats (e.g., hairy-nosed wombats *Lasiorhinus latifrons*), which rest in self-dug burrows during the heat of the day and emerge late in summer to exploit the coolness, but adjust their activity timing during cooler periods of the year such that they become active earlier in the day, and are active for longer times (Finlayson et al., 2003). By delaying the onset of evaporative cooling, such heat-avoidance responses may save animals considerable amounts of body water, which is of high priority in a hot, arid environment: the oryx likely reduced water loss by up to 19 % (Ostrowski et al., 2003). However, time spent in cooler locations to preserve water may limit the time animals can spend on other fitness-enhancing activities, such as energy acquisition, territory maintenance, mating, or offspring care. Moreover, not all species are equally able to switch from daytime to night-time activity because of limiting adaptations, predator or competitor presence, or reduced prey availability at night (Kronfeld-Schor et al., 2001; Fuller et al., 2016).

If species are unable to entirely buffer heat loads through appropriate microclimate selection, they might have to alter autonomic thermoregulatory responses. Some mammals might allow their body temperatures to rise when facing water scarcity, a mechanism termed dehydration-induced hyperthermia (Fuller et al., 2016; Hetem et al., 2016). However, hyperthermia may impair the performance of mammals and put them at risk of heat illness (Fuller et al., 2016). In recent decades, the increasing rate and intensity at which heat waves occurred in already hot regions of the world have caused mass mortalities of endotherms. Perhaps the most well-known events are the catastrophic mass mortalities of populations of birds (Finlayson 1932, Keast 1960, Miller 1963, McKechnie & Wolf 2010) and flying-foxes (*Pteropus* spp., Welbergen et al., 2008) during climate change-related heat waves in Australia. Extreme heat prevented these animals from maintaining homeostasis, and they died of dehydration and hyperthermia (McKechnie & Wolf, 2010). During a heat wave in Queensland, up to 63 % of the koala (*Phascolarctos cinereus*) population died of heat stress and dehydration linked to a decline in foliage quality, from which koalas usually obtain fluids (Gordon et al., 1988). The recovery of the koala population was prevented by continuing drought conditions for several years (Gordon et al., 1988). In India, recurring unprecedented droughts and heat waves between 2000 and 2016, with record temperatures of 52.4 °C in 2016 (WMO 2015; Mazdiyasni et al., 2017), have killed several thousand humans and countless domestic animals such as dogs (Bhatti, 2015; Reuters, 2015). North American pika are sensitive to heat stress (MacArthur & Wang, 1973, 1974; Stafl & O'Connor, 2015), and have undergone reductions in distribution in response to changes in ambient temperature and water availability (Beever et al., 2016). Such direct heat-related calamities underline the importance of investigating consequences of increasing ambient temperatures and aridity on animal populations, as well as the thermal physiology of free-living individuals (Walsberg, 2000).

Warmer winters have also been of benefit to some mammals both directly through temperature changes and indirectly through food abundance changes. For example, wild boars (*Sus scrofa*) have increased reproduction in response to climate change-related milder winter temperatures as well as to climate-change mediated increasing frequency of beech nut mast events in Europe in recent decades (Vetter et al., 2015). While such studies integrating direct and indirect ecological effects of climate change on species or ecosystems are scarce, they nevertheless highlight the need for a better understanding of the complex cascading effects of climate change.

1.3.2 Indirect climate change impacts through ecosystem changes

Different responses of organisms to climate change will cause variation in the patterns and pace of range shifts, alterations in population size and structure, and variation in individual performance and behaviour, which in turn will result in novel biotic assemblages as current interactions fall apart and new ones arise (Gilman et al., 2010; Chen et al., 2011). Modifications in trophic interactions (predator-prey dynamics, plant consumption, parasitism), host-distributions, mutualism and inter- and intraspecific competition may have considerable impacts at all community levels (De Ruiter et al., 1995; Cahill et al., 2012). These factors need to be integrated into assessments of climate change impacts on species responses (Araújo and Luoto 2007; Alexander et al., 2015). Species composition might indeed change at such a great scale in response to climate change that the functionality of entire ecosystems might be impeded (Lawler et al., 2009).

1.3.2.1 Changes in trophic interactions

Decreasing food availability has been identified as a relevant proximate cause of climate change-related extinctions (Cahill et al., 2012), and climate change impacts on biodiversity in ecological networks may be amplified if trophic cascades between levels of producers (plants) and consumers (animals) are disrupted (Schleuning et al., 2016), with impacts increasing with trophic level (Voigt et al., 2003). Indeed, adverse impacts of climate change via trophic cascades have already manifested in a plant-herbivore-predator association that is highly dependent on synchrony of productivity: earlier springtime warming induced a disruption of growth cues for oak trees that provide food for caterpillars, which in turn are the prey of a songbird. The moth displayed phenotypic plasticity in that its biomass peak advanced in step with its plant food availability (Visser & Holleman, 2001). The birds, however, responded to different springtime cues and were thus unable to match the timing of their reproduction with peak availability of moth caterpillars as food for chicks (Visser et al., 1998). Such disparity between reproduction timing and resource abundance through three or more trophic levels may negatively affect population viability. Some published examples describe the effects of climate-induced resource reductions on primary consumers that will likely be amplified in future climatic conditions. For example, Malayan sun bears (*Helarctos malayanus*) experienced a major loss of habitat and important food trees as a result of drought and fire events throughout Indonesia associated with ENSO-events (Fredriksson et al., 2007). However, little is known about the cascading impacts of climate-induced resource reductions on mammalian consumers, and consequences on secondary consumers.

Range shifts of many plant species will not be able to keep up with the rapid rate of climate change (Foden et al., 2007; Corlett and Westcott 2013), resulting in a geographic discrepancy of resource availability and consumer presence. In dry ecosystems, where precipitation is a key driver of plant productivity, future precipitation decline will likely reduce or change vegetation cover, thereby potentially impacting herbivores. For example, decreased rainfall resulted in changed plant community assemblages, leading to reduced food availability for desert bighorn sheep (*Ovis canadensis*), and in synergy with other factors such as anthropogenic habitat degradation, might increase the risk of the bighorn sheep's extirpation or even extinction (Epps et al., 2004; 2006). Drought-conditions stemming from increased heat and aridity often have severe impacts on resource availability, particularly in arid regions, such that endotherms are faced not only with reduced access to water, but also to food energy, requiring the use of additional physiological and behavioural mechanisms to preserve energy (Fuller et al., 2016). The maintenance of body temperature at high, narrowly controlled ranges is energetically costly. Many endotherms reduce their minimum 24-h body temperature in response to food shortage, resulting in heterothermy. This phenomenon is well-described for small endotherms that make use of daily torpor (daily heterotherms, reviewed in Geiser et al., 2008; Ruf and Geiser 2015, but not described in detail here), and also occurs in large mammals that do not undergo torpor (reviewed in Hetem et al., 2016). For example, numerous large mammals inhabiting hot-arid zones such as antelope (Hetem et al., 2010, 2012b) and western grey kangaroos (*Macropus fuliginosus,* Maloney et al., 2011) exhibited progressive declines in body temperatures in response to resource scarcity, likely as a response to energy deficit. Similar patterns were observed in some large cold-zone mammals such as polar bears (*Ursus maritimus,* Whiteman et al., 2015) and alpine ibex (Signer et al., 2011). Allowing body temperature to decline may result in considerable energy savings, however these savings might not suffice to sustain a large mammal through prolonged drought and resource scarcity. Blue wildebeest (*Connochaetes taurinus*) and Arabian sand gazelle (*Gazella subgutturosa marica*) died after displaying hypothermic heterothermy over several days when resources were scarce (Hetem et al., 2016). In the case of the sand gazelle, a mass mortality of up to 50 % of the resident gazelle population was recorded at the same time as the study individuals' deaths after an exceptionally hot and dry period with scarce resources (Hetem et al., 2012b).

Climate change-related reductions in primary productivity may also have bottom-up effects on predators (Letnic et al., 2005) and, with climate change, species may not only track climatic conditions suitable for them, but also the distributions of accessible resources. Predators may obtain fluids from prey to supplement their water intake while at the same time covering their energy requirements, and may in future track their prey distribution rather than their climatic niche (Thuiller et al., 2006). As an example, leopards (*Panthera pardus*) in the African Kalahari semi-desert can go without drinking water for up to 15 days if they hunt successfully (Bothma & Le Riche, 1984). However, as many habitats become hotter and drier, sources of both drinking water and food will likely decline, while the demand for water will increase due to greater water loss required for evaporative cooling. At the same time, higher energy and water expenditure during activity in search of prey may offset any energy or water savings obtained from consuming prey fluids, potentially even compromising the animal´s metabolic balance (Fuller et al., 2016).

1.3.2.2 Habitat alterations

All of the Earth´s ecosystems are influenced by human activities in some way, and the consequences of our direct, local alterations such as land transformation for agricultural purposes, interact strongly with our global environmental impacts, including emissions-associated climate change (Vitousek, 1997). While in some habitats, especially at higher latitudes, biodiversity will predominantly be affected by climate change, in other regions it will be more strongly altered through effects of land use change, such as in the Atlantic forest of Brazil and the Amazon basin in South America (Sala, 2000). Here, drought risk is greatest in areas of most active deforestation: indeed, large-scale reductions in forest cover (caused by deforestation and fires) induce rainfall reductions and exacerbate drought risk in the Amazonian forest biome (Baidya Roy and Avissar 2002; Andreae 2004; Malhi et al., 2008). The combined effects of deforestation and climate change on the charismatic mammal fauna of Central and South America are becoming increasingly severe. For example, because giant armadillos (*Priodontes maximus*) are facing an ongoing decline of habitat size and quality, as well as impacts of hunting, and a declining number of mature individuals, they have been categorised as ‘Vulnerable’ by the IUCN (Anacleto et al., 2014). For some Central and South American mammal species, including giant anteaters (*Myrmecophaga tridactyla*), giant armadillos, and three-banded armadillos (*Tolypeutes tricinctus*), 10 % or less of their present distributions will remain protected under climate change scenarios, with little connectivity between occupied patches (Zimbres et al., 2012). Of course, the impacts of habitat change are not necessarily always entirely negative: some mammals, such as the aforementioned southern African Cape fox (*V. chama*) or the North American red fox (*V. vulpes*) have expanded their ranges in response to changing conditions (MacPherson 1964; Berteaux et al., 2015; Rich et al., 2016; see sections 1.2.1.2 and 1.3.2.3). Increased aridity is typically associated with habitat degradation, reduced primary productivity, fewer trees, and thus less shade availability. Such degraded habitats generally have lower carrying capacity, and likely impose greater physiological stress such as higher water requirements, on animals than do intact rangelands (Hetem et al., 2011; Milton et al., 2013). Many mammals other than the Cape fox will thus more likely reduce their range in response to increasing aridity.

1.3.2.3 Changes in interspecific competition

Not only are interactions across trophic levels likely to be disrupted, so too are species interactions within a trophic level, for example through inter- and intraspecific competition, as well as new assemblages of predator and prey species. Range expansions can also bring about a variety of impacts on potential prey or competitive species that had not previously been confronted with this predator, and knowledge merely on the presence or absence of an organism in an ecosystem does not suffice to adequately forecast the potential impacts (Chapin et al., 2000). Since the early 20th century, the geographic range of red foxes in North America has been extending northward. The resulting range overlap with that of Arctic foxes (MacPherson, 1964) has led to increased competition for resources (Hersteinsson & MacDonald, 1992), interspecific killing, and even predation (Pamperin et al., 2006) to the disadvantage of Arctic foxes, causing a northward retraction of the Arctic fox' southern range boundary. Further stress has been imposed on Arctic foxes as a reduction in the geographic range of grey wolves (*Canis lupus*) resulted in decreased carcass availability for the Arctic fox (Hersteinsson et al., 1989).

Changes in species distribution may cause changes in predation patterns, such as asymmetrical intraguild predation, for example of red foxes prey upon young and adult Arctic foxes but not vice versa, and might be an extreme form of competition, where predation may eliminate a competitor (Palomares and Caro 1999; Pamperin et al., 2006). This form of intraguild predation is likely to occur more often as the range of red foxes increases with the ongoing warming of the Arctic zone. Moreover, when denning, Arctic foxes tend to avoid areas where red foxes co-occur (Tannerfeldt et al., 2002). The recent range overlap of these foxes in the Arctic zone might, however, not only be of advantage for the red fox, as Arctic foxes are known to transmit rabies, and increased physical encounters between the two foxes will increase the likelihood of disease transmission and spread (Pamperin et al., 2006).

Recently, another example of a predator expanding its range into that of a potential competitor has been reported for leopards of Nepal: for the first time, a common leopard (*P. pardus*) was sighted in the same habitat on the Tibetan plateau as the snow leopard (*P. uncia*). Occurrences of common leopards at higher-than-usual altitudes match predictions of species' ranges extending upwards in altitude as climate change progresses (Singh Khadka, 2017). However, it is unknown how increasing range overlap with common leopards will affect the endangered snow leopard, which is already facing the threats of habitat loss and hunting (Jackson et al., 2008).

Alterations in species interactions (notably trophic interactions and interspecific competition) are likely to be even more important than the direct impacts of a changing climate on species (Ockendon et al., 2014). However, the complexity of this relationship demands a better understanding of species responses to a changing environment through long-term field studies that quantify the capacity of populations to respond to change and identify keystone species that may be particularly vulnerable.

1.3.3 Animal species at particular risk from climate change

Some animals may be at greater risk from climate change impacts than others due to certain lifestyle traits, or because they occupy habitats more strongly affected by climate change. Those populations living at natural boundaries of the species' range are often living under climatic conditions at the limit of this species' physiological tolerance (Parmesan et al., 2000). These individuals are more likely to experience extreme weather events than those living in the interior of the species' range, as well as diminishing resource availability, and ultimately will experience decreased fitness (Carter and Prince 1988; Brown et al., 1996; Hoffman and Parsons 1997; Parmesan et al., 2000). Hence, climate change could drive extinctions and extirpations particularly at the warm edges of species distributions (Parsons 1990; Cahill et al., 2012, 2013).

Until recently, animals viewed at particular risk were ectotherms of tropical forests, such as amphibians, reptiles (Huey et al., 2009; Urban 2015) and invertebrates (Kingsolver et al., 2013), because ectotherm species are dependent on temperatures in their external environment, and because tropical species are considered to have narrower thermal ranges and may already be existing near their thermal limit (Deutsch et al., 2008). In addition to existence near a thermal limit, longevity and traits associated with it have been advocated as factors that put animals at explicit risk of climate-driven extinction. The reproduction rate of large, long-lived mammals is generally slow, with a long generation interval, low offspring numbers, and slow population growth (Cardillo et al., 2005). For particularly long-lived mammals, severe environmental changes will become evident within their lifespan, disqualifying the option of a genetic response (Fuller et al., 2014). Mammal populations may be further affected by temperature or rainfall, and in areas of low productivity or resource availability will become increasingly vulnerable to extinction as resources become more sparse (Owen-Smith 1990; Owen-Smith et al., 2005). Mammals with a specialized diet are even more likely to be negatively affected by climate change than generalist feeders (Gehring and Swihart 2003; Pacifici et al., 2017). For example, the giant anteater is considered the most threatened mammal of Central America, mostly due to habitat degradation, extensive fires during sugar cane harvest, increasing infrastructure, and human interference, and is unlikely to easily recover due to its slow reproduction, dietary specialisation, and large size (Miranda et al., 2014). In general, organisms with any specialised life-style traits are more likely to be adversely affected by changing conditions than are generalists, with severe cascading effects on their community if the organism happens to hold a keystone position in that community (Chapin et al., 2000).

1.4 The aardvark: a specialist ecosystem engineer

1.4.1 General information

The aardvark (*O. afer*, order: Tubulidentata, family: Orycteropodidae; Figure 1.1) is a large (30 to 60 kg) African mammal with a long lifespan (25 years in captivity; Goldman 1986; Nel et al., 2000; Reason et al., 2005; Rey et al., 2014). Aardvarks are generally solitary, predominantly nocturnal, and semi-fossorial. They spend their resting time in self-dug burrows from which they emerge at night to forage (Taylor, 2013; see Figure 1.1A). Aardvark gestation lasts approximately seven months, after which the female gives birth to one young which stays with the mother for several months; however, little only is known about aardvark reproduction in the wild (Taylor, 2013). Aardvarks have internal genitalia, and male and female aardvarks cannot easily be distinguished (Pocock, 1924)

Aardvarks are currently categorised as ‘Least Concern’ by the IUCN (Taylor & Lehmann, 2015), although their population size and density in the wild have not been assessed.

1.4.2 Aardvark phylogeny

The aardvark species *O. afer* is the only extant species of its family, Orycteropodidae, and although 18 subspecies have been described, their validity has not yet been confirmed (Meester, 1971; Lehmann, 2009). Orycteropodidae is the only family in the order Tubulidentata, which is unique among mammals in that it includes only one living species, the aardvark. Tubulidentates are members of the mammalian superorder Afrotheria which also includes elephants (Proboscidea), dugongs and manatees (Sirenia), hyraxes (Hyracoidea), tenrecs and golden moles (Tenrecoidea), and elephant shrews (Macroscelidea) (De Jong et al., 1981; Madsen et al., 1997; Springer et al., 1997; Stanhope et al., 1998; Murata et al., 2003; Tabuce et al., 2008). Molecular data and fossil evidence suggest that Afrotheria evolved on the Afro-Arabian continent during the Cretaceous (Tabuce et al., 2008). The lineage of the Tubulidentates can be traced back ~20 million years, with earliest ascertained aardvark fossils, *Myorycteropus*, originating from East Africa from the early Miocene (MacInnes, 1956; Pickford, 1974). They are thus considered a phylogenetically ancient lineage of mammals. The oldest fossil of the extant aardvark *O. afer*, located in South Africa, was dated to around five million years (Pickford, 2005).

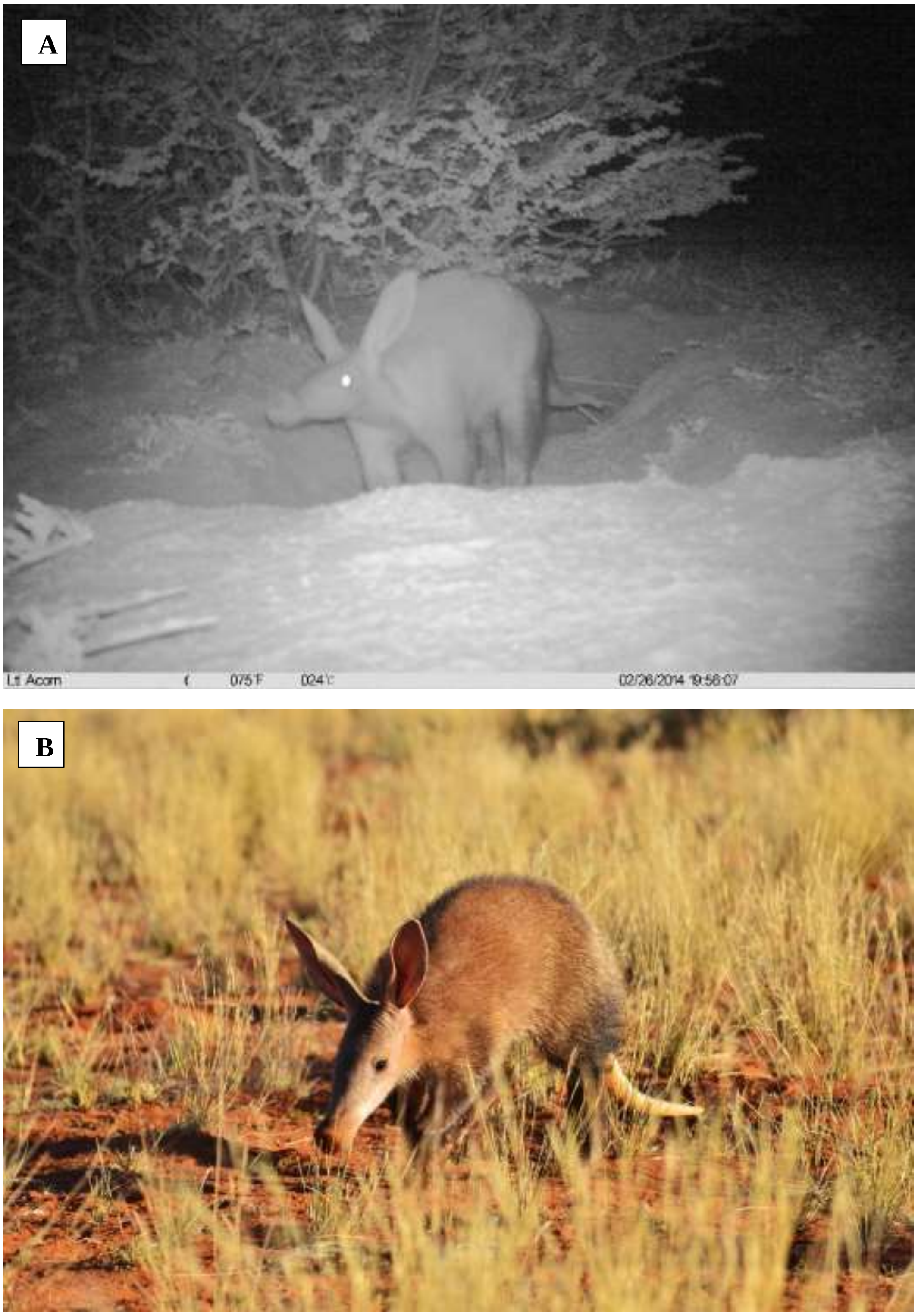

Figure 1.1 Aardvarks in the Kalahari. A) An aardvark just emerged from its burrow, where a camera trap was placed (photo credit: Nora Weyer, Tswalu Kalahari Reserve). B) A young aardvark foraging during daytime in winter (photo credit: Kelsey Green).

1.4.3 Aardvark distribution and habitats

Although the fossil record indicates a past distribution of Tubulidentates throughout Africa and Madagascar and into Eurasia, extant aardvarks are now restricted to Africa south of the Sahara (Lehmann, 2009; Figure 1.2). Aardvarks inhabit a variety of habitats, including open grasslands, savannahs, scrublands and even thick forest (Pagès, 1970; Lehmann, 2009), and are therefore exposed to considerable variation in climates and vegetation throughout their range. Although aardvarks do occur at high elevations (Yalden et al., 1996), they are generally absent from rocky mountainous environments in which they cannot dig burrows (Taylor, 2013). The presence of sufficient ant and termite prey populations proposedly determines aardvark distribution (Cilliers, 2002; Taylor, 2013). However, the abiotic environment may also contribute to aardvark distribution, because climatic conditions can form a ‘climatic envelope’ of species-specific physiological thresholds of temperature and rainfall tolerance, thereby influencing a species’ distribution (Walther et al., 2002). The only habitat that aardvarks are entirely absent from is the arid desert habitat (Taylor, 2013). In an arid environment, the maintenance of water balance (osmoregulation) rather than energetic needs might well be the range-limiting factor for aardvarks, as proposed for koalas in Australia (Ellis et al., 2010) and for several African large mammals (Fuller et al., 2016).

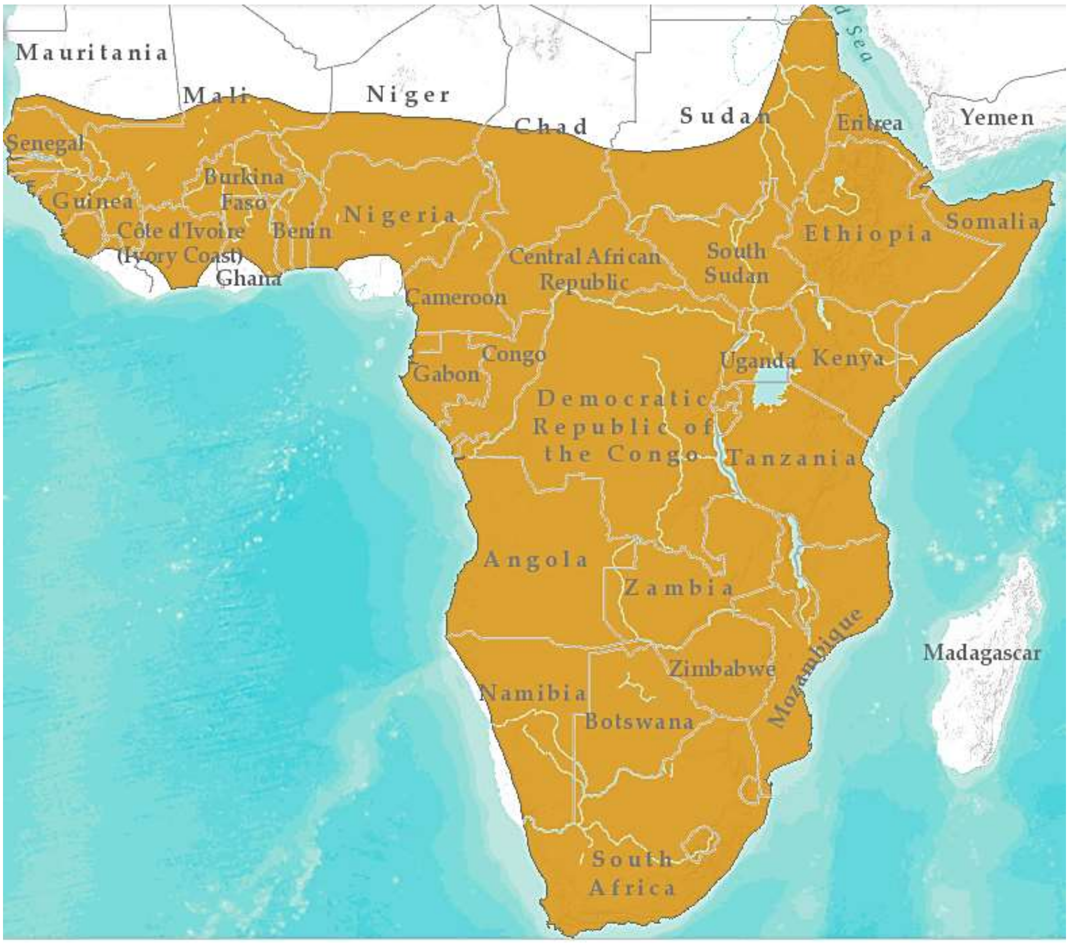

Figure 1.2 Geographic distribution of aardvarks in sub-Saharan Africa (map obtained from the IUCN at http://www.iucnredlist.org/details/full/41504/0#end_uses). The aardvark occurs in all regions except for the arid Namib and Sahara deserts.

1.4.4 Aardvark diet

The aardvark is a dedicated myrmecophage, feeding almost exclusively on ants and termites in many parts of its range, and very rarely, stomach contents have indicated that locusts, beetle pupae, or fruit pulp and seeds might occasionally be consumed (Melton, 1976; Taylor, 2013). To date, four studies have examined the diet of free-living aardvarks (Melton 1975; Melton and Daniels 1986; Willis et al., 1992; Taylor et al., 2002), revealing a varied species composition of ants and termites in different geographical regions of the aardvark's range (Table 1.1). In all studies, the diet of the aardvark was dominated by ants throughout the year, and was supported with termites during the winter (Table 1.1), except in the study in Uganda where diet of aardvarks differed in different sections of the study area (Melton, 1975). The dominant prey species consumed differed between studies (Table 1.1). The variation in diet in all studies was most likely a result of varying prey availability across habitat and season. For example, in the semi-arid South African False Karoo, ants are usually more abundant during summer and become less available to aardvarks in the colder winter months, resulting in higher ant intake in summer and greater termite consumption in winter (Lindsey & Skinner, 2001; Taylor et al., 2002). Termites such as the northern harvester termite (*Hodotermes mossambicus*) harvest mostly dried, frost-killed grass and are more active during winter months (Nel & Hewitt, 1969a; Duncan & Hewitt, 1989). To date, variation in the contributions of ants and termites to aardvark diet have not been assessed across seasons varying in resource availability, nor in geographic regions with low primary productivity.

Table 1.1 Aardvark diet in different regions of aardvark distribution in sub-Saharan Africa. For main aardvark prey, the genus of each aardvark main prey items is presented. Note that Melton (1975) did not report the genus of ants consumed.

Study conducted by	Taylor et al., 2002	Willis et al., 1992	Melton and Daniels 1986	Melton 1975
Study area	Tussen die Riviere		Umgeni Valley	Ruwenzori
Country	South Africa		South Africa	Uganda
Habitat	Nama Karoo		Natal Highlands	Savanna
Aridity level	semi-arid		warm-temperate	tropical
Total annual rainfall (mm)	420		900	600 to 1200
Rainy season	summer		summer	spring, autumn
Air temperature (°C)				
annual maximum	> 30		28	35
annual minimum	< 0		5	18
24-h amplitude	NA		NA	11-14
Main aardvark prey				
summer	ants (*Anoplolepis*)	ants (*Anoplolepis*), termites (*Trinervitermes*)	ants (*Dorylus*), termites (*Odontotermes*)	ants (genus not given), termites (*Macrotermes*)
winter	ants (*Anoplolepis*), termites (*Trinervitermes*)	ants (*Anoplolepis*), termites (*Hodotermes*)	NA	ants (genus not given), termites (*Macrotermes*)
N (scat samples)	350	20	5	23
n (study aardvarks)	4	NA	NA	NA

1.4.5 Morphological adaptations to myrmecophagy and a semi-fossorial lifestyle

Ants and termites typically occur in large underground colonies. Some species emerge from their colonies to forage above ground and store their harvest in their underground galleries. Aardvarks, however, do not feed on surface-foraging insects, but rather detect their prey's superficial soil galleries using their highly specialised sense of smell, then extract prey by cracking open the soil and digging up aggregations of ants or termites. The aardvark is an efficient digger, and its extremities form a specialised system: when digging, the aardvark's strong claws can break soil surface, and its fingers perform a crush-and-sweep motion (Endo et al., 2003), and webbing between the fingers allows for efficient soil movement (Taylor & Skinner, 2004). Special bone and musculature anatomy allows for effective force-generation, while an ulnar process ensures great leverage (Thewissen & Badoux, 1986). The aardvark's tail provides a counterweight for the body weight and lends force when the aardvark conducts its power-stroke (Endo et al., 2013). The morphology of the aardvark's head and teeth is modified in adaptation to their myrmecophageous and fossorial habits, though its head is more elongate than that of other anteaters (Sonntag & Le Gros Clark, 1926). The rather rudimentary teeth of aardvarks have a unique structure of hexagonal dentine prisms surrounding tubular pulp cavities, responsible for the name of the Tubulidentate clade (Melton, 1976). Large salivary glands keep the elongate tongue moist and sticky for licking up their prey, which is then ground up by the gizzard-like, muscular stomach to aid digestion (Sonntag & Le Gros Clark, 1926). Aardvark eyes are protected from debris by long, dense lashes and keratinisation of the cornea, and are dark-adapted, lacking retinal cone cells for colour-vision and acuity, and a tapetum lucidum (Sonntag & Woollard, 1925). The aardvark's complex nasal system has more turbinal processes than any other mammal, and highly developed olfactory regions combined with large second olfactory cortex in the brain point towards a highly developed sense of smell (Sonntag & Woollard, 1925; Sonntag & Le Gros Clark, 1926).

1.4.6 Aardvarks as keystone species and ecosystem engineers

Species that have an impact on their community and ecosystem that is disproportionately large compared to their abundance are considered keystone species (Power et al., 1996). A prime example of a keystone species is the grey wolf in Yellowstone National Park. After ~70 years of absence from the Park, grey wolves were reintroduced in the mid-1990s, which caused large herbivores such as bison (*Bison bison*) and elk (*C. elaphus canadensis*) to prefer using more densely vegetated sections, thereby allowing riverine trees that had been diminished by herbivore activity to regrow (Ripple and Larsen 2000; Fortin et al., 2005; Ripple and Beschta 2006). Wolves are successful in hunting large animals even in winter; as a consequence, their presence in Yellowstone also increases carrion availability, thereby buffering resource bottlenecks for scavengers stemming from climate-change-related winter-shortening (Wilmers & Getz, 2005). Another classic example of a keystone species is the North American beaver (*Castor canadensis*); by constructing massive dams, beavers change hydrology and create large wetlands that persist for centuries, thereby increasing species richness at landscape scale (Wright et al., 2002). Lack of keystone species that buffer other species from environmental fluctuations may render these communities more vulnerable to detrimental effects of global climate change (Wilmers & Getz, 2005).

Organisms that physically modify, maintain or generate habitats and thereby influence other organisms are generally referred to as ecosystem engineers (Mills et al., 1993; Jones et al., 1994). An ecosystem engineer that influences other organisms, for example through trophic cascades, is often also considered a keystone species (Mills et al., 1993; Jones et al., 1994; Power et al., 1996). Burrowing mammals are considered ecosystem engineers because they actively change their environment, as well as keystone species because they provide valuable microhabitats used by other species (Kinlaw, 1999; Pike & Mitchell, 2013). Examples include numerous small (Davidson et al., 2012) as well as large and medium-sized mammals such as the Eurasian badger (*Meles meles;* Smal, 1995; Kowalczyk et al., 2008), wombats (e.g., *L. latifrons*) in Australia (Shimmin et al., 2002; Davidson et al., 2012), giant armadillos in South America (Desbiez et al., 2014), and aardvarks in sub-Saharan Africa (Cilliers 2002; Whittington-Jones et al., 2011). Burrows constructed by one animal can offer other animals vital thermal refuges from temperature extremes and environmental fluctuations (Pike & Mitchell, 2013). For example, during a severe heat wave in South Australia in 1982, numerous birds made increased use of the cooler mammal burrows to find shade and shelter from the heat while others not utilising this refugium died (Attwood, 1982). The presence of ecosystem engineers that provide such microhabitats might become crucial for the continued existence of their beneficiaries under future climate change impacts (Pike & Mitchell, 2013; Cahill et al., 2013), particularly in hot arid and semi-arid habitats. It is therefore pertinent to include climatic microrefugia into models of future distribution changes (Lenoir et al., 2017).

The aardvark is considered an ecosystem engineer (Whittington-Jones et al., 2011) as well as an African keystone species (Cilliers, 2002) because it actively modifies its environment via its extensive digging activity in three ways, namely (1) construction of burrows (Whittington-Jones et al., 2011), (2) exposure of food sources for commensal feeders (Taylor, 2013), and (3) promoting plant germination (Dean & Milton, 1991). The aardvark's presence in an ecosystem is thus beneficial for many other animal and plant species.

Each aardvark generates many burrows (Figure 1.3A) in its home range (Whittington-Jones et al., 2011), which are often used for brief periods only before abandonment (Taylor & Skinner, 2003). At least 30 different vertebrate species reportedly use vacant aardvark burrows as refuges, including the vulnerable blue swallow (*Hirundo atrocaerulea*; Boycott & Parker, 2003), the vulnerable Temminck's ground pangolin (*Manis temminckii*); Pietersen et al., 2014), larger mammals such as leopards and warthogs (*Phacochoerus africanus*) and reptiles such as rock monitor lizards (*Varanus albigularis*; Cumming 1975; Bothma and Le Riche 1984; White and Cameron 2009; Whittington-Jones et al., 2011). Aardvarks also generate nest sites and microclimates for small animals by hollowing-out termite mounds (Cilliers, 2002).

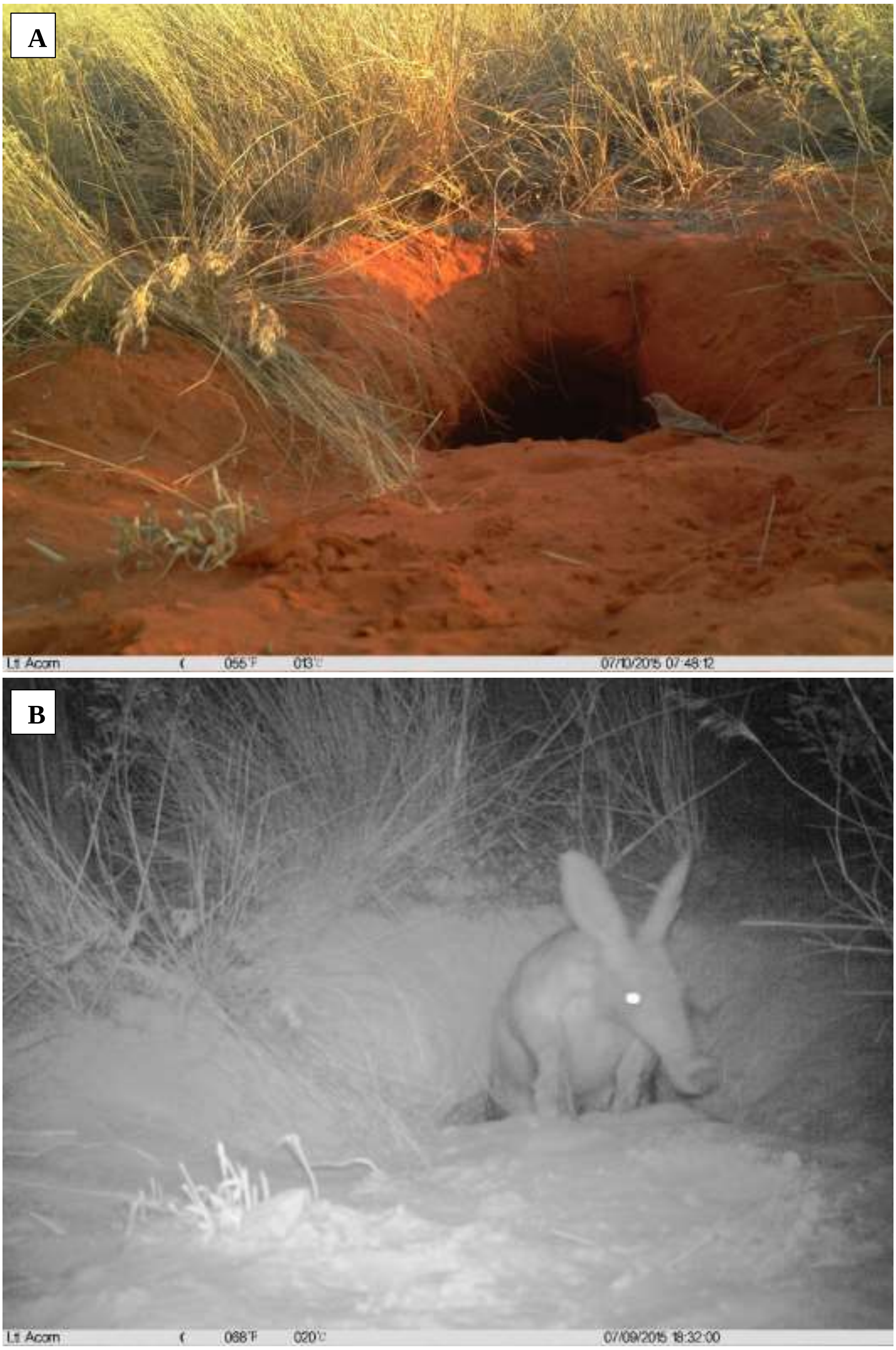

Figure 1.3 Camera trap footage of an aardvark burrow in the Kalahari. A) during the day, an aardvark is resting inside the burrow, concealed by sand in the entrance tunnel; B) at night, the aardvark emerges from the burrow to forage (Photo credit: Nora Weyer, Tswalu Kalahari Reserve).

In addition to the sheltering functions of their burrows, aardvarks' feeding excavations also have beneficial functions. Firstly, they facilitate access to insect prey for various opportunistic feeders. Their feeding pits serve as important food supplementation for opportunists that would otherwise not be able to reach deeper soil levels where ants and termites are abundant, especially during winter, when the surface-foraging activity of ants is reduced and aardvarks often forage during daylight hours (Cilliers, 2002; Taylor, 2013). Animals that exploit aardvark feeding sites include aardwolves (*Proteles cristatus*), bat-eared foxes (*Otocyon megalotis*), ant-eating chats (*Myrmecocichla formicivora*), and yellow-billed hornbills (*Tockus leucomelas*; Taylor & Skinner, 2000, 2009; Taylor, 2013). Secondly, aardvarks are so-called 'prime-movers' of soil and provide important seed germination sites (Dean & Milton, 1991).

1.4.7 Behavioural ecology of the aardvark

Aardvarks are predominantly nocturnal and emerge from burrows (Figure 1.3B) to forage on their subterranean prey. In the False Karoo, aardvarks began to forage after sunset and returned to burrows before or during sunrise during the warm seasons of the year (Taylor & Skinner, 2003). In winter, however, aardvarks often left their burrows in the afternoon and ceased above-ground activity during the coldest parts of the night several hours before sunrise (Taylor & Skinner, 2003). In the False Karoo, aardvarks were never observed above ground at temperatures lower than 2 °C, possibly because aardvarks were sensitive to cold with their sparse fur (Figure 1.1B) providing poor insulation (Taylor & Skinner, 2003). However, this explanation does not integrate other factors that might compensate for poor insulation and contribute to a mammal's capacity to tolerate ambient temperatures, such as body size and shape, changes in peripheral blood flow, and the use of vascularised body parts serving as thermal windows (Fuller et al., 2010, 2016). Nevertheless, aardvarks in the False Karoo spent less time outside burrows and moved more slowly during cold, dry months of winter than during the warmer and wetter summer months (Van Aarde et al., 1992). Several anecdotal reports based on field observations and aardvark spoor tracking have estimated the travelling distance of aardvarks to range from 2 to 30 km in one night (Pagès 1970; Melton

1975, 1976; Van Aarde et al., 1992; Taylor 2013). However, no study has quantified the duration and intensity of aardvark activity, and changes in activity level in response to seasonal environmental fluctuations in resource availability or climate.

1.4.8 Aardvark activity and body temperature

Aardvarks have a unique physiology in that their metabolism and body temperature are generally lower than expected for a mammal of their size (McNab, 1984). These low metabolic rates and body temperatures are characteristic of other large ant- and termite-eating mammals, and have been proposed as adaptations for a semi-fossorial lifestyle and specialisation on a low-energy diet of ants and termites (McNab, 1984). However, until recently, little was known about aardvark physiology under natural conditions. Taylor & Skinner (2004) investigated body temperature of aardvarks in the False Karoo. Body temperature recorded using intra-abdominally implanted biologgers was reported over five consecutive days during winter and summer for three individuals. Body temperature of these aardvarks ranged from about 34.5 to 37.5 °C in summer and 33.5 to 37.5 °C during winter, and the animals had a day-night nychthemeral rhythm, with lower body temperature occurring during periods spent inactively inside burrows, and higher temperatures during the active phase. The body temperature increase during the active phase was proposed to be a result of the metabolically intensive digging action producing body heat (McNab, 2002; Taylor & Skinner, 2004). Thus, foraging in aardvarks during summer was proposed to be limited to cooler night-times to avoid possible overheating that could result from daytime foraging, when exposure to heat and solar radiation would make dissipation of metabolic heat difficult (Taylor & Skinner, 2004). Their burrows provide a buffered environment that allows aardvarks to avoid extremely high temperatures during summer days and low temperatures during winter nights (Taylor & Skinner, 2004). Foraging activity at night may also reflect the time when prey is most available; although aardvarks are able to reach the deep nests of some of their prey insects, they generally target prey concentrated in superficial nests and storage chambers just below the soil surface (A. Taylor, pers. comm.). Thus, temporal shifts in aardvark activity patterns from summer nocturnality to winter diurnality may reflect a response to both thermoregulatory needs and prey activity patterns.

In a recent study, body temperature and activity patterns of six wild aardvarks were recorded using abdominally implanted biologgers in six free-living aardvarks in the Kalahari (Rey et al., 2017). During the study period, a particularly hot and dry summer occurred, and five of the study aardvarks and several other resident aardvarks at the study site died (Rey et al., 2017). Their body temperature patterns indicated that the aardvarks had likely been experiencing starvation during the drought, as their 24-h minimum body temperatures progressively declined, resulting in pronounced heterothermy (Rey et al., 2017). Several individuals shifted from nocturnal to diurnal activity during the summer drought, presumably to save energy, given that they were unable to maintain high body temperatures. Only one study aardvark survived the drought (Rey et al., 2017).

Rey et al. (2017) showed that while aardvarks employed physiological plasticity, this was an insufficient response to the extreme summer drought conditions. They proposed that the decline in body temperatures was indicative of a negative energy balance caused by drought-related resource decline, which also resulted in poor body condition. The authors did not, however, directly assess seasonal fluctuations in body condition, diet, or resource availability of aardvarks in the Kalahari. Populations of ants and termites, which are the main prey of aardvarks, are susceptible to seasonal vegetation abundance and to rainfall, and their colonies thrive when vegetation is plentiful but can crash following drought-induced vegetation declines (Tevis, 1958; Nel & Hewitt, 1969a). On the other hand, it has been proposed that some termites might do well under drought conditions if there sufficient dry vegetation is available to harvest (Braack, 1995), and thus the impacts of drought on ant and termite availability as aardvarks prey demands elucidation.

The semi-arid Kalahari desert is the hottest and most arid environment inhabited by aardvarks (Taylor & Lehmann, 2015), and rapidly is becoming hotter and drier with ongoing climate change (Pachauri et al., 2014). As summer droughts will likely become the rule rather than the exception in the Kalahari, an improved understanding of aardvark responses to such harsh conditions is needed. The initial study by Rey et al. (2017) provided a basis to broaden the investigation of drought stress on aardvarks in the Kalahari semi-desert, and by assessing diet, resource availability, body condition, body temperature, and activity patterns of aardvarks in the Kalahari over a three-year period, I aimed to identify the proximate causes behind the observed aardvark deaths and physiological stress.

1.5 Thesis aims and hypotheses

As a large, long-lived, nocturnal, non-migratory mammal with a specialised diet, the aardvark would likely be highly susceptible to the rapid climatic changes expected throughout much of its range. As an ecological engineer providing thermal refuges and food sources for other animal species (Whittington-Jones *et al.,* 2011), as well as germination sites for plants (Dean & Milton 1991), declines in aardvark numbers, particularly in hot and arid environments, are likely to have extensive impacts on various organisms reliant on aardvark digging activity. However, despite the aardvark's ecological importance, very little is known about the feeding ecology, physiology, and capacity of free-living aardvarks to adapt to seasonal and interannual changes in their natural habitat, particularly in hot and arid habitats - environments which may become more common following climate change in Africa. To understand the capacity of the aardvark to survive future environmental changes, it is necessary to determine its current success in coping with challenges in its natural habitat, particularly in regions where aardvarks are (1) an increasingly relevant provider of thermally buffered microclimates for many species, and (2) exposed to conditions similar to those predicted for much of its range in future climatic scenarios. One such region is the Kalahari semi-desert at the south-western edge of the aardvark's distribution, where current climatic extremes have resulted in aardvark deaths (Rey et al., 2017). Within this framework, I set out to achieve the following objectives:

Chapter 3: Investigate the link between aardvark body condition and seasonal and inter-annual changes in resource availability in the Kalahari.

To assess the abundance of resources relevant to the aardvarks, it was necessary to confirm the diet of Kalahari aardvarks, and to quantify the energy and water provided by prey species. Based on aardvark studies elsewhere, I expected Tswalu aardvark diet to consist of ants and termites in proportions reflecting the different seasonal availabilities of these insect groups, with ants more available during summer and termites during winter. I also hypothesised that, congruent with other studies, ants would be higher in energy but lower in water content than termites.

Since many ant and all termite species are herbivorous, I hypothesised that ant and termite abundance would be dependent on the vegetation productivity, which in turn would depend on rainfall. Consequently, I hypothesised that following drought, the abundance and activity of ants (which can be herbivorous or omnivorous) would be somewhat reduced, and that termite and ant abundance would be directly related to the amount of standing crop, i.e., vegetation productivity. I hypothesised that low prey abundance associated with low vegetation productivity would result in a decline in body condition, whereas high resource abundance would be associated with good body condition of aardvarks.

Chapter 4: Investigate patterns of aardvark activity (timing, intensity, duration) in response to seasonal and annual fluctuations in rainfall, temperature and resource availability.

I hypothesised that when aardvarks are in good body condition, intensity of activity, such as from digging, would be high, and activity would be restricted to the cooler evening. Activity intensity and duration of the active phase would decline during periods of very low air temperature. When aardvark body condition was poor, I expected that the intensity of aardvark activity would decline, but the duration of the active phase would expand to compensate for increased energetic needs, possibly resulting in diurnal activity.

Chapter 5: Investigate long-term records and 24-h rhythms of body temperature patterns as an indicator of aardvark well-being and activity rhythms.

I hypothesised that under favourable environmental conditions (moderate air temperature, abundant resources) when aardvarks are likely in good body condition, aardvark body temperature would be lower than that of other mammals of similar size, but tightly controlled, with a small 24-h amplitude of body temperature rhythm. However, during periods of low resource availability (reflected in poor body condition), I expected that minimum body temperature of aardvarks would decline as a result of an inability to sustain energetically costly homeothermy, resulting in increased 24-h body temperature amplitude. During periods of high air temperature and low resource availability, aardvark maximum body temperature might show unusually high peaks as a result of dehydration. I hypothesised that activity intensity would also influence body temperature, with body temperature increasing during the active (foraging) phase and decreasing during the inactive phase of the aardvark, and possibly being higher on days when aardvarks were more active.

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Chapter 2 - Methods and materials

2.1 Study site

2.1.1 Location

This study was carried out at Tswalu Kalahari Reserve from July 2013 until September 2015. Tswalu is a semi-arid private nature reserve situated along the Korannaberg mountains about 160 km north-east of Upington in the Northern Cape Province of South Africa (Figure 2.1) at an altitude of 1020 to 1586 m above sea level (S 27°14’57.50”, E 22°22’52.00”). Tswalu currently encompasses an area of ~1100 km^2, separated into a smaller (fenced) camp of ~200 km^2 which contains lions (*P. leo*), and a larger section of ~900 km^2 from which lions are absent, although leopards and cheetahs (*Acinonyx jubatus*) roam freely. From 2014 to 2015, African wild dogs (*Lycaon pictus*) were also present on the larger section of the reserve. Ant- and termite-consuming (myrmecophageous) mammals present in the reserve include the aardvark, aardwolf, pangolin, and bat-eared fox. Another burrowing mammal at Tswalu is the porcupine (*Hystrix africaeaustralis*), a medium-sized rodent. Unlike aardvarks however, they often re-use or expand existing burrows (often originally created by aardvarks), and are thus not considered primary ecosystem engineers (Bragg et al., 2005). The study was carried out in the central region of the lion-free section, where the landscape is dominated by distinctive NNE-SSW-aligned undulating dune strips at intervals of 0.5 to 1 km, parallel to the Korannaberg mountains.

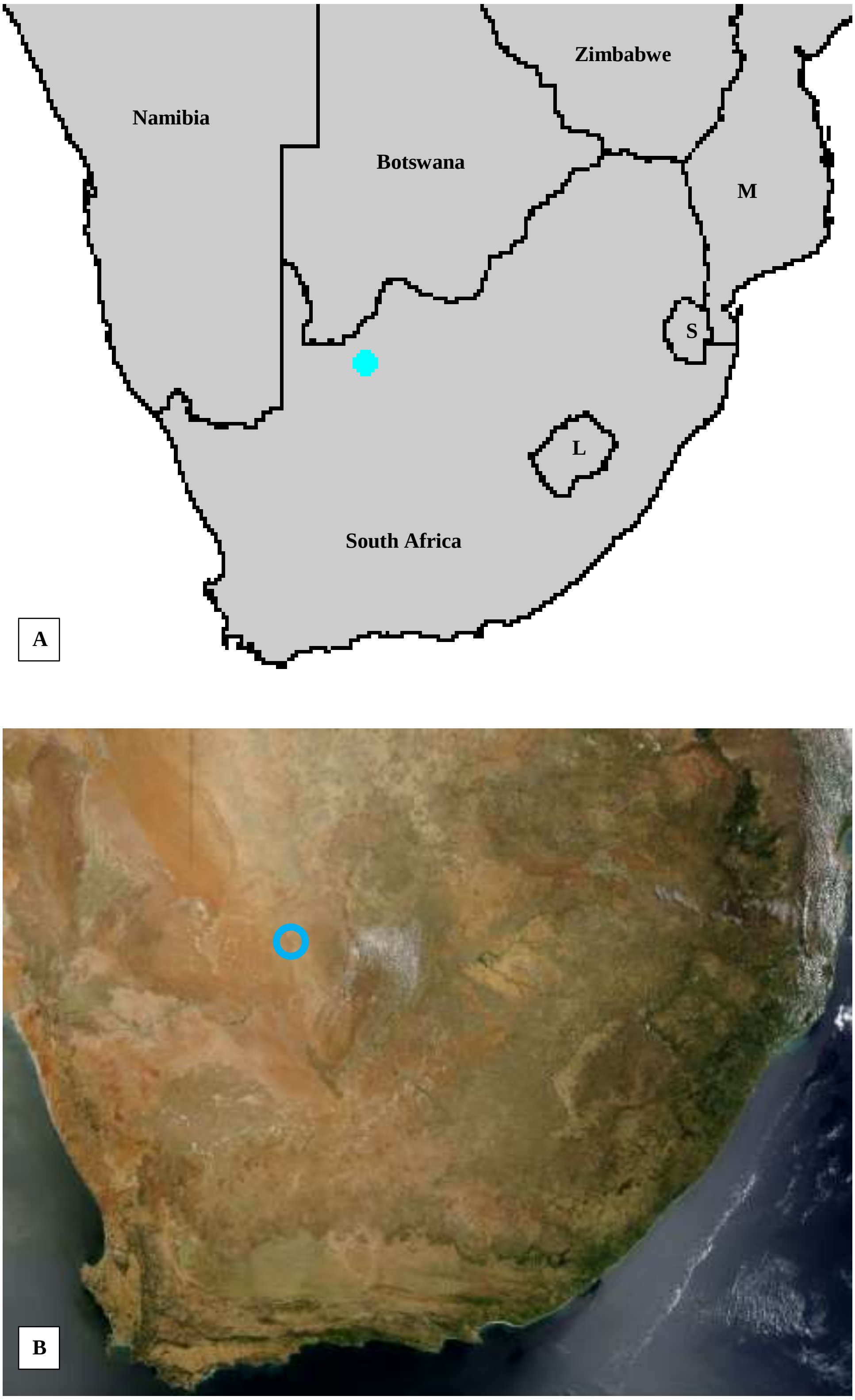

Figure 2.1 Geographic position of Tswalu Kalahari Reserve (blue circle). A) Tswalu within the southern African region (map created in R / RStudio), L - Lesotho, M - Mozambique, S - Swaziland; B) Tswalu within the Republic of South Africa (satellite image by Jaques Descloitres, MODIS Rapid Response Team, NASA / GSFC, cropped from http://visibleearth.nasa.gov/view_rec.php?id=4265, Public Domain, https://commons.wikimedia.org/w/index.php?curid=30922).

2.1.2 Vegetation

Tswalu’s dominant vegetation type comprises Kalahari thornveld (Acocks, 1988) and includes shrubby Kalahari dune bushveld on the plains, and Kalahari mountain bushveld in the mountainous areas (Low & Rebelo, 1998). Individual areas of the reserve are dominated by different vegetation types (Figure 2.2). The aardvark study site was dominated by Gordonia duneveld vegetation (Tokura, 2016). Dominant plant types on Tswalu and within the study site (Figure 2.3) include grasses such as *Anthephora*, *Aristida*, *Stipagrostis,* and *Eragrostis*, shrubs, such as *Rhigozum* and *Senegalia*, and few tree species such as *Boscia albitrunca*, *Acacia erioloba*, and *A. haematoxylon*. Tswalu falls within the Savannah Biome (Mucina & Rutherford, 2006), where the average plant growth season begins in late October, reaching its maximum between late January and February, while the end of the growing season is highly varied and may occur anytime between June and August (Wessels et al, 2011). Therefore, the Savanna Biome has a shorter and more variable growing season length with lower total annual productivity than other South African biomes, while the range of its annual productivity is similar to that of the Thicket and the Grassland Biomes (Wessels et al, 2011).

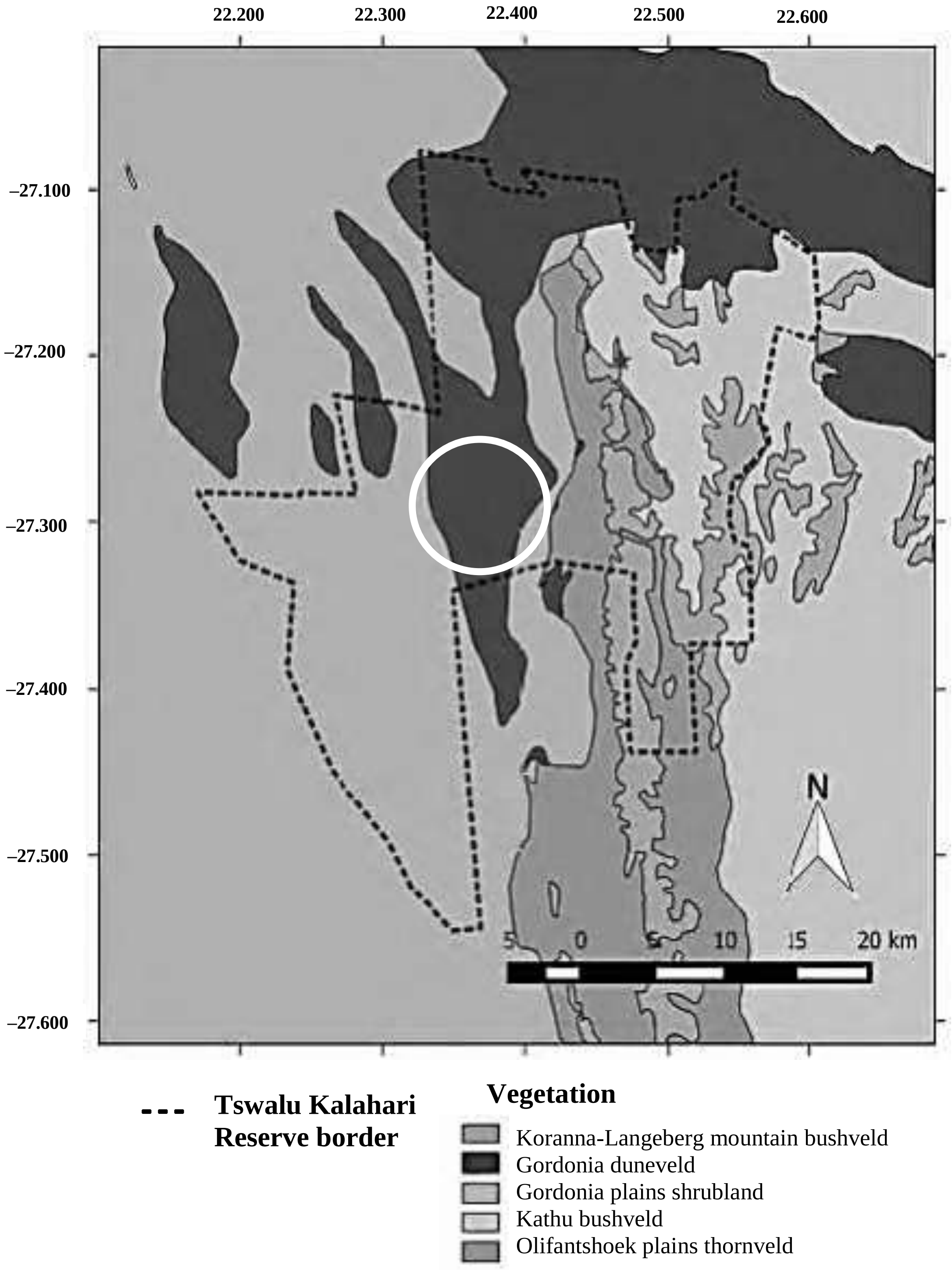

Figure 2.2 Map of Tswalu Kalahari Reserve indicating five different dominant vegetation types, adapted from Tokura (2016). The location of my study aardvarks (white circle) was situated mainly within Gordonia duneveld vegetation.

Figure 2.3 Example of vegetation coverage within a study aardvark's home range in Gordonia duneveld vegetation during summer 2014-15 following good rains. View from west to east towards the Korannaberg mountains (photo credit: Nora Weyer).

2.1.3 Climate and measurements of climatic variables at Tswalu

Tswalu is situated within an area that is predicted to become hotter and drier under future climate change (Niang et al., 2014), and already experiences low and highly variable rainfall, including sporadic droughts (Thomas et al., 2007). Average annual rainfall over the past 25 years was highly variable (~360 ± 170 mm), the majority of which fell in the warm period between December and April (Davis et al., 2010; Tokura, 2016). The dry period generally coincided with the coldest months of June to September, and rainfall generally occurred during the hottest months from November to February, during which maximum air temperatures occur (Van Rooyen et al., 1999). Air temperatures at Tswalu range from a winter nighttime minimum of -6.6 °C to a summer daytime maximum of 42.5 °C (Van Rooyen et al., 1999).

Wind speed and air temperature at the study site were recorded automatically at 30-minute-intervals (Watchdog 2700 weather station, Spectrum Technologies Inc., USA; data provided by A. Young, Exeter University). From these data, I calculated 24-h maximum wind speed, and 24-h minimum, maximum and mean air temperatures. To obtain monthly minimum, maximum and mean air temperatures, I averaged 24-h minimum, maximum and mean air temperatures for each month. I also calculated mean ± SD air temperature at 1-h-intervals for each season (summer: December to February, autumn: March to May, winter: June to August, spring: September to November) from winter 2012 to spring 2015 (Figure 2.4).

Rainfall (mm) was measured at 0.2-mm-intervals, using an event logger (HOBO Pendant Event data logger, Onset Computer Corporation, USA) and tipping bucket (Davis Instruments Corporation, USA). To assess rainfall during the growing season before our study started, I obtained rainfall data for the period of January to December 2012 from the Tswalu Rainfall Database. These data had been recorded by Tswalu staff using commercially available rain gauges within a few km of my weather station, and data from both sources were nearly identical during overlapping measuring periods. I calculated total rainfall per month for the period January 2012 to December 2015.

I obtained daily times of sunset, sunrise and % moonlight illumination for the nearest town Upington, Northern Cape Province (~200 km southwest of Tswalu) for January 2012 to December 2015 (Time and Date AS, Norway; http://staging.timeanddate.com), and calculated the duration of the daily photoperiod as the time elapsed between sunrise and sunset.

Air temperatures inside vacant burrows of study aardvarks were recorded during ad-hoc measurements over several days in early summer 2013-14 at a depth of ~1 m. using A temperature logger (DS1921G-F5 Thermochron iButton®, Dallas Semiconductor / Maxim Integrated Products, USA, accuracy 1.0 °C within an operating temperature range –30 °C to +70 °C, resolution 0.5 °C) attached to a string were pushed through the soil over a burrow cavity with the help of a metal pipe, so that the logger could loosely dangle inside the burrow just beneath the ceiling. The pipe was then removed and the insertion hole closed again with soil. Burrow air temperatures varied between 25 and 32 °C, while air temperatures outside ranged from 15° to 40 °C.

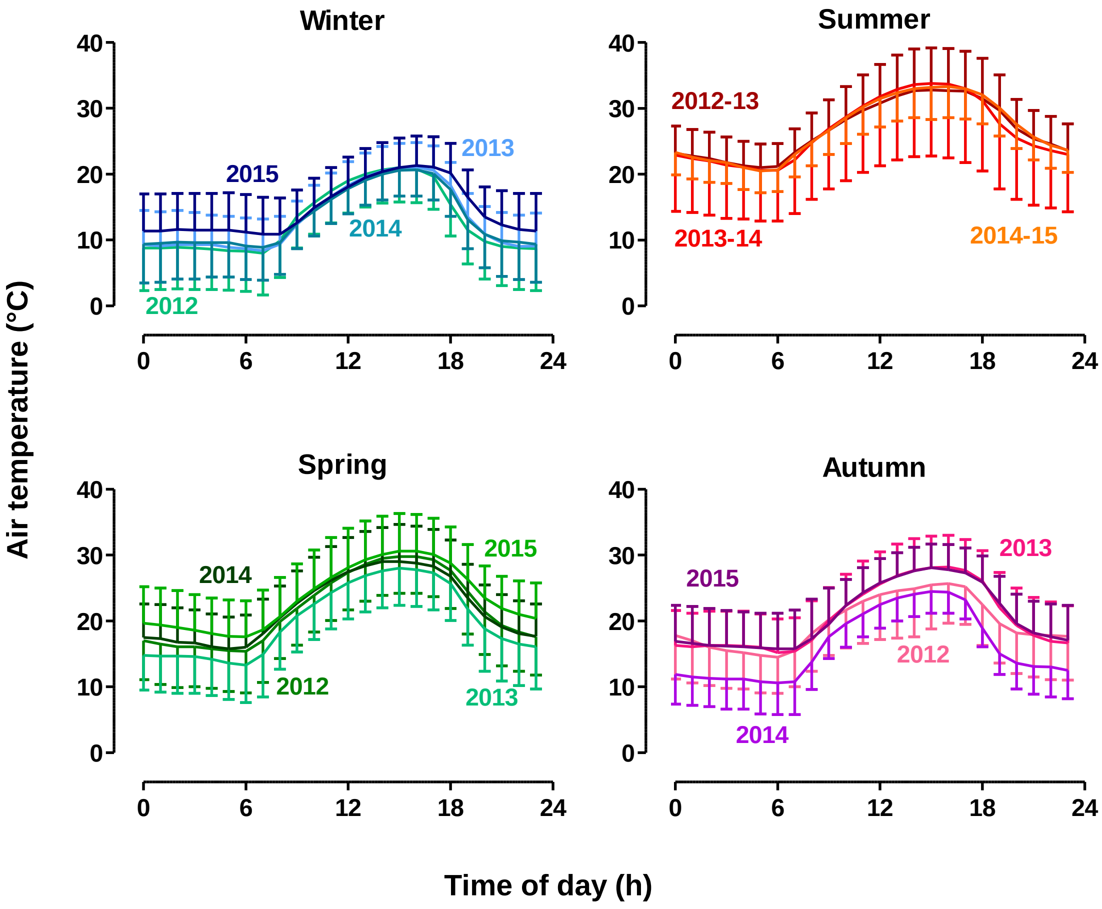

Figure 2.4 Seasonal mean ± SD air temperatures over 24 hours at Tswalu Kalahari Reserve between 2012 and 2015.

2.2 Aardvark capture and surgery

To implant tracking devices and data loggers to record body temperature and activity, seven aardvarks were initially captured and anaesthetised at Tswalu in July 2012 for the period July 2012 to July 2013. The anaesthetic procedure used in this study followed procedures described by Rey et al. (2014), which had been based on previous studies on aardvark anaesthesia (Robinson 1983, Nel et al. 2000, Stetter 2003, Vodicka 2004, Gers et al. 2011), and consultation with various veterinarians experienced in anaesthetizing and operating on wild mammals. The genitalia of aardvarks are internal and only have partial external protuberances, making it difficult to determine their sex. Hence, the sexes of the first six aardvarks (1 to 6) could not be determined with certainty. The sexes of all aardvarks (7 to 17) captured between July 2013 to 2015 were determined using a published description of aardvark genitalia (Pocock, 1924). Nine more aardvarks (two male aardvarks 10 and 11; seven female aardvarks 8, 9, 12 to 16) were captured in July 2013 for the second study year (July 2013 to July 2014), and another female aardvark was added to the study in July 2014 for the third study year (July 2014 to September 2015). In total, 17 different aardvarks were captured and implanted for this study (see below). All procedures conformed to the ethical requirements of the Department of Environment and Nature Conservation of South Africa (Northern Cape Province Government, permits no. FAUNA 1000/2013, 1000/2/2013, 1001/2013) and the Animal Ethics Screening Committee of the University of the Witwatersrand (clearance certificate no. AESC 2013/29/05).

Each aardvark was immobilised by wildlife veterinarians with a projectile dart (‘P’-type disposable RDD devices with flight stabiliser, 32-mm needle with 2-mm barb, 1 cc volume, Pneu-dart Inc., USA) propelled from a gas-pressurized (4,5 to 10 bar) dart gun (CO_2-injection rifle, DAN-INJECT ApS, Denmark) from a distance of 10 to 25 metres. When we located an aardvark foraging in daylight, a veterinarian approached it on foot as silently as possible and from a downwind direction until the animal was close enough to be darted. When an aardvark that needed to be recaptured did not become active during the day, I located it inside its burrow in the early morning. Before sunset, the veterinarian waited silently for the aardvark to emergence, which often took hours. I used a dim light to illuminate the area around the burrow entrance allowing the veterinarian to detect any movement at the burrow entrance, and dart the target aardvark as it was walking away from the burrow. These capture methods were safe and efficient because a darted aardvark generally did not run far (if at all), and only on very few occasions did a darted aardvark hide inside a burrow, from which we then excavated it once it had become recumbent.

Each aardvark was darted using a combination of an anaesthetic (Anaket-V, ketamine hydrochloride: 200 mg mL^{-1}, 0.5 mg kg^{-1}, Animal Health Division - Bayer HealthCare (Pty) Ltd., South Africa), a short-acting benzodiazepine (Dormicum, midazolam hydrochloride: 50 mg mL^{-1}, 0.2 mg kg^{-1}; Roche Products (Pty) Ltd., South Africa) and a surgical sedative and analgesic (Domitor®, medetomidine hydrochloride: 20 mg mL^{-1}, 0.08 mg kg^{-1}, Pfizer Animal Health, USA). Dart dosages were calculated for a 50 kg aardvark to ensure sedation. The aardvark was then transported to a temporary field surgery station, where we provided an environment as sterile as possible to implant each aardvark with miniature data loggers and a tracking transmitter via laparotomy. During transport, the aardvark was placed sternally (Figure 2.5) on an animal mattress (The Bakkie Mattress Ltd., South Africa) and kept warm with warm-water bottles and shock blankets. Its eyes were covered with a blindfold, and the ears were protected by inserting a finger-thick cotton plug. Anaesthesia during transport was maintained by administration of inhalation anaesthetic (ISOFOR, isoflurane: 0.5 to 6 %, SafeLine Pharmaceuticals (Pty) Ltd., South Africa) in 100 % medical oxygen supplied from an anaesthetic machine (Ohmeda portable anaesthetic machine, Datex-Ohmeda Medical Equipment, USA; now GE Healthcare, General Electric, USA) via a face mask.

Figure 2.5 Anaesthetised aardvark on the back of a vehicle before transport to the surgical theatre (Photo credit: Mary-Ann Costello).

Once a captured and transported to the temporary surgery theatre, the aardvark was placed on its side on a table atop heating pads (DisChem Pharmacies, South Africa) and towels, and partially covered with shock blankets, to keep it warm on a cushioned surface. An eye ointment (ISEE Eye Ointment, chloramphenicol: 20 mg g^{-1}, vitamin A: 15 000 IU g^{-1}, VIRBAC RSA (Pty) Ltd., South Africa) was applied to the eyes to keep them moist. To maintain anaesthesia using inhalation anaesthetic (ISOFOR, isoflurane: 0.5 to 6 %, SafeLine Pharmaceuticals (Pty) Ltd., South Africa) in medical oxygen, each aardvark was intubated. The snout was held open by tying a piece of crepe bandage around the upper jaw underneath the hard palate, and topical anaesthetic spray (Xylocaine, lidocaine: 10 mg 0.1 mL^{-1}, AstraZeneca, South Africa) was applied on the larynx. The aardvark was then intubated through its snout using a laryngoscope set (Miller Sololite®, Medical Devices (Pvt) Ltd., Pakistan) and a stylet to insert an endotracheal intubation pipe (6.5 or 7 mm, Kyron Laboratories, South Africa). On very few occasions, breathing ceased during anaesthesia, at which point a breathing stimulant was administered (Dopram®-Fresenius, doxapram hydrochloride: 20 mg mL^{-1}, Bodene (Pty) Ltd., South Africa). During surgery, each aardvark received a lactated saline solution drip (Ringer's Lactate Intravenous Infusion, B. Braun Medical (Pty) Ltd., South Africa, or Sabax Ringer-Lactate - Hartmann's solution, Adcock Ingram Critical Care (Pty) Ltd., South Africa) administered at a maintenance rate of 5 mL kg^{-1} h^{-1}. We inserted a catheter (Jelco® 20 gauge, Smiths Medical (Pty) Ltd., South Africa) into the marginal ear vein and ear artery. A pressure transducer (DPT-200 Deltran®, Utah Medical Products, Inc., USA) served to link the catheter to a veterinary vital signs monitor (Cardell® Model 9403, Sharn Veterinary Inc., USA) that recorded systolic, diastolic, and average arterial blood pressure of the aardvark. These blood pressures, as well as respiratory rate, heart rate, peripheral haemoglobin oxygen saturation, end-tidal carbon dioxide (LifeSense® Vet LS1-10R, Medair AB, Sweden), and rectal temperature (BAT-12 thermocouple thermometer, Physitemp Instruments Inc., USA) were monitored at 5-minute intervals throughout surgery. Before the veterinarian commenced surgery, a patch of approximately 100 x 100 mm on the abdomen around the paralumbar region of the aardvark was shaved, washed and sterilized using antiseptic solutions (Hibitane, chlorhexidine: 5 %, and Hibicol, chlorhexidine gluconate: 0.5 % in spirit, F10 Health and Hygiene (Pty) Ltd., South Africa). A local anaesthetic (lignocaine hydrochloride: 2 %, 3 mL, Animal Health Division - Bayer (Pty) Ltd., South Africa) was injected subcutaneously at the surgical site. Additionally, each aardvark received a non-steroidal anti-inflammatory (Metacam®, meloxicam: 20 mg mL^{-1}, 0.5 mg kg^{-1}, Boehringer Ingelheim Pharmaceuticals (Pty) Ltd., South Africa), and an opioid analgesic (Temgesic, buprenorphine hydrochloride: 0.3 mg mL^{-1}, 0.01 mg kg^{-1}, Reckitt Beckinser Healthcare Ltd., UK) subcutaneously, and a long-acting antibiotic intramuscularly (Duplocillin, procaine benzylpenicillin: 0.04 mL kg^{-1} 6 000 IU kg^{-1}, Intervet (Pty) Ltd. / MSD

Animal Health, South Africa). A 30 to 50 mm incision was made through skin, muscle layers, and parietal peritoneum in the paralumbar region, through which the wax-coated temperature data loggers and radio transmitter were inserted (see below, Figure 2.6A). All devices were dry-sterilised in formaldehyde vapour for at least 24 h before surgery, and rinsed in sterile water before implantation into the aardvark. The data logger that recorded locomotor activity of the aardvark was tethered to a muscle (*M. transversus abdominis*) inside the abdominal cavity, using non-absorbable polyamide suture (Nylon, Scimitar Surgical Sutures, Gabler Medical Ltd., UK), to ensure that the activity records were not affected by free movement of the logger inside the animal's body (Figure 2.6B). Each incision was sutured close using absorbable polyglycolic acid suture material (Viamac (USP), Scimitar Surgical Sutures, Gabler Medical Ltd., UK), sprayed with a topical antiseptic spray (Necrospray, oxytetracycline hydrochloride: 40 mg, gentian violet: 4 mg, Animal Health Division - Bayer HealthCare (Pty) Ltd., South Africa) and coated with a topical ectoparasite repellent (Tick Grease, chlorfenvinphos: 0.3 %, SWAVET RSA (Pty) Ltd., South Africa).

Figure 2.6 Wax-coated devices before sterilisation and surgical implantation into aardvarks for this study. A) VHF tracking transmitter (30 mm Ø, 110 mm length) with StarOddi temperature logger attached to one of the short sides of the transmitter. B) Locomotor activity data logger with surgical-steel-tethers to be attached to musculature inside the abdominal cavity of an aardvark; actual dimensions: ~ 20 x 40 x 40 mm; small arrow indicates the front of the logger to ensure all loggers were positioned inside different aardvarks in the same way.

After surgery, each study aardvark was released as close as possible to its respective capture site. During transport to release sites, each aardvark was given 100 % oxygen through a face mask. At the site, an intravenous medetomidine-reversal drug was administered (Antisedan, atipamezole hydrochloride: 5 mg mL^{-1}, 0.2 mL kg^{-1}, Pfizer Laboratories, South Africa), after which catheters were removed. Endotracheal tubes, earplugs, and the blindfold were removed when the aardvark showed signs of arousal. Each aardvark was monitored during recovery until it entered a burrow or walked out of sight at a fast pace and could no longer be observed. I closely observed the post-surgical recovery of each aardvark during the weeks following surgery.

At the end of the data collection period, each study aardvark was recaptured, and a similar procedure to that used for implants was followed to replace, or remove, the loggers and tracking transmitter. The implant sites had healed and no signs of infection from the implantation surgery were visible. It had originally been intended to recapture each aardvark in July each year, to allow implanted biologgers to record data over a period of ~12 months after which they would be replaced with new loggers and a new VHF tracking device. However, several aardvarks died from natural causes such as starvation, others could not be retrieved because their tracking devices ceased to work, and the remaining aardvarks proved very difficult to recapture so that several capture attempts had to be made before we succeeded. Moreover, some of the biologgers stopped recording data at varying time points throughout the study. Table 2.1 details for each aardvark the period for which it was part of the study, which data were successfully recorded, and whether records ended due to recapture, death, or failure to retrieve the animal.

Table 2.1 Gantt chart indicating for which time periods activity and body core temperature data were obtained from each study aardvark (1 to 17) at Tswalu Kalahari Reserve between July 2012 and September 2015. ID - aardvark identity; green - activity logger; grey - temperature logger; blank fields - no data available; * - implantation; # - logger failure; Ɨ - death of the aardvark; Ω - logger not retrieved; z - loss of the aardvark due to VHF transmitter failure; x - logger removal.

	2012						2013												2014												2015								
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2.3 Devices implanted

Two data loggers and one tracking device were implanted into each study aardvark. The tracking device was a very high frequency (VHF) radio transmitter (30 mm diameter, 110 mm length, ~100 g mass; Africa Wildlife Tracking, South Africa) which emitted a unique signal at a frequency between 149 and 150 MHz. The VHF implant allowed for locating a study aardvark from a distance of up to 3 km depending on terrain conditions, using a directional antenna and receiver kit (Three-Element Folding Yagi Antenna; R1000 Receiver, frequency range 148 to 152 MHz, Sirtrack Ltd., New Zealand). The tracking device was covered in inert wax (Sasolwax 1276, Sasol Ltd., South Africa). During the first year of study, several aardvarks died and some of the dataloggers could not be retrieved because scavengers had dispersed parts of the aardvarks, and other parts were lost in the sand. To find the body temperature dataloggers and retrieve data in case of further aardvarks' deaths, in the following study years I attached the body temperature data logger to the VHF transmitter with sterile wax (Figure 2.6A). I dry-sterilised the VHF-trackers together with the loggers in formaldehyde vapour until implantation. The total mass of all equipment implanted per aardvark did not exceed 350 g, i.e., ~1 %, of aardvark body mass.

2.3.1 Body core temperature

One data logger recorded abdominal body temperature in each study aardvark (2012 to 2013: DS1922L Thermochron iButton®, Dallas Semiconductor / Maxim Integrated Products, USA, resolution 0.0625 °C, accuracy ~0.5 °C within an operating temperature range between –40 °C and 85 °C; 2013 to 2015: DST centi-T implantable temperature data logger, Star-Oddi, Iceland; mass < 20 g, resolution 0.032 °C, accuracy ˜0.1 °C between –1 °C and 45 °C). Before implantation, I programmed each data logger to record at 5-minute-intervals, sealed it in antistatic cellophane and rubber tape, and encased it in three smooth layers of inert wax (Sasolwax 1276, Sasol Ltd., South Africa). I calibrated each data logger in an insulated water bath against a high accuracy thermometer (Quat 100, Heraeus, Germany) over a temperature range of 28 to 42 °C in 2 °C increments before implantation. To investigate if drift in temperature measurements might have had occurred during the period over which a logger was implanted, I re-calibrated each logger with the same method once it had been removed from an aardvark. No drift had occurred, as the mean difference between the data points after the first calibration and the temperature at the second calibration as measured by the high accuracy thermometer remained < 0.1 °C. After calibration, the loggers measured body temperature to an accuracy of better than 0.05 °C.

2.3.2 Activity

Activity loggers recorded locomotor activity of each study aardvark. Different loggers were used during different years of the study. In the first year (2012 to 2013), I used Actical loggers (Mini-Mitter Corporation, USA; mass ~40 g when covered in wax). Acticals were tri-axial piezoelectrical accelerometers sensitive to forces of > 0.05 *g*, and were set to record whole-body movement over full 5-minute-periods.

In the following years (2013 to 2015), manufactured activity loggers (MLOG_AT1, Sigma Delta Technologies (Pty) Ltd., Australia) with a triaxial accelerometer sensitive to forces of > 0.04 *g* (ADXL345 Digital Accelerometer, Analog Devices, Inc., USA; mass ~25 g when covered in wax) served to record aardvark locomotor activity over a period of 10 seconds at 5-minute intervals. The use of these biologgers, validated with visual field observations, has previously proven successful in assessing behavioural activity in a wild, free-living large mammal (McFarland et al., 2013). Although these loggers measured activity as well as temperature data, we only used the activity data from these loggers as the StarOddi temperature data loggers had a better resolution.

To account for differences in the sensitivity of individual activity loggers (both models) and in activity intensity of individual aardvarks, each 5-minute reading of activity was expressed as a percentage of the maximum activity reading for each logger while implanted in an aardvark (% of maximum). For each aardvark and each 24-h period, I calculated mean activity (% of maximum), maximum activity (% of maximum) and total activity (sum of counts across 24-h).

2.4 Aardvark observations

2.4.1 Behavioural observations

I observed aardvarks and recorded their behaviour to determine their time of emergence, body condition, and general behavioural repertoire. I conducted behavioural observations from a nearby, downwind location to avoid interfering with an aardvark's behaviour. However, the wary, elusive and generally nocturnal nature of aardvarks, and inability to habituate the aardvarks, made observations difficult. When an aardvark was diurnal, I was able to observe it from a distance using binoculars, thus preventing the aardvark from hearing me, as well as from likely seeing me (as aardvarks are considered short-sighted). However, when an aardvark was nocturnal, I had to get within torch range (≤ 20 metres) of the animal to observe behaviours, making it difficult not to alert it as it could hear the slightest rustling of leaves or clothes, or footsteps crunching on dry grass. Since the objective of the study was to obtain data from undisturbed animals, I was only able to record behavioural data from diurnal aardvarks from July to September 2013, and for a brief period in July 2014. During aardvark observations, I used category codes (Table 2.2) to record different types of behaviour based on Altmann (1974). I recorded aardvark behaviour in 5-minute-intervals, timed to match the automated recordings of activity data loggers. Often, an aardvark was obscured by vegetation during the moment I had to observe its behaviour, resulting in a gap in the observation record. Whenever I had the impression that an aardvark's behaviour was affected by my presence (e.g., increased vigilance behaviour), I aborted the observation and left the aardvark. I obtained a total of 458 observations, or ~38 hours of observations, on 9 aardvarks on 29 different days. I later compared aardvark behavioural observation data to activity data from loggers (see Chapter 4).

2.4.2 Camera trap footage

Camera trap footage served to determine the time of emergence from a burrow, and time of departure to forage when an aardvark did not leave the burrow location immediately after its emergence. I also used camera trap footage to determine the time of return to a burrow after foraging, in those cases when an aardvark returned to the same burrow from which it had emerged. Between July 2013 and September 2015, I located each aardvark inside its burrows several times per month using VHF tracking and placed camera traps (MMS wireless scouting camera, LTL-6210MC HD series, Ltl Acorn, China) at burrow entrances to record the aardvark's emergence and its body condition. Each aardvark changed burrows frequently, therefore I could not use a fixed camera trap system. Instead, I attached these camera traps to large-diameter sticks embedded in the ground either behind the burrow entrance or downwind of the burrow to minimize disturbance of the aardvark. I usually programmed the camera traps to take 3 photographs in 1-second-intervals, followed by a 10-second video. Camera traps then had a period of ~1 minute during which time they could not be triggered. Occasionally, camera traps fell over due to strong winds, were knocked over or carried away by animals (notably porcupines and warthogs), or suffered technical failure. Over the study period, I obtained 18 records of an aardvark emerging from a burrow to bask, 408 emergences to forage (including the departures after basking bouts), and 107 recordings of an aardvark returning to a burrow. I analysed all camera trap footage manually image by image.

Table 2.2 Behavioural observation coding system used to record aardvark behaviour.

Variable	Subcategory	Intensity	Type of behaviour
Activity	Movement	0	none
		1	walking
		2	trotting
		3	running
	Digging	0	none
		1	light digging (forelegs only)
		2	heavy digging (fore- and hindlegs)
	Foraging	0	none
		1	sniffing for prey
		2	scratching ground
		3	digging
		4	feeding
	Vigilance	0	none
		1	freezing / sniffing air / ear-movement / other
	Other	-	defaecating / basking / grooming / scratching / drinking / mating / ...
Microhabitat	Sun	0	none (cloud cover / night)
		1	yes (exposed to direct sunlight)
		2	no (in shade)
	Wind exposure	0	none
		1	yes (exposed to wind)
		2	no (sheltered)
	Habitat	1	completely open (road / no vegetation)
		2	grass
		3	shrubs
		4	thick bush
	Location relative to dune	1	on dune crest
		2	eastern slope
		3	western slope
		4	in dune valley (no slope)
Encounters (animals closer to aardvark than observer)		0	no other animals present
		1	birds
		2	herbivores
		3	carnivores
		4	other ant-eating specialists and opportunists
		5	other aardvarks (ID recorded if known)
Weather	Cloud cover	0	none
		1	25 % cloud cover
		2	50 % cloud cover
		3	75 % cloud cover
		4	100% cloud cover
	Wind	0	still or breezy
		1	windy

2.4.3 Notes on burrow use

Between July 2013 and September 2015, I located each aardvark inside its burrows several times per month using VHF tracking. During the dry winter of 2013 after the drought, when the aardvarks were in poor condition, I observed that aardvarks frequently re-used the same burrow for several consecutive nights or switched between the same two or three burrows over several weeks. The longest period of consecutive use of the same burrow in one aardvark (aardvark 9) was 14 days during the winter 2013 after a summer drought. During all other seasons and years, my study aardvarks changed burrows nearly every day, and seldom re-used burrows on consecutive days, such that on 620 non-consecutive days between July 2013 and September 2015, I located twelve study aardvarks in 362 individual burrows, with aardvark 9 alone in over 100 different burrows. During the entire duration of the study, Aardvarks seldom refurbished burrows in which I had previously located them.

2.4.4 Body condition

During aardvark observations and analysis of camera trap footage, I scored aardvark body condition on a visual appearance scale (Figure 2.7 A, B) based on a system commonly used for scoring physical condition of livestock (Russel, 1991; Thompson & Meyer, 1994). The scale ranged from 1 = ‘emaciated’ to 5 = ‘obese’, which I termed ‘overweight’ for this study since pathological obesity is unlikely to occur in an animal in its natural environment (Table 2.3). This non-invasive scoring system worked reliably on aardvarks because their body shape and musculature are readily visible and not concealed by dense pelage. I analysed all camera trap footage manually image by image. I found no discrepancy between body condition scores obtained from simultaneous live observations and camera trap imagery of the same animal. I recorded a total of 314 aardvark body condition scores from 12 study aardvarks in the period from July 2013 to September 2015, with varying numbers of observations per aardvark.

Table 2.3 Aardvark body condition scoring system (adapted from Russel, 1991; Thompson & Meyer, 1994)

Score	Body condition characteristics
1	emaciated, severely underconditioned (hip bones, spine processes & small ribs well visible)
2	thin (hip bones & spine processes fairly visible)
3	ideal / average (defined muscles)
4	fat (muscles covered with fat layer)
5	overweight

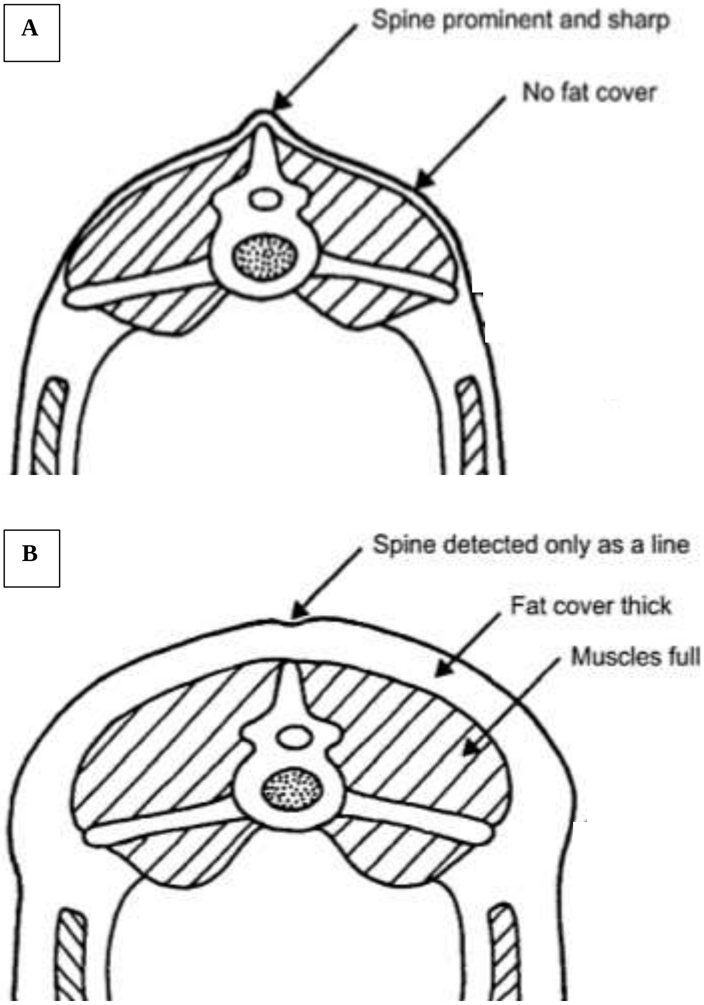


Figure 2.7 Body condition scoring in aardvarks adapted from a livestock body condition scoring system by Thompson and Meyer (1994): A) characteristics of body condition score 1; B) characteristics of body condition score 4.

2.5 Aardvark diet

2.5.1 Scat collection

I collected scats from six non-habituated study aardvarks at Tswalu between July 2013 and September 2015, either at night by following an aardvark after its emergence, or by tracking its fresh spoor from a burrow the following morning until at least one and up to three defaecation sites along the spoor trail were located (Figure 2.8). To locate as many defaecation sites as possible, I traced an aardvark’s spoor back in the direction from which it had entered the burrow, as well as the spoor that led away from the burrow after it had emerged. On several occasions, I was able to trace one or both these spoor trails far enough to locate multiple defaecation sites, however, sometimes I could not find any scats as the spoor had been destroyed by strong wind or rain, or overlaid by other animals’ tracks. Study aardvarks generally defaecated either shortly before entering or after leaving a burrow, in varying distances along the spoor trail. An aardvark deposits its scats in a shallow furrow which it then covers up, leaving behind a distinctly shaped mound of soil. In a previous study on aardvarks in the Karoo (Taylor, 1998), some individuals became habituated to human presence, and these individuals could be followed closely for entire nights. They were found to defaecate on average six times per night (Taylor, 1998). Similar to aardvarks in the Karoo (Taylor et al., 2002), the scats of aardvarks (Figure 2.9) at Tswalu generally comprised collections of 20 to 50 oval-shaped, 15 to 20 g pellets which had a large sand component, ingested by the aardvark during foraging. The pellets were dark in colour and glistened with chitinous remains of the insect prey. I collected a total of 133 scats from 6 study aardvarks at Tswalu between July 2013 and September 2015.

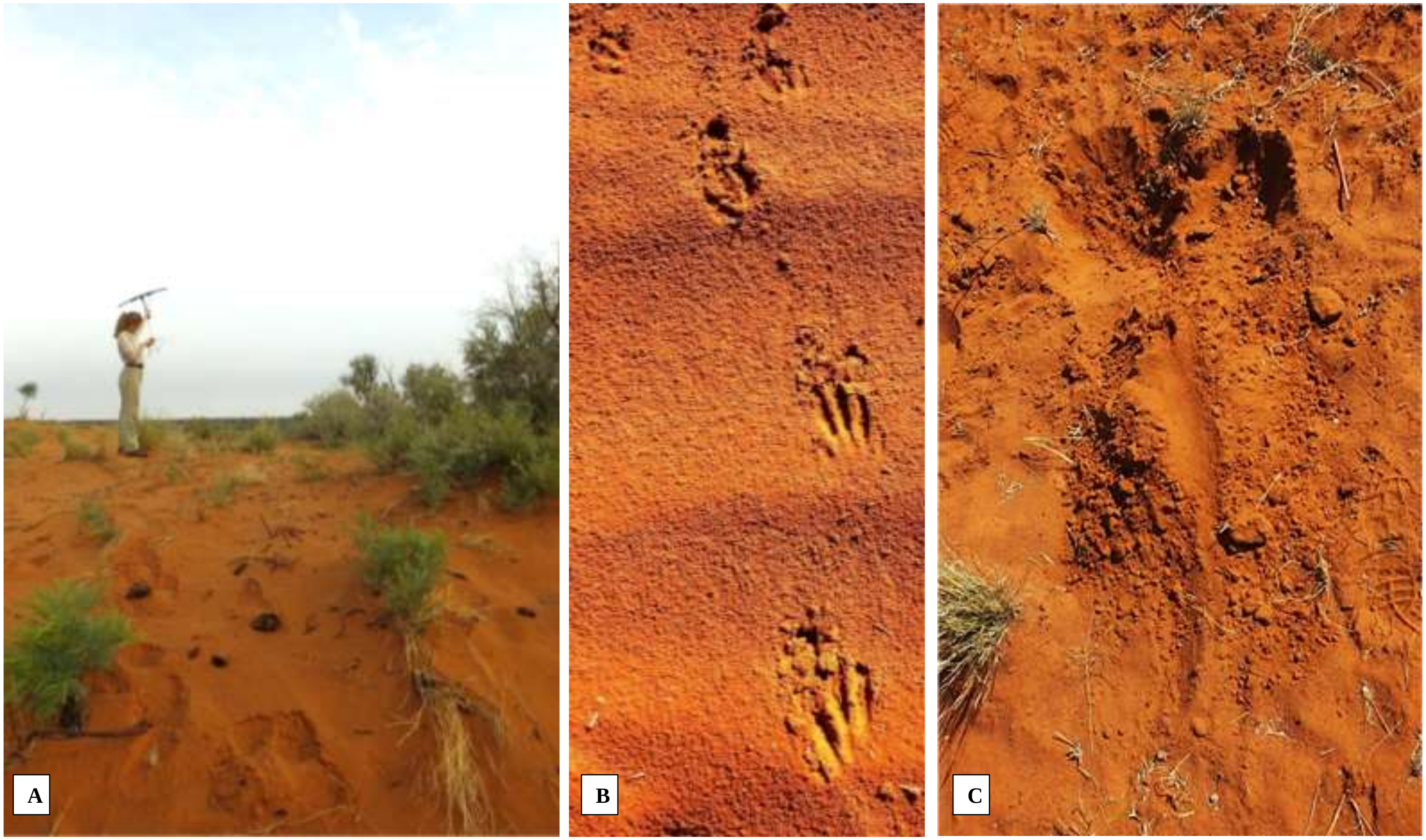


Figure 2.8 Aardvark tracking. A) Myself on a dune top at Tswalu Kalahari Reserve, using a VHF tracking kit to locate a study aardvark (photo credit: Alex Baade); B) aardvark spoor trail in the sand (photo credit: Nora Weyer); C) aardvark defaecation site (photo credit: Nora Weyer).

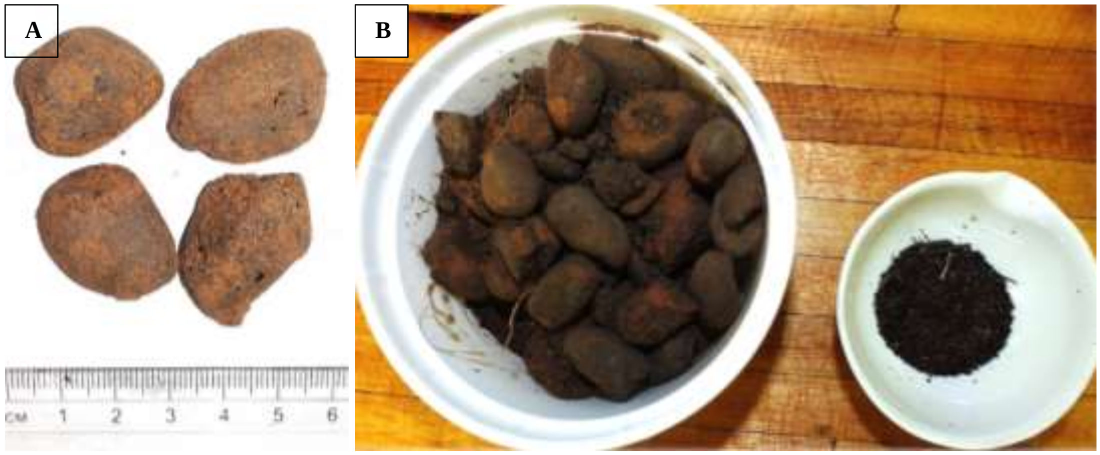


Figure 2.9 Aardvark scats. A) Four aardvark scat pellets. B) Left bowl contains a complete aardvark scat deposit, right bowl contains the dried prey remains isolated from a scat deposit by the washing procedure described in section 2.5.2.

2.5.2 Aardvark scat analysis

I adapted sample preparation protocols for scat analysis from previous studies on aardvark diet (Melton & Daniels, 1986; Taylor et al., 2002). I did not include wet mass of fresh scats in the analyses because of a number of variables that could influence scat wet mass, for example aardvarks often urinated into their defaecation furrows, thereby affecting the moisture content and mass of the scats, and because of variation in time elapsed between defaecation and sample collection (from 5 minutes to several days). I allowed all scats to air-dry for at least 14 days before analysis, and I recorded the dry mass of each scat deposit to the nearest 0.5 g before separating the organic from inorganic fractions contained in the scat. I gently dissolved the pellets of each scat deposit in a 5 L bucket containing ~2 L hot water, and soaked them for ~15 minutes to allow the organic matter contained in the dried scats to float to the surface and to subsequently separate them from the heavier sand fraction using a fine mesh net (0.1 mm mesh diameter). Insect remains floated to the surface as the insect cuticle contains lipids (Hackman, 1974). Without stirring, I poured the suspension through the fine mesh net to isolate the organic (floating) component. I again mixed any sand remaining at the bottom of the bucket with ~4 L cold water under high pressure and poured suspended matter through the net. I repeated this procedure until no further suspended matter appeared in the sample. The organic matter isolated from each scat deposit was dried in a ventilated oven at ~60 °C for 3 days to constant mass, and re-weighed to obtain the proportion of organic material contained in each aardvark scat sample (Figure 2.9). As scats contained very large numbers of individual insect fragments, I employed a subsampling system to quantify the number of each prey species present. I used a range of subsample masses where I counted each insect fragment to compare, to determine an appropriate minimum subsample size. I counted the number and proportions of various prey items (ant and termite head capsules and jaws) in the scats in subsamples ranging from 0.04 to 0.32 % of the scat deposit (0.1 to 0.8 g) and extrapolated these values to the real numbers and proportions to the total mass of the entire scat deposit. Subsamples of ≥ 0.3 g resulted in nearly identical estimates of total prey item numbers in the whole scat. Thus, I subsequently subsampled an aliquot of 0.4 to 0.7 g of the dry organic contents of each scat sample, and thinly spread the contents onto a transparent polyacrylamide gel plate overlying a grid under a dissection microscope (SMZ800 zoom stereomicroscope, maximum magnification 63x, Nikon Instruments Europe B.V.) for analysis of prey items using a genus reference collection (see section 2.9). Prey items occurred in three forms: (1) head capsules with a mandible pair attached, (2) head capsules with mandibles missing, and (3) individual mandibles detached from head capsules. To standardise counts, I made a score of a single individual when (1) both mandibles were still attached to the head capsule and (2) when I found a head capsule missing mandibles + a pair of loose mandibles of the same prey item. I counted a total of 76 200 identifiable prey remains within the different categories: (1) 25 414 mandible pairs (50 828 single mandibles), (2) 13 527 heads with mandibles attached, and (3) 11 845 heads without mandibles in the aardvark scat subsamples. In 422 cases (0.9 % of all samples), discrepancies between categories 1 (mandible pairs) and 3 (heads lacking mandibles) occurred. For these cases I chose the greater of the two values for all subsequent calculations, to avoid underestimating the occurrence of a prey item, and added this value to the count of intact head capsules with mandibles still attached, resulting in a total of 46 794 individual ants and termites counted in the subsamples. Discrepancies of categories 1 and 3 for the Northern harvester termite *H. mossambicus* occurred in only 0.01 % of all samples. The mandibles of the snouted termite *T. trinervoides* are minute and were too small to be isolated by the fractionation methodology, although their head capsules and 'snouts' (i.e., the characteristic conical process of the head capsule) were captured. I thus counted heads with snouts, without snouts, and snouts detached from heads, and found virtually no discrepancy in numbers of head capsules without snout, and numbers of loose snouts. For the three most important ant genera in Tswalu aardvark diet, such discrepancies were also few (*A. custodiens* 1.7 %, *Dorylus* sp. 1.8 %, *Pheidole* sp. 2.5 %). For subsequent analyses, I extrapolated counts of prey items in the subsample to counts per 1 g dry scat mass.

2.6 Plant productivity and aardvark prey abundance

2.6.1 Plant productivity

I assessed grass cover as a proxy for plant productivity at the study site, because grass is the primary food source of many ant and termite species occurring at the study site (Nel & Hewitt, 1969a; Ohiagu, 1979; Marsh, 1987). I conducted estimates monthly at 30 permanent sites for 16 months (May 2014 to August 2015). I randomly selected the sites in grass- and shrub-dominated areas within the foraging range of the study aardvarks. Sites were at least 300 m apart from one another and consisted of a 50 m line-transect between two permanent markers. I placed 2 x 2 m quadrats at 10-metre-intervals along the 50 m line-transect at each of the 30 permanent sites (i.e., 5 quadrants per line-transect, resulting in 150 grass cover estimates per month), within which I (1) counted all grass clumps with more than approximately 30 green culms; (2) measured the height of five randomly chosen green grass clumps (where fewer than five grass clumps were available, I scored the missing grass clumps as 0 mm); and (3) estimated grass cover (%) within the quadrat. I first obtained a median value for each measured variable per site, and then calculated a median value across the 30 sites for each of the 16 months of measures of plant productivity within the aardvark study site. For a long-term plant productivity index that encompassed the full duration of this study, I obtained mean values of MODIS-derived time-series enhanced vegetation index (EVI) for the Gordonia duneveld vegetation type predominant at the study site at Tswalu (Figure 2.2) for January 2012 to December 2015 from Tokura (2016), which I compared to my monthly data for grass cover from May 2014 to August 2015 to validate the use of EVI with on-site measurements as I describe in Chapter 3.

2.6.2 Social insect abundance

Potential aardvark prey items at Tswalu exhibited different activity patterns: ants were active surface-foragers, while termites were more cryptic and did not forage far from their colonies. The predominant ant and termite species at the study site formed extensive subterranean colonies often many metres below soil surface, and also with superficial galleries (Figure 2.10); ant and termite species in other arid zones also have colonies deep in the soil profile (Hartwig, 1965; Mitchell et al., 1993; Tevis, 1958; Tschinkel, 2011). There were no mounds of any ant or termite species above the soil surface at the study site. A direct method of scoring absolute numbers of subterranean ants and termites does not exist. While pitfall-traps adequately sample ants (Andersen, 1991), they are less effective in sampling subterranean termites which either forage under soil sheetings or in grass clumps and rarely fall in pitfall traps. Termites are thus more commonly assessed using indirect, visual methods (Picker & Moore, 1991; Geerts et al., 2016). *H. mossambicus* termites deposit excavated debris and other waste material from their colony activity in soil-dumps (soil heaps, frass heaps) at the surface. These soil-dumps are distinctly cone-shaped and easily visible on the ground (Figure 2.11A), and reliably indicate activity of below-ground *H. mossambicus* colonies (e.g., Hartwig, 1965; Nel & Hewitt, 1969a; Braack, 1995). I focussed on this termite as it was a dominant termite dietary item in aardvark scats. *H. mossambicus* (Figure 2.11B) is a harvester species that forages mainly on frost-killed dry grass, but also on green grass (Nel & Hewitt, 1969a; Duncan & Hewitt, 1989).

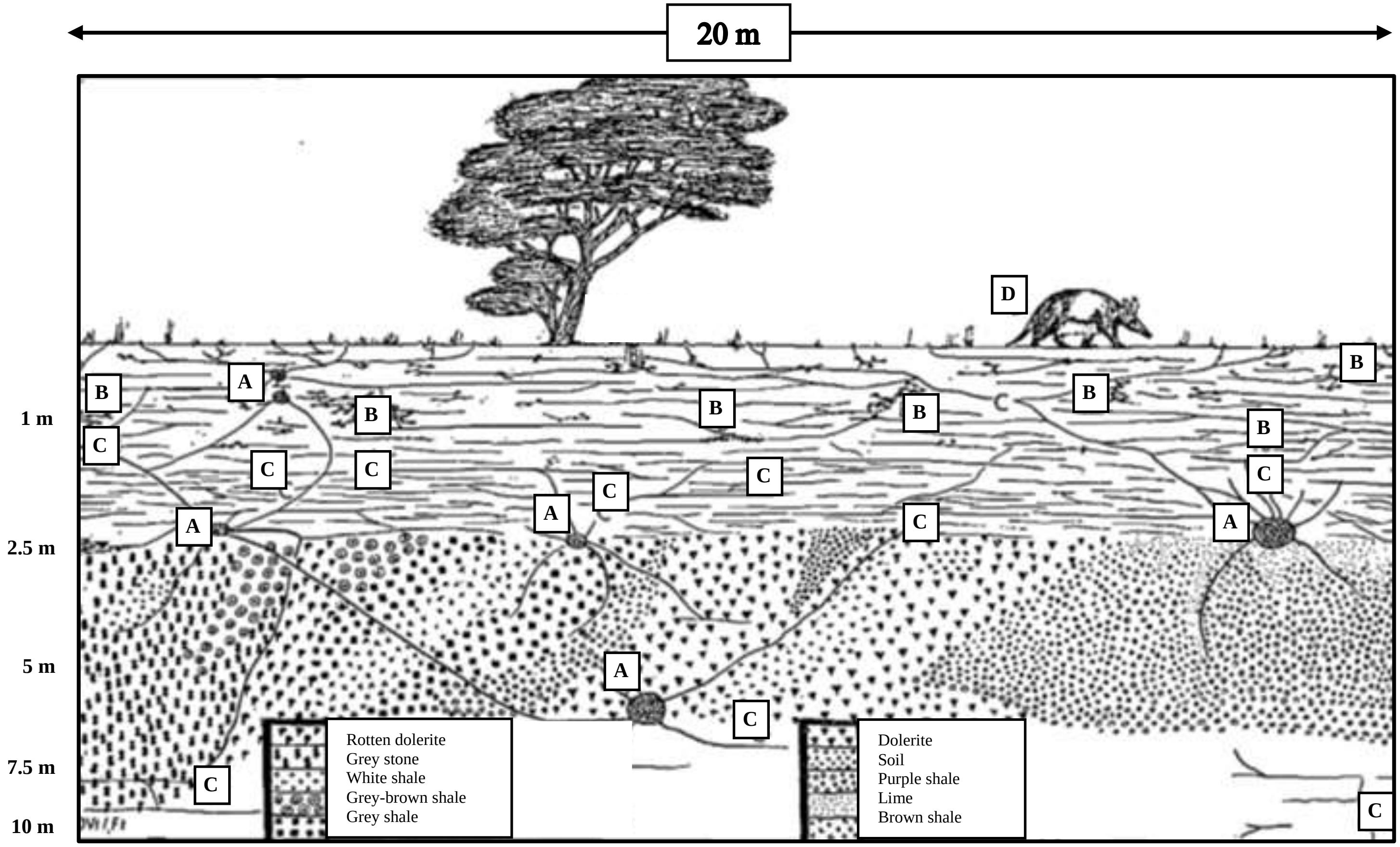


Figure 2.10 Typical colony structure of an important aardvark prey species, the northern harvester termite Hodotermes mossambicus, through varying types and depths characteristic of the area near Bloemfontein in the Freestate Province of South Africa, adapted from Hartwig (1965). A - termite hives; B - temporary storage chambers for harvested grass; C - passages connecting hives, storage chambers, and soil surface; D - a foraging aardvark. Note that some passages can reach many metres deeper but are only depicted to a depth of ~10 m below ground here. Though soil characteristics of the Bloemfontein area differ from those of the Kalahari (Johnson et al., 2008; Pietersen et al., 2010), the colony structure can be expected to be similar in both regions as harvester termites use similar colony structures in different habitat types (Becker & Getzin, 2000).

Figure 2.11 Field signs of the northern harvester termite *Hodotermes mossambicus* at Tswalu Kalahari Reserve. A) Soil excavations indicating tunnelling activity underground; B) *H. mossambicus*-workers actively harvesting dry grass at the soil surface.

Therefore, during monthly plant-productivity-assessments, I assessed the abundance of ants and termites along the same 30 permanent sites using the following sampling routines. (1) Along the 50 m line-transect and within 1 m to each side of the line, I assessed the activity of *H. mossambicus* colonies visually, by counting frass heaps and soil dumps, and scoring surface foraging-activity of *H. mossambicus* workers on an approximate scale from 0 (absent) to 5 (intense). I calculated monthly median values for frass heap and soil dump counts and for surface activity scores for each of the 30 sites. (2) Along the same 50 m line-transect, I dug 10 pitfall-traps into the ground at 5-metre-intervals, and added 3 spare traps randomly in-between. After 4 days, I collected the trap contents of 10 traps and discarded the contents of the spare traps, or if a trap had been removed or sand-filled by wind or animal activity, I replaced it with the contents of a spare trap placed at that transect to ensure collecting contents of 10 traps per transect in each month, generating a trapping sampling intensity of 1 200 trapping days per month, and 19 200 trapping days in total. Traps consisted of 50 mL centrifuge vials (mouth diameter 27 mm; Falcon®, Corning Inc., USA) filled with 20 mL non-attractant fluid (1:10 commercial glycerol-based antifreeze-agent in water, modified after Majer, 1978). I combined trap-contents at each site, resulting in 30 samples per month, and a total collection of 480 samples over the 16-month sampling period. I stored trapped ants and termites in 90 % ethanol at room temperature (~25 °C). For microscopic identification, I first separated ants and termites into different morphospecies, which I then identified to genus-level using a reference collection compiled from samples I had collected previously over a year at Tswalu (see sections 2.9 and 2.10). When traps from a single site contained > 500 ants and termites from one sampling event, I analysed a subsample of ~20 % of the original wet volume, and extrapolated numbers of ants and termites counted in the subsample to the full sample volume. On occasion, more pitfall traps than replaceable with spare traps were excavated by various fossorial animals, filled with sand due to strong wind, or flooded with rainwater. Thus, for each month, I combined the counts of all transects and divided them by the number of traps collected to obtain an average value per trap. I provide a detailed description of further analyses of the insect abundance sampling in Chapter 3.

2.7 Overview of data collected between January 2012 and September 2015

The presented study started in July (winter) 2012, and rainfall and vegetation productivity of the preceding summer were considered in this study. During the first year of the study, study aardvarks were implanted with data loggers and tracking devices, but were not visually observed, and no camera traps were placed regularly. I was based on-site at Tswalu from July 2013 to September 2015 to validate biologger data on aardvark activity via behavioural observations and camera trap footage, to collect scats, and to record aardvark body condition. I also assessed on-site vegetation productivity and aardvark prey abundance from May 2014 to August 2015. A timeline of the data collected for this study is presented in Table 2.4. Following the field research period (January to July 2015), I conducted laboratory-based analyses of aardvark diet, prey abundance samples, and energy and water content of aardvark prey insects.

Table 2.4 Overview of data collected for this study at Tswalu Kalahari Reserve between January 2012 and September 2015. MODIS-EVI data on Gordonia duneveld vegetation productivity were kindly provided by Mr Wataru Tokura (pers. comm.; see also Tokura, 2016). Air temperature data were kindly provided by Dr. Andy Young, Tswalu White-Browed Sparrow Weaver Research Group, Exeter University. Rainfall data for Tswalu for January to December 2012 from the Tswalu Rainfall Database were kindly provided by Mr Dylan Smith, Tswalu Kalahari Reserve. Timing of sunrise and sunset, and % lunar illumination were obtained online for the town of Upington from Time and Date AS, Norway, http://staging.timeanddate.com. Aardvark body temperature and activity data from implanted data loggers for July 2012 to July 2013 kindly provided by Dr Benjamin Rey, Brain Function Research Group, University of the Witwatersrand.

Year	2012												2013												2014												2015								
Month	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S
Rainfall	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
Air temperature	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨		▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
Sunrise time	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
Sunset time	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
Lunar illumination	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
EVI	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
On-site vegetation																													▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
Prey abundance																													▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
Scats																			▨	▨	▨	▨	▨	▨		▨	▨	▨	▨		▨	▨		▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
Body condition																			▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
Body temperature							▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
Activity (logger)							▨	▨	▨	▨	▨	▨	▨	▨	▨				▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨				
Activity (camera trap)																			▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨

2.8 Energy and water content of prey

2.8.1 Wet and dry mass

After having determined that aardvark diet was dominated by three prey items (the termites *H. mossambicus*, *T. trinervoides* and the ant *A. custodiens*), I collected large numbers of live individuals of these species at Tswalu. Once freed from adhering debris such as sand or plant matter, I counted live individuals, weighed them collectively to the nearest 0.0001 g (Ohaus® Adventurer^{TM} AR 3130 electronic balance, Ohaus Corporation, USA) to obtain wet mass, then froze, and subsequently dried them in a ventilated oven at ~48 °C for 72 h to constant mass, after which I recorded the dry mass of the insects. I carried out the same procedure for eight samples of *T. trinervoides* (workers and soldiers mixed), two samples of *A. custodiens* (workers and soldiers mixed), and two samples of *H. mossambicus* (workers only). Numbers of individuals varied in each sample but included a minimum of 50 individuals per sample.

2.8.2 Bomb calorimetry

To maintain dryness, I stored dried prey insects inside a sealed desiccator containing silica gel. For measurements of each species' energy content, I combined its dried samples and ground them to a fine powder using mortar and pestle. For each of the three species, I subsampled 10 aliquots of 0.2 to 0.3 g and measured their energy content using a bomb calorimeter (Cal2K Calorimeter System, Digital Data Systems (Pty) Ltd., South Africa), calibrated with benzoic acid as a standard. I averaged the energy values (kJ g^{-1}) of the 10 replicates per prey item and then calculated the energy value of a single prey individual (kJ $individual^{-1}$) of that particular species.

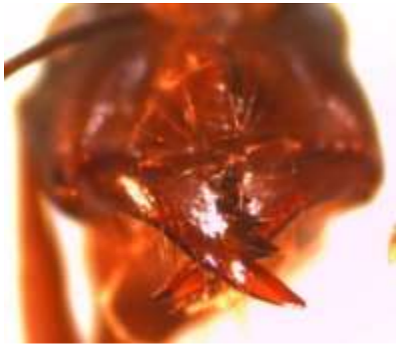
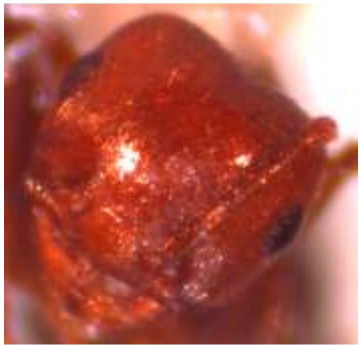
2.9 Insect reference collection

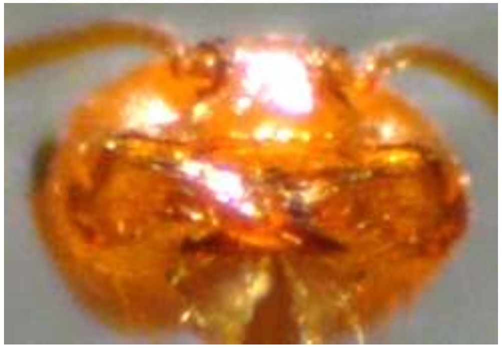
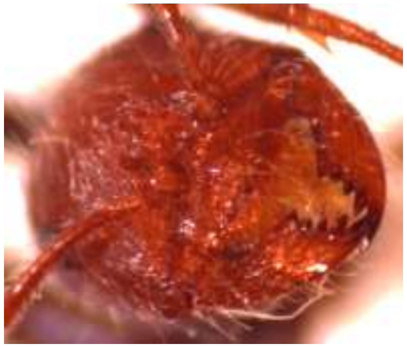
I compiled a photo-reference collection to identify isolated mandibles and head capsules of all prey items contained in aardvark scats (see section 2.10) to genus level. This reference collection comprised pitfall-trapped and hand-collected ants and termites across the study site. Insects caught from one colony were kept separately from insects caught at another colony to avoid potential mixing of different taxa. All insects were stored in 90 % ethanol until further processing in the lab. From this collection, I generated a photo-reference collection of the mandibles of all collected ant and termite genera. Some images from this photo-reference collection are shown in Table 2.5 and Figure 2.12. Ant mandibles are highly variable in shape and number of teeth (Hölldobler & Wilson, 1990), providing multiple identifying characters. Much of an insect's body is destroyed by aardvarks′ digestive tract and the grinding action in combination with large volumes of ingested sand, with the result that typically only head capsules (with or without attached jaws) and isolated jaws remain in the scats (Figure 2.12). I identified the dry, carded reference collection of ants (including their dissected out mandibles) and alcohol-preserved collection of termites to genus level using available ant (Scholtz & Holm, 1985; Hölldobler & Wilson, 1990) and termite (Uys, 2002) keys and photographed them using a photomicroscope (Leica LasEZ photomicroscope and image processing software, Leica Microsystems Ltd., Switzerland). For subsequent identification of ants and termites caught in pitfall traps, as well as those contained in aardvark faecal samples, I also created a photographic collection of ants and termites noting diagnostic details (Table 2.5). Of each taxon, I took full-body photographs in dorsal and lateral view, and of the head capsule (all aspects including frontal view with mandibles and antennae spread away from the face where possible to expose the face, allow for counts of antennae segments, and later be able to link mandibles to the head and body to which they were attached by their shape). I then carefully detached the mandibles from the head and photographed them separately.

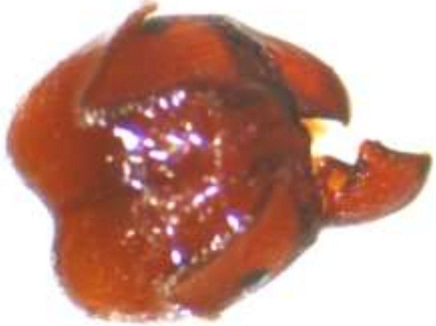
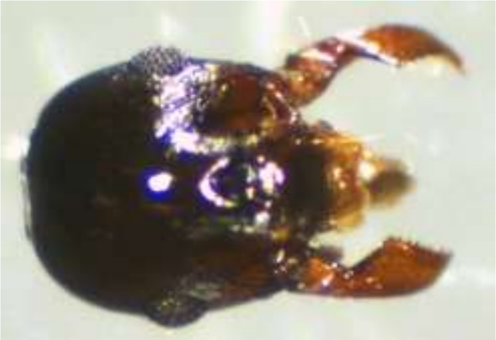
2.10 Photo-reference collection

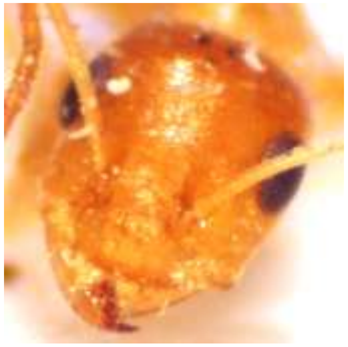
Table 2.5 A selection of intact ants and termites, with their head capsules and mandibles occurring in the diet of aardvarks at Tswalu Kalahari Reserve (photo credit: Nora Weyer).

Genus and relevant notes	Full body view	Facial view showing mandibles
Anochetus - Large, slender ant - Unusual head shape - Mandibles long, with two teeth bent inwards by >45° - Mandibles can open nearly 180°		
Anoplolepis - Large, orange or red, with dark abdomen - Much larger than *Pheidole* - Head heart-shaped, red - Mandibles with 6 to 9 teeth - unarmed		

Camponotus - Large ant - Abdomen smooth in some species, hairy in others - Large round head - Large eyes - Colour: dark brown to orange to yellow - Mandibles with 5 teeth, no ridges, smooth surface - unarmed		
Cerapachys - Large, slender, black ant - Long head - Giant eyes - Mandibles large, shovel-shaped with serrated edge - unarmed		
Crematogaster - Eyes on the side of the head - Abdomen (missing on photo) can bend upwards via special joint - Wide distance between antennae - Mandibles with 4 teeth - Armed with spines		

Meranoplus - Very small, golden, hairy ant - Armed with large spines - Club-like antennae - Mandibles very small, golden, with few orange teeth		 ,
Monomorium - Small, yellow ant - Head almost square-shaped - Mandibles small, with few teeth - unarmed		
Ocymyrmex - Long legs - small, stalked abdomen - very hairy - mandibles large, with ridges, 5 teeth - unarmed		

***Pheidole* (dimorphic) - large worker** - seed-cracker worker - large, almost hear-shaped head head - large, blunted mandibles, often no teeth left - small spines		
***Pheidole* (dimorphic) - small worker** - small, round head - Beady, protruding eyes - Elongate, serrated mandibles - Small spines		
Plagiolepis - Black body - Dark red mandibles with 5 teeth - unarmed		

Tapinolepis - Yellow ant - size and shape very similar to *Anoplolepis* - only ant with 3 ocelli in triangle on forehead - mandibles yellow, with 5 orange teeth - unarmed		
Tetramorium - head square-shaped - mandibles with 6 to 11 teeth, often filed off - armed with spines		

Psammotermes - head square-shaped, sandy-beige - mandibles orange-red to purple, curved inward and upward - full body photo not available	- - -	
Hodotermes - head black, glossy - body large, yellowish-brown - thick, broad mandibles, orange at base, dark to black teeth		
Trinervitermes - small termite, light body colour - head capsule orange-brown, with rostrum in the soldier caste - photo shows two soldier individuals; worker photo not available		

Figure 2.12 Comparison of head capsules and corresponding mandibles of three main aardvark prey items at Tswalu Kalahari Reserve, isolated from aardvark scats, indicating size differences of the different prey items. All images at the same scale. A) Northern harvester termite *Hodotermes mossambicus*, head capsule and mandible of a soldier; smaller mandibles belong to a worker; B) pugnacious ant *Anoplolepis custodiens* worker head capsules and isolated mandibles, as well as one partially-preserved worker head; C) snouted termite *Trinervitermes trinervoides* soldier head capsule (mandibles not displayed), with snout-like rostrum (photo credit: Nora Weyer).

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Chapter 3 - Drought reduces aardvark body condition and survival in a semi-desert through disruption of trophic cascades

3.1 Introduction

Rapid climate change is expected to drastically alter rainfall patterns, and to increase temperatures and surface evapotranspiration in southern African semi-arid zones such as the Kalahari (Le Roux et al., 2016; Niang et al., 2014; Pachauri et al., 2014; Russo et al., 2016). Increasing heat and aridity directly impacts the physiological performance of animals, as greater heat load can compromise their water economy (Fuller et al., 2014; Fuller et al., 2016; Hetem et al., 2014). Indirectly, animals might be affected by trophic cascade interruptions originating from reduced primary productivity that affects prey species abundance (Schleuning et al., 2016). The rapid rate of current climate change puts large mammals at a pronounced disadvantage because of the lifestyle characteristics associated with large body mass (Cardillo, 2005). Indeed, climate change has already negatively affected numerous animal species, including hundreds of mammal and bird species (Parmesan & Yohe, 2003; Pacifici et al., 2017). In addition, specialist feeders are particularly vulnerable to the consequences of climate change (Pacifici et al., 2017).

Aardvarks are large mammals that are dedicated myrmecophages, specialising on a diet of ants and termites (Melton & Daniels, 1986; Taylor et al., 2002; Willis et al., 1992). Aardvarks have to cover all their nutritional (and often water) requirements from their insect prey (Taylor et al., 2002, Redford & Dorea, 1984, Redford 1987). Although the impact of climate change on social insect populations in hot and arid climates is still uncertain (Jenkins et al., 2011; Shiday et al., 2011; Huey et al., 2012), they are likely to be impacted in similar ways to vertebrates (Ehrlich et al., 1980; Huey et al., 2012; Kearney et al., 2009; Kingsolver et al., 2013; Parmesan, 2006). Drought-related reductions in primary productivity can result in severe crashes of termite populations, and affect ant abundance (Nel & Hewitt, 1969a; Marsh, 1987). As a result, summer droughts might indirectly compromise the survival of aardvarks, and other myrmecophages, through trophic cascades linked to reduced primary productivity.

Mass mortality and poor nutritional state of aardvarks has been observed during and after severe summer drought periods in southern African semi-arid zones (Stuart & Stuart, 2007; Rey et al., 2017). Increased frequency and intensity of summer drought in the Kalahari, a consequence of climate change (Russo et al., 2016), might therefore have devastating consequences on the aardvark population, in turn jeopardizing the continued existence of those animal species dependent on aardvarks' burrows (Whittington-Jones et al., 2011). However, no studies have examined the diet, seasonal fluctuations in resource availability, and their impacts on the physiological well-being of aardvarks in the Kalahari, an area where these cryptic mammals exist at the arid extreme of their range. An understanding of the dietary requirements of aardvarks under current conditions is crucial to predicting their ability to tolerate increasing aridity and heat anticipated across their range.

Although the dietary composition of aardvarks in the Kalahari has not been studied, they reportedly consume those species most abundant in their home ranges (Willis et al., 1992). The northern harvester termite *H. mossambicus*, which contributes to diet of aardvarks in the Karoo, is abundant in the southern African summer rainfall region, where it is a key grass-harvesting animal (Hartwig, 1965; Nel, 1968, 1970). I hypothesized that summer drought in the Kalahari would impact standing crop of vegetation in semi-arid habitats, thereby generating reduced primary productivity (lower grass abundance), which would directly impact grass- and plant seed-harvesting insects such as ants and termites (Nel & Hewitt, 1969a; Ohiagu, 1979; Marsh, 1987). Secondary consumers having a strong and specific reliance on these particular prey items (Kok & Hewitt, 1990) would in turn face increasing shortages of ant and termite prey as these social insect colonies decline following drought (Nel & Hewitt, 1969a), leading to physiological stress and possible death of the secondary consumers.

To understand responses of aardvarks to seasonal fluctuations in resource availability, I recorded seasonal changes in body condition of aardvarks over more than two years (26 months). I assessed seasonal variation in abundance and availability of termites and ants in relation to inter-annual and seasonal fluctuations in temperature, rainfall and measures of vegetation productivity in the Kalahari semi-desert over 17 months. I then compared these patterns with prey composition in aardvark scats across different seasons over two years. I also measured water and energy content of major prey items to establish their contribution to and importance in Kalahari aardvark diet. I present the first records of nutritional compromise and subsequent recovery of aardvarks in response to summer drought, and propose that the threat of climate change on aardvarks is greater than previously considered.

3.2 Methods and materials

3.2.1 Climatic variables at the study site

Climatic variables were recorded within a few kilometres of the study site over the period January 2012 to September 2015 (Chapter 2). To obtain monthly minimum, mean, and maximum air temperatures, I averaged 24-h minimum, mean, and maximum air temperatures, respectively, for each month. Similarly, I calculated mean ± SD air temperature at 1-h-intervals for each season (summer: December to February, autumn: March to May, winter: June to August, spring: September to November) from winter 2012 to spring 2015 (Figure 2.4). I calculated total rainfall per month based on daily rainfall data from the Tswalu rainfall database for the period January to December 2012, and from a rainfall event logger (HOBO Pendant Event data logger, Onset Computer Corporation, USA) and tipping bucket (Davis Instruments Corporation, USA) for the remainder of the study.

3.2.2 Vegetation productivity

I conducted estimates of vegetation productivity at Tswalu Kalahari Reserve monthly at 30 permanent sites for 16 months (May 2014 to August 2015, Chapter 2). I used grass cover as an index of vegetation productivity because grass and grass seed are the primary food sources of many ant and termite species occurring at the study site (Nel & Hewitt, 1969a; Ohiagu, 1979; Marsh, 1987). For a long-term vegetation productivity index that encompassed the full duration of this study, I obtained data of moderate-resolution imaging spectroradiometry-derived time-series enhanced vegetation index (MODIS-EVI, hereafter EVI) for the Gordonia duneveld vegetation type predominant at my study site for January 2012 to December 2015 from Tokura (2016). These data were based on 16-day-interval mean EVI values, which I used to calculate monthly means. To validate the use of

EVI data when on-site measures of vegetation productivity were unavailable, I tested whether a relationship existed between my monthly grass cover data from May 2014 to August 2015 with the corresponding EVI-value using nonparametric Spearman rank correlation analysis. Similarly, I used nonparametric Spearman rank correlation analyses and linear regressions where appropriate to detect and assess the individual relationships between EVI, grass cover, grass clump count and grass height (see Chapter 2 for details of data collection) with total monthly rainfall of the same month, the previous month, as well as two, and three months before the sampling or EVI-recording.

3.2.3 Social insect abundance

During monthly vegetation-productivity-assessments along 30 permanent sites between May 2014 and August 2015, I used both pitfall traps and visual observations to assess the abundance of ants and termites (Chapter 2). I subsequently identified these ants and termites to genus-level using a reference collection compiled from samples I had collected over a year at Tswalu (Chapter 2). To obtain ant and termite abundances in pitfalls, I combined all monthly counts for each morphospecies, and converted them into %-proportions of trap contents over the sampling period. I used Spearman rank correlation and linear regression analyses to explore relationships between (1) monthly ant abundance, and (2) *H. mossambicus*-termite abundance, namely (a) soil-dump abundance (an index of underground colony tunnelling activity and waste deposition) and (b) surface foraging activity of workers (scored from 0 = absent to 5 = intense), with total monthly rainfall, monthly mean air temperature, and with the four vegetation scores (monthly medians of grass cover density, height, and clump count, and monthly mean EVI).

3.2.4 Aardvark scat analysis

I collected a total of 133 scats from six study aardvarks at Tswalu between July 2013 and September 2015 (Chapter 2). Due to the difficulty in finding aardvark scats, numbers of scat samples per month varied between 1 and 18, and no samples were collected in January, June, and September 2014.

I quantified the prey contents of the scats (Chapter 2), and then obtained the overall contribution of different prey items to aardvark diet by calculating total counts of individual prey taxa (by morphospecies) in each individual scat sample, then averaged these counts across all samples collected, and converted the values into a percentage. Mean monthly total scat contents were obtained by calculating total counts of individual prey taxa in each aardvark's scats in each month, averaging the counts across each aardvark's scat collection for that month, then averaging these monthly means across all aardvarks for that month, and converting the values into %-contributions of prey species for the aardvark population of a particular month (Taylor et al., 2002). Similarly, I obtained mean seasonal total scat contents by calculating total counts of individual prey taxa in each aardvark's scats in each season, averaging the counts across each aardvark's scat collection for that season, then averaging these seasonal means across all aardvarks for that season, and converting the values into %-contributions of prey species for the aardvark population of a particular season. Since the termites *H. mossambicus* and *Trinervitermes trinervoides* and the ant *Anoplolepis custodiens* comprised the main prey items, they were analysed as individual prey categories, while all other ant and termite taxa found in smaller abundances in scat samples were combined in the category 'other ants and termites'. Since different developmental stages of ants and termites show differential digestibility due to varying sclerotisation of the exoskeleton, particularly the head cuticle, and do not always retain diagnostic characters used in identification, I only included adult workers and soldiers in analyses and excluded any immature stages. This method has been used previously to determine aardvark diet (Taylor et al., 2002). For each month, I examined the relationships of ant numbers in scats with ant numbers in pitfall traps, and of *H. mossambicus* numbers in scats with both of the two *H. mossambicus* abundance indices, using Spearman rank correlation and linear regression analysis.

3.2.5 Aardvark body condition assessments

Throughout the study period, I located all aardvarks several times per month to obtain scats and assess body condition (Chapter 2). I recorded a total of 314 aardvark body condition scores from 12 study aardvarks over the period July 2013 to September 2015, with varying numbers of observations per aardvark. I calculated median monthly body condition scores for each aardvark. To identify changes in aardvark body condition over time, I used an ordinal logistic regression of the type "cumulative link mixed model" fitted with the Laplace approximation that laid a smoothed curve through each aardvark's data points as a visual guide. To allow changes in body condition over time to be detected, I only included those aardvarks in further analyses for which median body condition scores during three or more months were available (264 observations, 26 months). I examined the relationship of overall aardvark monthly median body condition with monthly mean EVI using Spearman rank correlation. To determine whether a simpler approach could be used to detect body condition, I categorised individual monthly median body condition values less than 3 as 'poor' (score of 1), and body condition values of 3 or higher as 'good' (score of 2), and analysed their relationship with monthly mean EVI using Spearman rank correlation.

3.2.6 Water and energy content of major prey items

I determined the energy and water content of each of the three major prey items (the termites *H. mossambicus*, *T. trinervoides* and the ant *A. custodiens*; Chapter 2). I used a one-way ANOVA assuming equal variances to compare the energy contents of the three species, and post-hoc comparisons with Bonferroni-correction to determine which of the three groups differed statistically significantly from one other. To obtain an average monthly value of the biomass, energy and water provided by these prey items in 1 g dry aardvark faecal material, I multiplied mean monthly counts of each prey item in 1 g dry faeces by the live (wet) mass, energy value, and water content of an individual of this prey item. I used *A. custodiens* values as a representative of all ant genera occurring in the diet, *T. trinervoides* values as a representative of all termites other than *H. mossambicus*, and *H.*

mossambicus values for *H. mossambicus*, because the contribution of prey items other than these three was low (~12 % to overall diet) and any termites and ants consumed other than *H. mossambicus* had similar dimensions to *T. trinervoides* and *A. custodiens*, respectively.

3.2.7 Aardvark energy requirements and intake

An animal's field metabolic rate, or its realistic energetic needs in the wild during activities such as foraging and predator avoidance, is invariably higher than its basal metabolic rate, which describes the energy expenditure of an inactive, resting animal (Brown et al., 2004; Nagy, 1987; Nagy et al., 1999). No study to date has investigated the daily energy requirements of aardvarks; however, basal metabolic rate of a captive aardvark was 0.128 mL O_2 g^{-1} per hour (n = 1 zoo animal, body mass 48 kg, sex unknown; McNab, 1984), equivalent to an energy expenditure of ~2 150 kJ per 24 h for my study aardvarks in the Kalahari (mean body mass 35 kg, range 29 to 42 kg). I used an equation that predicts energy expenditure of desert mammals (Nagy et al., 1999, equ. 8) toestimate the field metabolic rate of Kalahari aardvarks. I chose this equation because body mass is the primary predictor of field metabolic rate, and aardvark mean body mass was within the body mass range of species used for generating this equation (Nagy, 1987; Nagy et al., 1999).

With the aim of estimating the 24-h energy input a Tswalu aardvark received from its prey, I generated the following equation:

$$E_{\mathrm{24h}} = \sum_{i=1}^{n} (proportion_i * E_i) * PI * m_{\mathrm{scats}} * n_{\mathrm{scats}} * AE$$

with E_{24h} = dietary energy input (kJ per aardvark per 24 h);

PI = prey items (no. per g dry scat mass);

$proportion_i$ = proportion of item i in diet;

E_i = energy content of *a* (kJ per individual);

m_{scats} = scat mass (g);

n_{scats} = defecations per night (no. per aardvark per 24 h);

AE = assimilation efficiency (proportion of 1).

I inserted into the equation the mean overall prey item count per gram dry scats, the mean dry mass of Tswalu aardvarks' scats, the overall contribution of the three main prey categories (Figure 3.3), and their energy content per individual (Table 3.3). Based on aardvark observations in the Karoo (Taylor, 1998), I estimated that my study aardvarks defecated 6 times in 24 h. I assumed an assimilation efficiency of 65 % as in other myrmecophageous mammals (Cooper & Withers, 2004; Williams et al., 1997).

3.2.8 Statistical analyses

I conducted all analyses in Excel 2016 (Microsoft Windows, USA), Prism 5 (GraphPad Software, Inc., USA) except for body condition analyses which were performed using R 3.4.4 (R Core Team, 2016, Austria), and RStudio 1.1.383 (RStudio, Inc.). Unless otherwise stated, I presented data values as mean ± SD, and considered $P < 0.05$ to be statistically significant.

3.3 Results

3.3.1 Climatic variables

Mean air temperature at Tswalu varied greatly between seasons (Figure 3.1A), ranging from an absolute minimum winter air temperature of –4.4 °C to a maximum summer air temperature of 39.9 °C during the course of the study. There was no notable interannual difference between seasonal mean 24-h air temperatures, although mean autumn air temperatures of 2013 and 2015 were slightly higher than those of 2012 and 2014 (Figure 2.4). The 2012-13 summer experienced a severe drought and the high temperatures typical of summer lasted nearly two months longer than in the 2013-14 and 2014-15 summers, with maximum air temperatures of 35 °C and higher and mean air temperatures of 25 °C and higher throughout October 2012 to March 2013, i.e., from mid-spring until autumn. Mean air temperature of February 2013 (the hottest summer month) exceeded that of February 2014 by ~5 °C, and of February 2015 by ~2 °C.

The amount, onset and termination of rainfall also varied greatly between years (Figure 3.1 B). Rainfall during the unusually dry 2012-13 summer was late and scarce: no rainfall events of greater than 10 mm occurred in the hot months before late March 2013, and total rainfall of this summer remained as low as ~80 mm, i.e., one-quarter of mean annual rainfall of the area over a period of 25 years. In contrast, the summer of 2013-14 experienced higher rainfall than the two other years of study: rainfall occurred during nine consecutive months (September 2013 to May 2014), and provided a total amount of ~450 mm rainfall, exceeding mean annual rainfall by ~100 mm and approaching upper annual records (~550 mm, Tokura, 2016). During this rainy season, each month from December 2013 to March 2014 experienced 80 mm rainfall or more, reaching a maximum of more than 150 mm in March (Figure 3.1B). In comparison, during the following summer of 2014-15 rainfall occurred during only five months (November 2014 to March 2015) and total rainfall amounted to as little as ~150 mm, 65 % of which occurred in one month (December 2015). Although the onset of rainfall in summer 2014-15 did not occur particularly late, the total amount remained 50 % below 25-year annual average (Figure 3.1B).

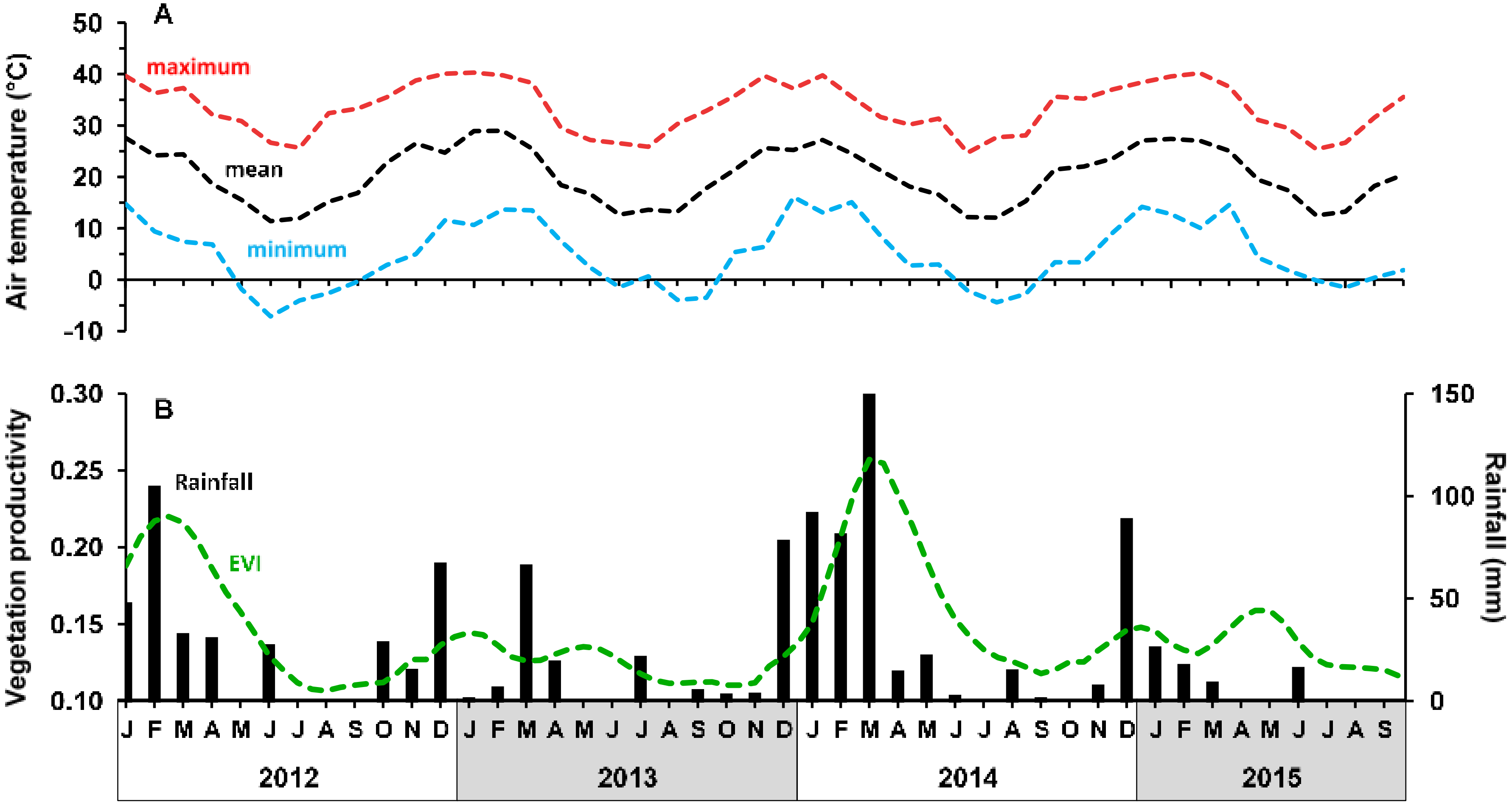

Figure 3.1 Monthly records of A) air temperature (°C), and B) total rainfall and mean EVI of Gordonia duneveld vegetation as a primary productivity index at Tswalu (January 2012 to September 2015).

The winter of mid-2013 after the 2012-13 summer's drought was cold and experienced minimum 24-h air temperatures of 0 °C and below during five subsequent months (May to September 2013), thus lasting two months longer than the winters of mid-2014 and mid-2015. Minor rainfall events of less than 20 mm occurred during winter in all three study years (Figure 3.1B).

3.3.2 Vegetation productivity

Annual productivity of the growing season as indicated by maximum mean EVI for the Gordonia duneveld vegetation characteristic of my study site at Tswalu was higher during 2012 (greater than 0.2) and 2014 (greater than 0.25), when there had been good rains, than during 2013 (less than 0.15) and 2015 (0.16) (Figure 3.1B). Maximum annual EVI was low when summer rains were poor and/or fell late (Figure 3.1B). EVI was strongly positively correlated with total monthly rainfall that had occurred three months earlier ($r^2 = 0.37$, $P = 0.012$). No significant relationship, however, was detected between EVI and rainfall of the same month ($r^2 = 0.12$), one month back ($r^2 = 0.0004$), or two months back ($r^2 = 0.045$). Each year, EVI was lowest in the cold-dry period, especially July to September (Figure 3.1B).

My shorter-term vegetation indices recorded on-site during monthly transect sampling from May 2014 to August 2015 correlated positively with the monthly mean EVI values of that period (monthly median grass height: $r^2 = 0.42$, $P = 0.0068$, monthly median grass clump count: $r^2 = 0.26$, $P = 0.042$). Vegetation productivity, as indexed by EVI and field measures, was greater in 2014 than 2015 (Figure 3.2A). Grass height and grass clump count were both greatest in May 2014, while grass cover was greatest in July 2014 (Table 3.1). Grass height, grass clump count, and grass cover had low values simultaneously in October 2014, before summer rainfall occurred in November 2014-15.

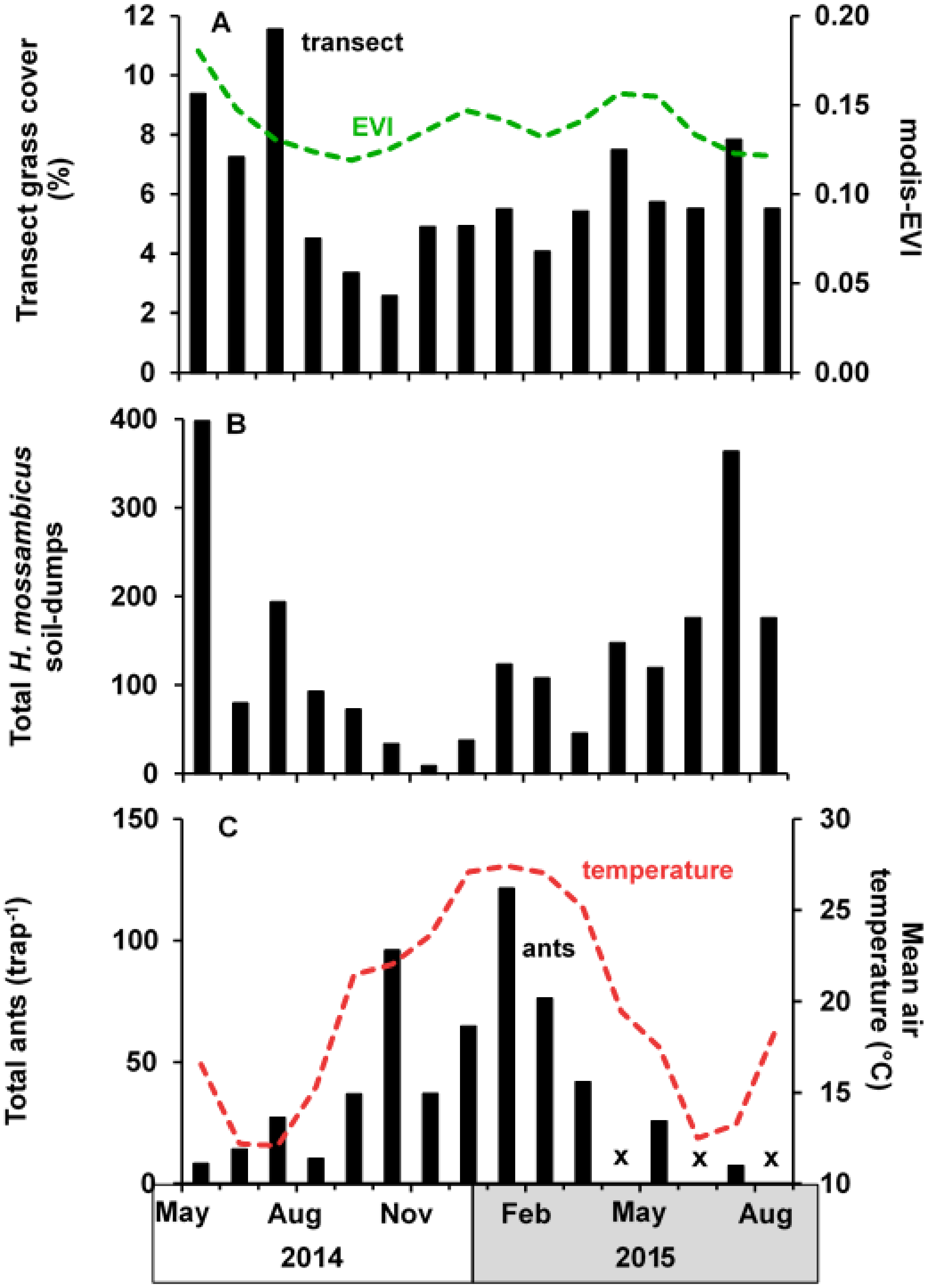

Figure 3.2 Vegetation productivity and aardvark prey insect abundance and activity assessed during monthly transect sampling at Tswalu Kalahari Reserve between May 2014 and August 2015. A) monthly vegetation indices (black bars indicate mean % grass coverage as a representative of three different vegetation indices recorded during monthly on-site transect sampling, green line indicates monthly mean EVI of the Gordonia duneveld vegetation predominant at the study site); B) monthly total soil-dumps as an activity index of *H. mossambicus* tunnelling activity; and C) total number of ants collected in pitfall traps (red dotted line indicates monthly mean air temperature; black bars indicate ants trapped per month; x indicates when no data were available).

A positive, significant relationship existed between grass height and the total monthly rainfall measured three months prior ($r^2 = 0.35$, $P = 0.016$). No significant relationships existed between monthly EVI and air temperature, nor with monthly median grass cover, rain of the same month, one month prior, or two months prior. Monthly medians of grass clump count and grass cover showed no significant correlation with total monthly rainfall of the same month, of the previous month, of two months prior, or three months prior. Similarly, no relationship existed between grass height and total monthly rainfall of the same month, of the previous month, or two months prior. Grass cover was inversely correlated with monthly mean air temperature ($r^2 = 0.35$, $P = 0.016$), while no correlation with mean air temperature existed for grass clump count or height.

Grass clump count was not significantly related to total monthly rainfall of the same month ($r^2 = 0.01$), of the previous month ($r^2 = 0.04$), of two previous months ($r^2 = 0.06$); or previous three months ($r^2 = 0.19$). Similarly, no relationship existed between grass height and total monthly rainfall of the same month ($r^2 = 0.06$), of the previous month ($r^2 = 0.03$), or two months back ($r^2 = 0.17$). Grass cover (%) had a negative, significant correlation with mean monthly air temperature ($r^2 = 0.35$, $P = 0.016$), while no correlation with air temperature existed for grass clump count ($r^2 = 0.19$) or grass height ($r^2 = 0.01$).

3.3.3 Prey abundance

Monthly *H. mossambicus* surface-foraging activity and soil-dump abundance (a result of excavations during underground tunnelling activity and excavation of frass) over the 16 transect sampling months were highest in cold, dry months (May 2014 and again in July 2015) and lowest in summer (December 2014) (Figure 3.2B and Table 3.1). Significant positive relationships existed between mean monthly *H. mossambicus* soil-dump abundance and grass cover ($r^2 = 0.60$, $P < 0.001$) as well as with grass clump count ($r^2 = 0.32$, $P = 0.022$), but not with grass height ($r^2 < 0.01$). Monthly mean soil-dump abundance was inversely correlated with air temperature ($r^2 = 0.30$, $P = 0.028$). Monthly mean surface foraging activity and soil-dump abundance of *H. mossambicus* were not significantly correlated with one another ($r^2 = 0.47$).

Median soil-dump abundance of *H. mossambicus* was not significantly correlated with monthly mean EVI of the same month ($r^2 < 0.01$) or the previous month ($r^2 < 0.11$), or with monthly mean air temperature ($r^2 = 0.01$). Median surface foraging activity of *H. mossambicus* was not significantly correlated with monthly mean EVI of the same month ($r^2 = 0.03$) or the previous month ($r^2 = 0.02$), or with monthly mean air temperature ($r^2 < 0.01$). There also was no relationship between *H. mossambicus* surface foraging activity and grass cover ($r^2 = 0.09$), number of grass clumps ($r^2 = 0.04$) or grass height ($r^2 = 0.02$).

Table 3.1 Assessments of vegetation productivity and aardvark prey abundance at Tswalu (May 2014 to Aug 2015). Monthly median values of three grass indices across all transects: cover (%), height (cm), number of grass clumps with 30 or more stems; monthly mean EVI of Gordonia duneveld vegetation characteristic of my study site; activity indices of *H. mossambicus* termites (number of frass heaps, surface foraging activity on a scale from 0 to 5) and average contents per pitfall trap (grouped into three classes: (1) *H. mossambicus*, (2) small termites (*T. trinervoides* and other termites), and (3) ants of all genera). Numbers of transect sites sampled, and pitfall traps collected at these transects, are presented. Number of traps in May 2015 was low because these traps were excavated by animals and flooded with rain. Trap contents from April, June, and August 2015 were not counted.

	Vegetation productivity				*H. mossambicus* colonies		Pitfall trap contents			Assessed	
Month	Cover (%) (median)	Clumps (count) (median)	Height (cm) (median)	EVI (mean)	Frass heaps (mean)	Surface activity (mean)	Ants (all genera)	Harvester termites	Small termites	Transects	Traps
May 2014	7.4	5.4	45.6	0.19	13.72	0.6	8.2	1.9	0.2	29	280
Jun 2014	6.2	3.6	31.6	0.15	3.0	0.1	13.8	0.7	0.2	27	270
Jul 2014	5.0	3.0	27.6	0.13	6.5	0.0	27.5	0.9	0.1	30	280
Aug 2014	3.6	2.4	16.0	0.13	3.1	0.0	10.4	0.1	0.5	30	290
Sep 2014	2.4	1.5	12.2	0.12	2.4	0.0	37.0	0.3	0.2	30	300
Oct 2014	1.7	1.2	9.4	0.13	1.1	0.0	96.0	0.1	0.1	30	240
Nov 2014	4.5	2.4	15.4	0.14	0.3	0.0	39.8	0.8	0.1	30	260
Dec 2014	4.8	2.1	17.8	0.15	1.3	0.0	65.0	0.7	0.2	30	270
Jan 2015	4.8	2.8	22.0	0.14	4.3	0.0	121.5	0.1	0.3	29	219
Feb 2015	4.0	2.2	13.2	0.13	3.7	0.2	76.4	0.5	1.9	29	250
Mar 2015	5.5	2.2	10.1	0.14	1.5	0.1	42.0	0.4	1.8	30	223
Apr 2015	7.7	3.8	20.3	0.15	4.9	0.1	-	-	-	30	-
May 2015	5.6	2.6	16.9	0.16	4.0	0.0	25.9	0.7	0.7	30	151
Jun 2015	5.7	2.5	11.5	0.14	5.9	0.1	-	-	-	30	-
Jul 2015	8.0	2.9	8.8	0.12	12.1	0.1	8.4	0.3	0.1	30	257
Aug 2015	5.7	2.5	11.5	0.12	5.9	0.1	-	-	-	30	-

A total of 22 different potential aardvark prey taxa occurred in the pitfall traps, of which 6 were termite morphospecies and 16 were ant morphospecies (Table 3.2). In terms of abundance scores, ants made up the majority of potential prey items in pitfalls (~97 %) over the 16 months of the assessments (Table 3.2). Monthly ant abundance was greatest during summer, with a maximum in January 2015, when temperatures were high and good rainfall occurred at Tswalu (Figure 3.2C). Throughout the cooler winter months, ant abundance was low (Figure 3.2C), a pattern that was confirmed by the strong positive, significant correlation of ant abundance with mean monthly air temperature ($r^2 = 0.62$, $P = 0.0015$). In contrast to termite colony activity as indexed by soil-dump abundance, ant abundance was inversely correlated with % grass cover ($r^2 = 0.38$, $P = 0.025$), and not significantly associated with grass clump count ($r^2 = 0.27$).

No relationship existed between ants trapped and grass height ($r^2 = 0.05$). More than one-third of trapped ants (Table 3.2) were *A. custodiens*, followed by *Monomorium* sp. (22.8 %) and *Pheidole* sp. (16.5 %). I grouped all ant and termite morphospecies that individually contributed less than 2 % to trap contents. When combined, they contributed ~5 % to trap contents. Of the comparatively small number of trapped termites (3 % of overall trap contents), *H. mossambicus* formed two thirds (~2 % of overall trap contents). *T. trinervoides* only ranked the ninth most important item trapped with a total contribution to overall trap contents of 1 %.

3.3.4 Dietary composition

Aardvark scats had a mean total dry mass of 276.6 ± 164.7 g (range 9.0 to 731.5 g, n = 133). The average proportion of organic matter in scats (including prey remains, and any plant matter involuntarily ingested by aardvarks) was 8.8 ± 6.1 % and varied greatly between samples (as indicated by the large SD) but without detectable seasonal patterns, and with no detectable relationship with any of the prey abundance measures.

Table 3.2 Ant and termite genera sampled in pitfall traps at Tswalu at monthly intervals (n = 300 traps per month, May 2014 to August 2015), their individual % overall contribution to trap contents, and their individual overall % contribution to the diet of aardvarks (n = 133 scat samples) at Tswalu (July 2013 to September 2015).

Genus	% overall occurrence in pitfall traps	% overall contribution to diet
Termites (total)	**3.3**	**74.9**
Hodotermes	2.2	58.6
Trinervitermes	1.0	15.7
Psammotermes	< 0.1	0.5
Termopsidae	< 0.1	–
Amitermes	< 0.1	< 0.1
Angulitermes	< 0.1	< 0.1
Ants (total)	**96.7**	**25.1**
Anoplolepis	38.3	13.5
Monomorium	22.8	0.1
Pheidole	16.5	5.5
Tetramorium	8.5	1.1
Ocymyrmex	4.9	0.9
Tapinolepis	3.6	< 0.1
Camponotus	1.1	0.3
Meranoplus	0.4	< 0.1
Acantholepis	0.3	< 0.1
Crematogaster	0.3	0.3
Plagiolepis	0.2	< 0.1
Cerapachys	0.1	0.2
Anochetus	0.03	< 0.1
Dorylus	0.01	3.4
Messor	< 0.1	-
Acropyga	< 0.1	-
Cataulacus	< 0.1	-

Organic matter only comprised less than 20 % of dry scat mass in all scat samples, as scats consisted largely of sand and inorganic termite colony debris. Aardvark scats contained 46 ± 23 items per g of dry scat mass (range 9 to 118 items per g, n = 133 scat samples). In terms of numbers, termites dominated the diet of aardvarks at Tswalu, with an overall contribution of ~74 % (Table 3.2; Figure 3.3A), and specifically, the termite *H. mossambicus* constituted nearly two-thirds of the diet. The remainder was made up of the following three categories which contributed nearly equal parts of ~15 %: (1) *T. trinervoides*, (2) *A. custodiens*, and (3) various other ant and termite genera combined. In total, I identified 19 different ant and termite taxa in the Tswalu aardvarks' diet (Table 3.2). *H. mossambicus* occurred in 100 % of examined scats, *T. trinervoides* in 87.2 %, and *A. custodiens* in 94.7 %.

The proportion of different prey types in scats, and thus dietary energy and water, of study aardvarks during the study period was greatest after summer 2014-15, and nearly twice that of the same period in the previous year (Figure 3.4). Although prey numbers in scats (Figure 3.4A) and thus their relative contributions (Figure 3.4B) varied greatly over time, the relative proportion of termites in Tswalu aardvark diet was greater than 50 % while ant contribution generally remained below 25 % during all seasons, except autumn and spring 2014, when more ants than termites occurred in aardvark diet. High ant intake during these periods resulted in a contribution to energy intake of nearly 50 % during these months due to their high relative energy value (see below). However, during most seasons, aardvarks consumed greater numbers of *H. mossambicus* than of all other prey items combined, with a maximum *H. mossambicus* contribution of ~80 % in summer 2014.

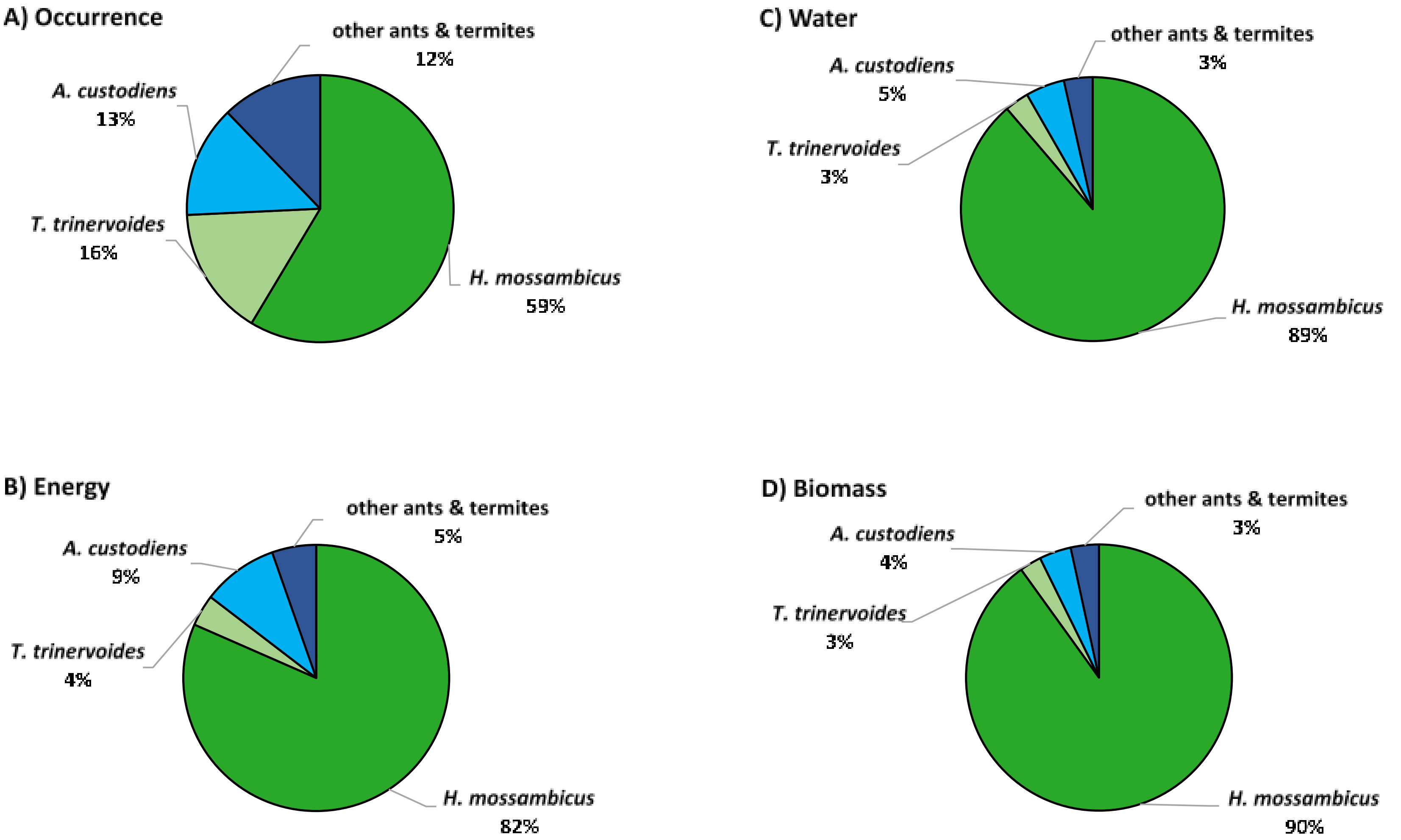

Figure 3.3 Overall contribution (%) of four main prey item categories to A) frequency of occurrence, B) energy content, C) water content and D) biomass of the diet of aardvarks at Tswalu between July 2013 and September 2015.

The second-most important dietary termite was the snouted termite *T. trinervoides*, included in the category "all other termite species combined" (Figure 3.4). The dominant dietary ant was *A. custodiens*, followed by *Pheidole* sp.; and although a single scat sample (excluded from Figure 3.4) obtained in October 2014 contained extraordinarily high numbers of prey items (~83 %) of which were *Dorylus* sp., this sample was the only one in which *Dorylus* ants occurred in such extraordinarily high numbers. No relationship existed between monthly numbers of ants in aardvark scats and in pitfall traps (n = 49 scat samples during 13 trapping months); similarly, no relationship existed between numbers of *H. mossambicus* in aardvark scats and *H. mossambicus* soil excavations or foraging activity.

3.3.5 Water and energy contribution of aardvark prey items to diet

Significant differences in the dry mass energy contents (Table 3.3) of the three main prey items *H. mossambicus*, *T. trinervoides* and *A. custodiens* were revealed by a one-way ANOVA ($F_{(2,\ 27)} = 477.4$; $P = < 0.0001$), and a Bonferroni post-hoc comparison indicated that all three items differed from one another (all *P*-values < 0.0001) in that *A. custodiens* contained the highest and *H. mossambicus* the lowest energy per unit dry mass. However, individual *H. mossambicus* workers had the highest energy and water content, and the highest live (wet) mass of the three species (Table 3.3), with a ~6-fold greater energy content, ~9-fold greater water content and ~11-fold greater wet mass compared to that of the smaller termite *T. trinervoides*. The main prey termites *H. mossambicus* and *T. trinervoides* accounted for ~90 % of dietary energy and water for aardvarks, largely attributable to *H. mossambicus*, while the remaining ~10 % of energy and water intake was derived from *A. custodiens* and other ants and small termites (Figure 3.3 C, D). Termites were also the main provider of biomass, energy and water to aardvark diet in each season (Figure 3.4 B, D, F). During all seasons except autumn 2014, termites delivered more than half of the energy intake (Figure 3.4D), and provided two-thirds to three-quarters of total energy intake during the study period (Figure 3.3B).

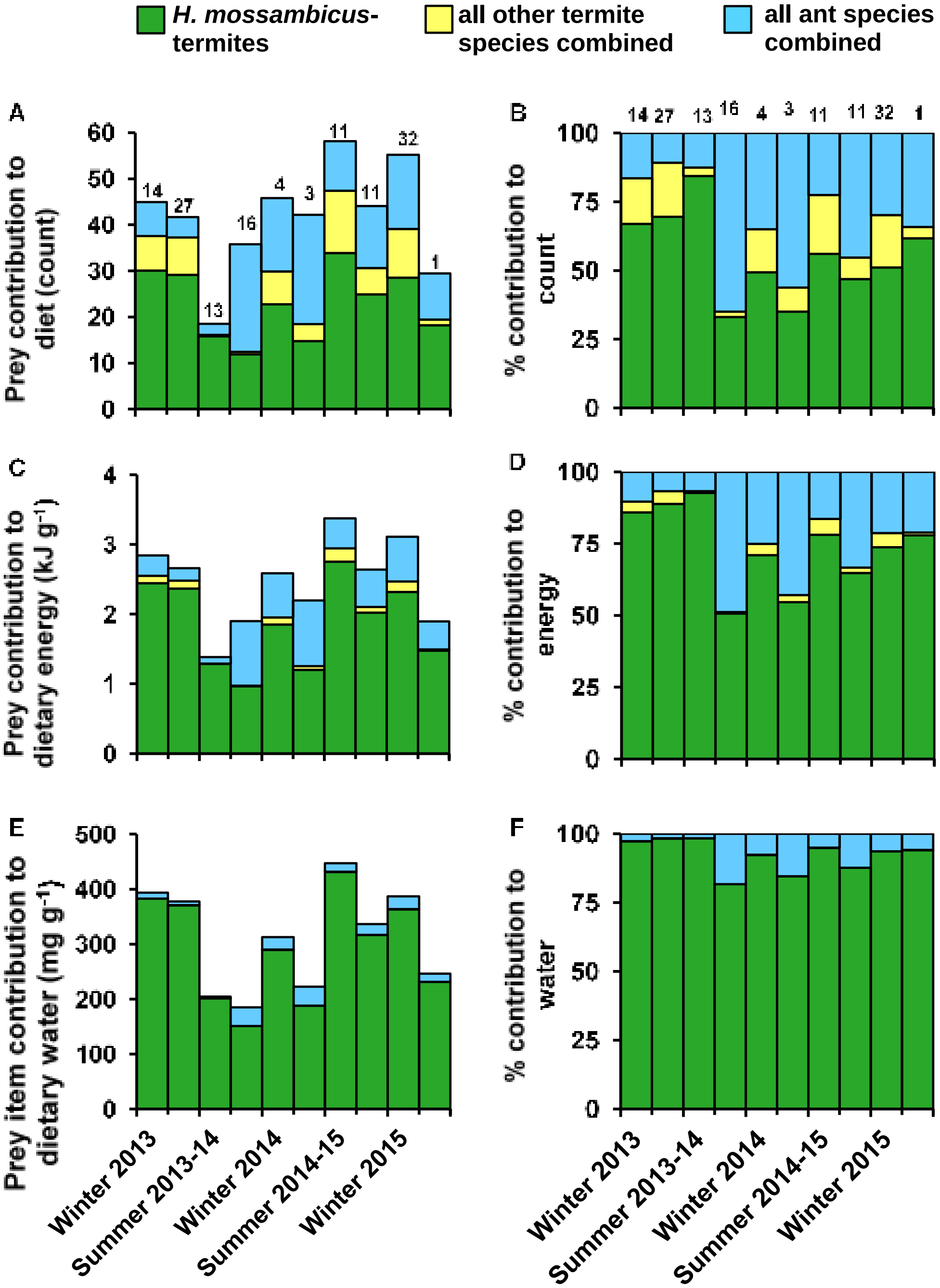

Figure 3.4 Seasonal variation in prey items in aardvark diet, and their contribution to diet in 133 scat samples from six study aardvarks at Tswalu Kalahari Reserve between August 2013 and September 2015. A) Abundance of different prey items per g dry scat mass and B) their % contribution, C) energy (kJ per g dry scat mass) and D) % energy contribution, and E) water (mg per g dry scat mass) and F) % water contribution of different prey item categories to aardvark diet. Numbers of scat samples obtained each month are indicated at the top of plates A and B. No scats were obtained in January, June, and September 2014. One scat sample, obtained in October 2014, contained exceptionally high numbers and a large proportion of ants of the genus *Dorylus* and was not included in data displayed here but is described in the text.

As a result of the numerical dominance of *H. mossambicus* in the aardvark diet and their large mass and high individual energy value, these termites dominated the energy and water contribution of prey items to aardvark diet (Figure 3.4 C - F). During each season, *H. mossambicus* alone accounted for at least 50 % and up to 95 % of energy provided in Tswalu aardvark diet, and for more than 75 % of dietary water.

3.3.6 Aardvark body condition

Monthly median body condition recorded on a scale from 1 (emaciated) to 5 (overweight) across all aardvarks was positively associated with monthly mean EVI ($r^2 = 0.19$, $P = 0.025$). Monthly body condition scores condensed into the two categories 'poor' (less than 3) and 'good' (3 or higher) also associated strongly significantly, positively with monthly mean EVI ($r^2 = 0.39$, $P = 0.0006$).

Most study aardvarks were in very poor condition during winter 2013 (July to September, Figure 3.5), and body condition of most aardvarks (individuals 9 to 15) had body condition scores as low as 1 to 2 (of a possible maximum of 5, Chapter 2). These animals appeared weak, apathetic and oblivious to observer presence when foraging. Aardvarks 10 and 11 died in July 2013, and aardvark 14 died in August 2013 after a sharp decline in body condition (pers. obs; data not displayed because less than 2 months of data were available for these individuals). Only study aardvarks 7 (not displayed, less than two months of data available) and 8 maintained good body condition (score 3) throughout July to September 2013 (Figure 3.5). From spring (October) 2013 onward, overall aardvark body condition continuously improved until all aardvarks were in good body condition (scores of 3 or higher, Figure 3.5), and aardvarks appeared stronger and more vigilant when foraging (e.g., head lifting, ear rotating, air sniffing).

Table 3.3 Energy content of dry mass (kJ per g), as well as individual wet mass (mg), energy (kJ) and water content (mg) of the three main aardvark prey items (*H. mossambicus* - workers only, *T. trinervoides* and *A. custodiens* - workers and soldiers combined, ca. 50 % of each) at Tswalu.

Species	**dry mass energy content (kJ per g)**	**individual wet mass (mg)**	**energy per individual (kJ)**	**water per individual (mg)**
H. mossambicus	18.02 ± 0.59	17.2	0.081	12.7
T. trinervoides	21.06 ± 0.23	1.9	0.014	1.2
A. custodiens	23.93 ± 0.38	3.2	0.039	1.5

Aardvark 13 maintained good body condition through winter 2014 and possibly managed to reproduce in 2014, since she was recorded on camera trap leaving her burrow together with a smaller, subadult aardvark in December 2014. However, the subadult aardvark died in February 2015 concomitant with a heat wave, and aardvark 13 began losing body condition at the same time with a (minimum) score of 1 in March 2015 (Figure 3.5). Despite a brief recovery of body condition over April and May, aardvark 13 died in winter (late July) 2015 after progressive body condition deterioration (Figure 3.5), weakness, apathy and unusually frequent diurnal activity, as observed in many aardvarks during the drought period of the 2012-13 summer and the 2013-winter (see also Chapter 4).

Aardvark 15 died unexpectedly inside her burrow at the end of November 2014, but had not shown a body condition decline or unusual behaviour before death (Figure 3.5). From December 2013, which marked the onset of the 2013-14 summer, until the end of the study in the following spring (September 2015; Figure 3.1), all study aardvarks except the aforementioned aardvark 13 maintained good body condition with scores of 3 or higher, with aardvark 8 reaching the maximum score of 5 in November 2014, and none lost condition in the winters of 2014 and 2015 (Figure 3.5).

3.3.8 Aardvark energy requirements and intake

I estimated that Tswalu aardvarks with a body mass of 35 kg would have a 24-h field metabolic rate of ~11 700 kJ (range of the 95% confidence interval for this prediction: ~4 700 to 29 100 kJ per 24 h). Considering the energy contents of their prey items (Table 3.3), aardvarks could meet their ideal energetic needs of ~11 700 kJ per 24h by consuming ~22 000 *H. mossambicus* and ~19 000 ants and 35 000 small termites per 24-h period combined. Alternatively, if only *H. mossambicus* were consumed, aardvarks would require at least 37 000 individuals per 24 h to match ideal energetic needs.

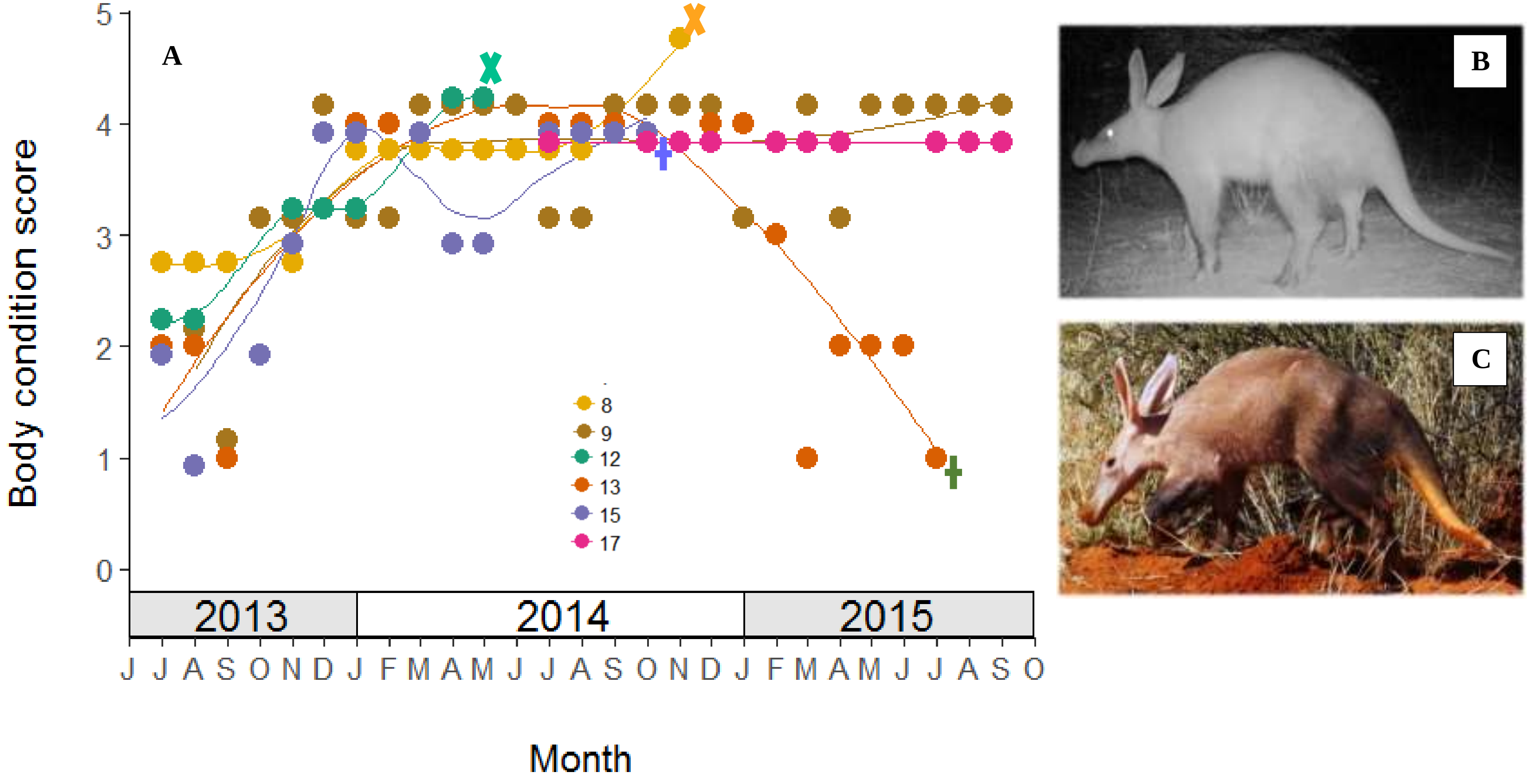

Figure 3.5 Aardvark body condition at Tswalu Kalahari Reserve. A) Monthly median body condition of study aardvarks at Tswalu from July 2013 to September 2015, scale from 1 = emaciated to 5 = overweight. Aardvarks displayed are those for which body condition was scored over at least 3 months. Overlapping data points are stacked to avoid concealing each other. Lines represent smoothed curves for each aardvark's body condition and serve as a visual guide. ┼ indicates death of the aardvark. X indicates loss of the aardvark due to tracker failure. B) An aardvark in very good body condition (score 4). C) An aardvark in very poor condition (score 1). Photo credit: Nora Weyer.

3.4 Discussion

This study is the first to examine aardvark well-being and nutritional stress in response to climatically-influenced resource abundance. I present the first records of nutritional compromise and subsequent recovery of Kalahari aardvarks in response to a summer drought. The large termite *H. mossambicus* dominated the diet of Kalahari aardvarks across all seasons and years, contributing ~90 % to dietary energy and water. *H. mossambicus* soil-dump abundance (an index of colony activity) was positively correlated with % grass cover, and aardvark body condition had a positive relationship with MODIS-derived time-series enhanced vegetation index (EVI). During and after a severe drought in summer 2012-13 and a less severe drought in summer 2014-15, reduced vegetation productivity likely caused local population crashes of the strongly vegetation-dependent termites, aardvark body condition deteriorated, and many aardvarks died. Following good rainfall, the body condition of surviving aardvarks improved, most likely in response to increasing vegetation productivity.

In agreement with other studies (Nel & Hewitt, 1969a; Duncan & Hewitt, 1989; Hewitt et al., 1990), I detected a strong dependence of *H. mossambicus* activity on the availability of plant matter. Field observations confirm that the typically brief foraging events of *H. mossambicus* can easily pass unnoticed (especially nocturnal foraging in summer) to an observer, and thereby lead to an underestimation of their abundance, or to an overestimation of *H. mossambicus* activity when encountering a colony during particularly intense localised foraging events. In contrast, soil-dump abundance resulting from tunnelling activity and frass deposition at the surface provides a more reliable, albeit indirect, index of termite abundance. A direct comparison between prey abundances, and the determination of whether aardvarks selected the most available resource, were impossible due to the differing foraging strategies of ants and termites, and difficulties in quantifying termite abundances. However, the predominant contribution of termites to aardvark diet, particularly *H. mossambicus*, reveals that aardvarks at Tswalu are strongly dependent on this dietary item. Thus, an event that negatively impacts numbers of the dominant termite (*H. mossambicus*) in the diet of aardvarks at Tswalu would reduce the physiological condition of the aardvarks, unless aardvarks are able to shift to another prey type such as ants to compensate for deficits in their staple termite prey, which did not occur during the present study at Tswalu, or if aardvarks were able to reduce their energy expenditure.

At my study site, vegetation productivity as measured in the shorter-term by transect sampling, and in the longer-term via EVI, was largely influenced by the extent of summer rainfall. EVI was a reliable indicator for summer-drought-induced low vegetation productivity, and for high productivity after good rainfall. During two years of the study, a summer drought occurred with high air temperatures and late and little rainfall, resulting in low vegetation productivity during the growing seasons of 2012-13 and 2014-15. The summer drought of 2012-13 was exacerbated by strong winds that contributed to soil desiccation (Rey et al., 2017). Underground tunnelling activity of *H. mossambicus* colonies, as indexed by soil-dump abundance, was predicted by the density of available grass year-round, and thus strongly linked to vegetation productivity, but negatively impacted by air temperature. In comparison, the aboveground-foraging activity of ants was positively related to air temperature, i.e., their foraging activity was greater in summer than winter. These results corroborate other studies which have also found a greater foraging activity of *H. mossambicus*-termites during winter than summer (Duncan & Hewitt, 1989), and greater activity during productive than unproductive years (Nel & Hewitt, 1969a), as well as temperature-related activity patterns of ant species (Hölldobler & Wilson, 1990; Cros et al., 1997; Drees et al., 2007).

Tswalu aardvark diet was numerically dominated by the termite *H. mossambicus*. As a consequence of their large size compared to other aardvark prey items at Tswalu, *H. mossambicus* also contributed the vast majority (over 50 %) of biomass, energy and water to aardvark diet throughout the study period, despite increased ant consumption by aardvarks during late summer. Considering the elusiveness of aardvarks, and despite losses of study animals due to drought-related deaths as well as tracking transmitter failures, I was able to obtain a relatively large sample of scats (n = 133) and body condition scores (n = 314) in twelve different aardvarks over more than two years. Body condition as an indicator for aardvark well-being fluctuated strongly in line with vegetation productivity, as indexed by EVI. Decreased vegetation productivity coincided with low rainfall, as well as with reduced termite activity. Late onset and low amounts of summer rainfall combined with high air temperature resulted in a drought during summer 2012-13 that caused low primary productivity, with EVI nearly 50 % lower than that of the following summer 2013-14, which experienced more and earlier rainfall. *H. mossambicus*' annual harvesting-activity usually peaks during winter (Duncan & Hewitt, 1989). The lack of plant-forage availability to grazers in winter 2013 possibly caused local collapse of *H. mossambicus* colonies, as reported for this termite previously (Nel & Hewitt, 1969a). Consequently, food availability to aardvarks was reduced due to their strong dependence on *H. mossambicus* termites, and body condition of many aardvarks declined following this summer drought, during which primary productivity was low (Tokura, 2016). Numerous aardvark mortalities (including five study aardvarks and at least 11 other aardvarks on a small section of Tswalu) occurred during and after the 2012-13 drought, while many surviving aardvarks appeared weak and were largely diurnal (Rey et al., 2017) despite their reported preference for nocturnal activity (Taylor and Skinner 2003; see Chapter 4). Recovery of the surviving aardvarks occurred over a period of more than six months, from August 2013 when their body condition was very poor, until body condition had returned to good levels (3 or higher) in February 2014, at the peak of the productive period of 2013-14. This summer brought about good rains, inducing comparably high vegetation productivity (Tokura, 2016), and Tswalu aardvarks consumed higher amounts of prey biomass and maintained good body condition. One study aardvark (out of four females under study at the time) possibly reproduced during this period. During arid but non-drought conditions between summer 2013-14 and spring 2015, study aardvarks maintained good body condition, which decreased only slightly during winter. Following a summer drought in 2014-15, I observed a similar pattern to that of 2012-13: the study aardvark that had likely reproduced in late 2014 showed a body condition decline during the hot month of February 2015. Her physical condition might have been impaired by the high energetic costs of lactation (Hamel et al., 2010; Oftedal, 2000; Speakman, 2008). Although this aardvark's condition appeared to improve for a short while during autumn, she rapidly lost body condition as winter progressed, and died during the coldest period of the year. Maintaining good body condition, especially during increased energy demands of the cold season, requires a high daily intake of prey insects, which is likely to be compromised when environmental conditions reduce prey availability. This argument is corroborated by my calculations on the prey intake of aardvarks at Tswalu. I estimated the average energetic input for Tswalu aardvarks to be ~2 865 kJ per day from their prey. This energetic input, although covering aardvark basal metabolic needs, only covered less than a quarter of their estimated total 24-h expenditure of ~12 000 kJ per day when active. Active, free-living aardvarks would have barely met their minimal energetic requirements in the Kalahari under arid but non-drought conditions during this study.

This study is the first to show that termites (Isoptera) were a more important dietary item than ants in the diet of aardvarks. Overall, I distinguished 22 different prey insect taxa in aardvark scats, more than the 14 found by Taylor et al. (2002) or the 15 of Willis et al. (1992) in studies of aardvarks in the Karoo. To compare whether Karoo aardvarks with an ant-dominated diet had a similar energy input as Kalahari aardvarks with termite-dominated diet, I calculated the average energetic input for Karoo aardvarks using the formula in section 3.2.7 of this thesis by inserting values from Taylor (1998) who found that Karoo aardvarks (mean body mass 37.5 kg) defecated on average 6 times in 24 h. Their mean dry scat mass was 215 g with ~39 prey items per g, consisting of 84.5 % ants, 13.6 % small termite species, and 1.9 % *H. mossambicus* termites. I calculated that my Kalahari study aardvarks, on average, consumed ~2 865 kJ per 24 h and had a dry scat mass of 1650 g per 24 h (including sand), and Karoo aardvarks, despite a lower scat mass of 1 290 g per 24 h (including sand) consumed more energy from their ant-dominated diet: 3 763 kJ per 24 h.

Drought-induced food scarcity, resulting from trophic cascades originated by depressed standing crop of grass, would further reduce the energetic input of aardvarks in the Kalahari, as observed after a summer drought in 2012-13 and again during 2014-15, when aardvark body condition declined and mass mortality occurred (the present study; and Rey et al. 2017). In addition, aardvarks likely depend on their prey intake to cover their water requirements (Taylor & Skinner, 2004), which would be compromised during periods of food scarcity. Although some records of aardvarks drinking water from accessible water holes exist for hot, arid regions of southern Africa, namely the Kalahari (Figure 3.6A, and pers. comm. with G. van Dyk, Manager at Tswalu Kalahari Reserve), the Karoo (Taylor & Skinner, 2004; Kerley & Tompkins, 2018), and the Limpopo Province (Figure 3.6B), such observations are rare. The aardvarks observed by Kerley & Tompkins (2017) were drinking after a summer drought had occurred over southern Africa. These aardvarks were visiting water holes during daytime in summer, suggesting that they were experiencing water as well as nutritional stress – indeed, the animals appeared to be in poor condition (as evidenced by protruding pelvic bones and vertebrae of aardvarks in the photographs in the report). In addition, some of these individuals appeared to be subadults and might thus have had increased resource requirements. In mammals, lean individuals, young-of-the-year, and females during gestation are most susceptible to energy-deficiency, particularly at the edge of their distribution where climatic conditions may be more extreme than in other parts of a given species' range (McNab, 1980). In the Karoo as well as the Kalahari, surface water is scarce, aardvarks do not have ready access to drinking water, and they therefore must rely on their prey to obtain fluids (Taylor & Skinner, 2004). A reduction of water-providing insect prey thus not only compromises supply of energy but also of water, an effect which is amplified during conditions of summer drought, with potential strong repercussions on aardvark survival. Evaporative water loss during forced summer daytime foraging as observed by Rey et al. (2017; see also Chapter 4) would further exacerbate physiological nutritional stress and water balance. Unfortunately, nothing is known about the capacity for evaporative water loss in aardvarks.

The results of my study, in combination with studies on aardvark diet from other regions, support the consensus that myrmecophageous mammals inhabiting arid regions are more reliant on termites than the same groups of mammals in semi-arid regions (Abensperg-Traun, 1994). Subterranean termites are well-adapted to life in extreme, arid environments, with large inter-seasonal environmental variation, because their large underground colonies with food storage provide a buffered environment (Wood & Johnson, 1986; Abensperg-Traun, 1994). *H. mossambicus* is distributed throughout the more arid summer rainfall regions of sub-Saharan Africa, particularly in low-rainfall areas, where they forage largely on dry grass (Coaton & Sheasby, 1975; Hewitt et al., 1990; Nel, 1965). Their large colonies provide a patchy but reliable food source in terms of energy and fat content (Redford, 1987; Bukkens, 1997), and these termites dominated aardvark diet in the Kalahari throughout the year. In regions less arid than the Kalahari, such as the False Karoo, ants might be more abundant than termites (Willis et al., 1992), and were also the predominant prey item of aardvarks (Smithers & Wilson, 1979; Melton & Daniels, 1986; Willis et al., 1992; Lindsey, 1999; Taylor & Skinner, 2000; Taylor et al., 2002), while *H. mossambicus* and other termites might serve mostly to top-up aardvark diet during winter when ant availability declines and nutritional stress for aardvarks is most likely (Taylor et al., 2002). The lower abundance of the grass-feeding *Hodotermes* termites in the False Karoo is likely a result of a predominance of woodier plants such as shrubs and trees compared to the grassy Kalahari region (Acocks, 1988; Mucina & Rutherford, 2006). In an equatorial climate in Uganda, aardvarks consumed more ants than termites in areas where ants dominated, but where *Macrotermes* termites were common compared to ants, they dominated the diet of aardvarks (Melton, 1975). The greater importance of termites in aardvark diet in hotter and drier environments could be a result of their higher abundance in these habitats, as well as of their greater potential as a source of dietary water than ants.

Indeed, regional alimentary flexibility might be an advantage for aardvarks in hotter, more arid regions such as the Kalahari, as very large, long-lived colonies of large termites such as *Macrotermes*, *Hodotermes* and *Microhodotermes* can provide a substantial and reliable food source for a relatively large mammal such as the aardvark (Melton, 1975; Picker & Moore, 1991; this study). However, in semi-arid, drought-prone regions, even termite colonies would appear to be susceptible to drought, influencing availability of this staple resource, and likely compromising aardvark energy and water intake, with subsequent deterioration of body condition as observed during this study.

Figure 3.6 Aardvarks drinking water from waterholes, A) at Tswalu Kalahari Reserve, on 01 January 2015 (screenshot of a camera trap video by Joe Gosling, obtained from https://twitter.com/JoeGosling2/status/838017615486464000), and B) in Limpopo during January 2014 (photographed on camera trap by Hennie Steyn, obtained from http://raptorsview.co.za/wp-content/uploads/2015/08/The-Raptor-January-2014.html).

With global climate change, the frequency, intensity, and duration of droughts over much of Africa has been increasing (Rouault & Richard, 2005; Russo et al., 2016), and for southern Africa and the Kalahari specifically, temperatures are expected to increase by twice the global rate, i.e., by ~4 °C by the end of the current century (Niang et al., 2014). Amplified droughts will exacerbate the desertification of semi-arid zones in southern Africa (Vetter, 2009), thereby potentially changing the distribution of subterranean termite and ant species and causing colony contractions and declines in areas at risk (Shiday et al., 2011). Termites are directly reliant on primary productivity and are known to experience population declines following drought: in the semi-arid Free State Province of South Africa, a severe, prolonged drought and heat wave in the 1960s resulted in reduced vegetation productivity and consequentially eliminated *H. mossambicus* colonies, which showed no signs of recovery within two years of that drought (Nel & Hewitt, 1969a). A severe drought in southern Africa during the 1980s strongly affected the activity patterns of several termite species (Braack, 1995), and aardvark deaths and starvation were recorded in Namibia during this period (Stuart & Stuart, 2007). Colony initiation by reproductive termites would also likely be less successful in drought years due to the termites' dependence on soil moisture (Abensperg-Traun & De Boer, 1990; Su & Puche, 2003), further reducing the biomass of termites. Similarly, although ants are often trophic generalists and exhibit a multitude of heat-coping strategies (Tevis, 1958; Kadochová & Frouz, 2014), they are sensitive to intensified heat and aridity, and climate-change-related habitat warming (Barrow & Parr, 2008; Diamond et al., 2016).

Species on higher trophic levels are more likely to be affected by indirect effects of climate change on their prey than by direct effects of climate change such as temperature (Ockendon et al., 2014), and reduced productivity as well as the demise of food or host plants can have severe cascading effects on consumers in ecological networks (Schleuning et al., 2016). Aardvarks, as higher-level consumers, are thus likely to be affected by direct impacts of reduced primary productivity on their prey. In many ecosystems in Africa and worldwide, termites such as *H. mossambicus* are considered both keystone organisms in trophic cascades, and ecological engineers in ecosystems they inhabit (Jones et al., 1994; Dangerfield et al., 1998; Jouquet et al., 2011). Termite biomass is comparable to that of ungulates and megaherbivores in African savannas (detailed in Jouquet et al. 2011), making them an essential resource to many other animals. In southern Africa, *H. mossambicus* termites are an important food source for at least 65 bird and 19 mammal species, particularly during periods of drought (Kok & Hewitt, 1990). Regular mammalian consumers apart from aardvarks include the aardwolf, bat-eared fox, meerkat (*Suricatta suricatta*), and yellow mongoose (*Cynictis penicillata*). The termites *H. mossambicus* and *T. trinervoides* account for up to 100 % of aardwolf diet (Cooper & Skinner, 1979). Termites and ants are vital resources for hundreds of mammal species worldwide, numerous of which are specialised myrmecophages (Redford, 1987). Interestingly, early hominids likely had a million-year-long tradition of termite-foraging in southern Africa, even developing tools for termite-harvest (Backwell & D'Errico, 2001). Termite mound structures may last thousands of years, can reach massive dimensions, and may accommodate many small and large animals including aardvarks (Picker & Moore, 1991). Moreover, termite tunnelling activity stabilises upper soil-levels and improve water filtration through soil in arid systems (Elkins et al., 1986). Termites also contribute to vegetation heterogeneity through energy release, soil turnover and nutrient redistribution, thereby providing 'islands of fertility' in semi-arid grasslands (Dangerfield et al., 1992; Fox-Dobbs et al., 2010; Sileshi et al., 2010). Such islands of fertility might indeed aid ecosystem stabilisation and drought recovery under global climate change (Bonachela et al., 2015), unless climate-change-induced rainfall decline causes termite colony extermination, resulting in subsequent homogenisation of termite structures (Whitford, 1993). Dramatic cascading effects on ecosystems where termites currently occur in high abundances and provide ecological key services (Shiday et al., 2011) might thus result from predicted and ongoing environmental changes in southern African semi-arid termite habitats with climate change (Geerts et al., 2016; Midgley et al., 2001; Pachauri et al., 2014).

For most of Africa, the rapidly increasing temperatures are predicted to raise evapotranspiration so strongly that even rainfall increases predicted for some areas will likely be offset by evapotranspiration (Le Roux et al., 2016; Rind et al., 1990). The decrease in net water availability through drought, more erratic rainfall, and higher evapotranspiration, will likely result in severe foreshortening of the growing season in the southern African region (Engelbrecht et al., 2015), thereby reducing the current number of 40 to 60 days per year with soil moisture and conditions suitable for vegetation growth in the Kalahari to as few as 20 to 40 days per year by 2050 (Midgley et al., 2001). Warming may affect vegetation directly by accelerating leaf ageing processes, further shortening the productive season (Zavaleta et al., 2003). Indeed, even arid-adapted plants have already shown a range contraction in response to recent climate change, indicating that desert ecosystems might be more sensitive to increasing heat and aridity than previously considered (Foden et al., 2007).

In many dry habitats, the perennial, sedentary colonies of termites and ants exhibit strong responses to seasonal and inter-annual fluctuations in environmental conditions and resource abundance (Barrow & Parr, 2008; Bernstein, 1974; Haverty et al., 1974; Marsh, 1985, 1987; Park et al., 1993). Synergistic influences might further exacerbate this impact, as dramatic increases in drought periods and atmospheric CO_2 levels anticipated for the current century will likely cause grass biomass in warm African regions to decline (Le Roux et al., 2016). The main reason herefore is thatthe prevailing grasses in these regions are C_4 grasses, which are considered less well-adapted to high atmospheric CO_2 levels (Ehleringer et al., 1997) and elevated temperatures (Zavaleta et al., 2003) than C_3 grasses. The diet of *H. mossambicus* termites in South Africa consists 93 % of grass, most of which is C_4 grass (Symes & Woodborne, 2011), thus the forage availability to termites might be reduced in future. In addition to reduced forage availability (Nel & Hewitt, 1969a), increased soil desiccation directly restricts the tunnelling activity of subterranean termites (Su & Puche, 2003; Cornelius & Osbrink, 2010), and the maintenance of vital high air moisture levels inside their colonies (Hartwig, 1965). Prolonged summer drought is known to have devastating long-term effects on *H. mossambicus* colonies, and the recovery of *H. mossambicus* colonies from drought is slow (Nel & Hewitt, 1969a). Shorter intervals between drought events might further exacerbate aridity impacts on the system by not leaving enough time for grass to regrow and termite populations to recover from drought-related damage before the next drought, with profound ecosystem cascades.

The vulnerability of aardvarks to drought-induced crashes in prey insect populations stresses the importance of the keystone termite *H. mossambicus*, and possible wider-reaching negative effects on dozens of myrmecophageous or insectivorous vertebrates in semi-arid southern Africa (Kok & Hewitt, 1990; Kok & Nel, 1992). Declines in *H. mossambicus* populations linked to climate change likely will have severe ecological impacts not only on its direct predators, such as the aardvark, but will also impact a large number of other organisms. These organisms include vertebrate and invertebrate species that are dependent on aardvark burrow refugia (Whittington-Jones et al., 2011), plants that use aardvark excavations as germination sites (Dean & Milton, 1991), and all animals that depend on these termites for food (Kok & Hewitt, 1990), often exposed by aardvark digging (Taylor & Skinner, 2000, 2009).

As the only animal providing a multitude of burrows across sub-Saharan Africa, aardvarks are primary ecosystem engineers. The burrows that they dig will likely gain importance as climatic refuges for many species as African climates become hotter (Pike & Mitchell, 2013). A loss of digging mammals, which contribute to soil turnover, water infiltration, and incorporation of organic matter in the soil (among other ecosystem functions), also has been linked to ecosystem deterioration in Australia (Fleming et al., 2014). Destructive cascades initiated by failure of vegetation productivity after successive droughts and heat waves will likely cause a level of degradation that prohibits a system to simply revert back to its original state even if the stress load ceases (Rapport & Whitford, 1999). My study shows that the environmental conditions global climate change is expected to bring about for southern Africa, and their negative impact on subterranean keystone termites as a resource and ecosystem service provider, are likely to be a greater threat to the region’s myrmecophages, such as aardvarks, than previously considered, with potentially severe impacts on southern African biodiversity and ecosystem stability.

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Chapter 4 - Aardvarks shift their activity patterns in response to season, air temperature, and drought-related resource limitation

4.1 Introduction

Flexibility in their behavioural patterns and activity timing may improve the resilience of large mammals to climate change impacts (McCain & King, 2014). Understanding flexibility in activity patterns of mammals is thus crucial for predicting adaptive capacity in future climate regimes. Climate change can affect mammals directly through increasing temperatures and aridity, and indirectly through changes in food availability, competition, and disease. Under normal conditions, many mammals adjust their activity to seasonal or daily environmental fluctuations. Daily activity patterns can be driven by abiotic factors, such as extreme environmental temperatures, rainfall and water availability, and biotic factors, such as prey availability or predation risk. Seasonal or inter-annual shifts in activity can be a response to photoperiod, environmental temperature, or seasonal resource abundance. Many animals avoid climatic extremes such as heat, cold, or aridity by seeking shelter and reducing activity to reduce water and energy expenditure (Hetem et al., 2012a; McFarland et al., 2014). For example, the Arabian oryx, a large diurnal mammal, shifted to a nocturnal pattern during very hot and dry periods, and rested in shade during the hot daytime (Hetem et al., 2012a). Not all species, however, may be able to adjust their activity to buffer themselves against extreme environmental conditions. Oryx in the Arabian desert had no natural predators, but an African antelope shifting its activity to the night may face increased predation. A nocturnal animal that responds to increased environmental heat by shifting its active phase to a later, cooler point of the night might face reduced time available for activity before dawn, potentially limiting its time to acquire nutrients or interact with conspecifics. Specialist species, such as obligate nocturnal animals, that are not able to evade adverse conditions by shifting their activity to a more favourable time have been deemed particularly likely to respond negatively to changing climates (McCain & King, 2014).

As a large nocturnal mammal and a dietary specialist, the aardvark will likely be strongly impacted by climate-change-related environmental changes throughout its range (Niang et al. 2014, see also Chapter 1) unless it can adequately adapt its behaviour and activity patterns to avoid climatic adversities (McCain & King, 2014). Despite the high ecological significance of the aardvark as an ecosystem engineer that actively creates shelter for other species (Cilliers, 2002; Whittington-Jones et al., 2011), not much is known about its capacity to respond behaviourally to extreme environmental conditions expected to become more prevalent throughout its distribution. Aardvarks generally emerge from their burrows at night to forage. During summer, when day-time temperatures were high (> 30 °C), aardvarks in the semi-arid Karoo region of South Africa restricted their activity to the cooler hours of the night, which led to the proposal that aardvarks may be heat-sensitive (Taylor & Skinner, 2004). However, during cold winter periods, aardvarks partly shifted their activity to daytime (Taylor & Skinner, 2004), demonstrating flexibility in their behaviour and activity patterns to environmental fluctuations. The aardvarks were presumed to have become diurnal to avoid the cold night-time because their sparse fur cover makes them cold-sensitive (Taylor & Skinner, 2004), but other factors such as nutritional state might also have affected their activity patterns. Indeed, during a recent drought in the more arid Kalahari semi-desert, aardvarks showed unusual diurnal behaviour during the drought summer as well as during the following winter, when many aardvarks died (presumably from starvation, see Chapter 3), and survivors were in poor condition (Rey et al., 2017). To date, no study has investigated whether and how aardvark locomotor activity and active phase timing and duration vary in response to fluctuations in resource availability or climatic conditions.

Like other nocturnal and cryptic animals, the aardvark is hard to observe in the wild, and therefore not much is known about its flexibility in responding to environmental change. Technological advances, however, permit long-term, continuous, unbiased quantifications of animal activity patterns and behaviours over extended periods using locomotor activity biologgers such as accelerometers, while the animal’s behaviour and physiology remain unaffected by human presence (Fuller et al., 2014). Moreover, such biologgers permit continuous activity records for animals difficult to access in the wild (Podolski et al., 2013). In the Kalahari, the south-western edge of aardvark distribution, air temperatures are extreme (below 0 °C in winter to above 40 °C in summer) and aridity is intense (dry winters, low summer rainfall). Resource abundance is dictated by rainfall, fluctuating strongly between seasons and years, and aardvark body condition decline and deaths have occurred in response to drought-related limitations in prey abundance (Chapter 3).

Here, using activity biologger records, which I validated using camera trap records and behavioural observations, I examine timing, duration, and intensity of aardvark activity in response to seasonal and inter-annual fluctuations in the abiotic and biotic environment in the Kalahari. I investigate three main hypotheses: (1) Seasonal activity patterns of Kalahari aardvarks will be similar to Karoo aardvarks, with generally nocturnal activity, and possibly some diurnal activity in winter; (2) Activity patterns will reflect responses to extreme temperatures, with aardvarks avoiding extremely high and low temperatures, and altering the intensity and timing of their activity; (3) Activity patterns will reflect nutritional compromise, with aardvarks attempting to compensate for decreased food intake by extending the duration of their active (foraging) phase, and decreasing their digging efforts to preserve energy.

4.2 Methods and materials

I obtained records of locomotor activity, activity patterns, and behaviour of aardvarks at Tswalu Kalahari Reserve between July 2012 and September 2015. A detailed description of behavioural observations, camera trap footage collection, and surgical instrumentation of aardvarks with data loggers recording activity is provided in Chapter 2. Locomotor activity of each study aardvark was recorded using implantable activity biologgers, with different logger models used in different years of the study. In the first year (July 2012 to July 2013), activity was recorded using Actical loggers (Mini-Mitter Corporation, USA; mass ~40 g when covered in wax). Acticals were tri-axial piezoelectrical accelerometers sensitive to forces of > 0.05 *g* and were set to record whole-body movement over full 5-minute-periods. In the following study years (July 2013 to September 2015), manufactured activity loggers (MLOG_AT1, Sigma Delta Technologies (Pty) Ltd., Australia) with a tri-axial accelerometer sensitive to forces of > 0.004 *g* (ADXL345 Digital

Accelerometer, Analog Devices, Inc., USA; mass ~25 g when covered in wax) served to record aardvark locomotor activity in the form of activity counts over a 10-second-period at the beginning of each 5-minute-interval. The use of these biologgers, validated with visual field observations, has previously proven successful in assessing behavioural activity in a wild, free-living large mammal (McFarland et al., 2013).

To assess how effectively activity loggers could detect certain types of behaviours, I compared biologger data with time-matched observation data (see details in Chapter 2). I compared 430 observations (~36 hours) for study aardvarks 8, 9, and 15 on 16 different days, to explore whether logger data could be used to determine the type of activity an aardvark was exhibiting. I compared the observation records of moving, foraging, and digging intensity to the data recorded by the logger at the same time, as well as five minutes before and after the observation. Although biologger activity data accurately reflected movement intensity, and resting could be distinguished from movement, it was not possible to distinguish any particular behaviours (digging, moving, or feeding) from one another.

To determine whether biologgers could reliably indicate the beginning and end of aboveground activity of aardvarks, I time-matched biologger data to observations and camera trap footage of an aardvark's times of emergence from a burrow, or an aardvark's time of return to a burrow after foraging. Occasionally after emergence from a burrow, an aardvark remained at the burrow to rest or bask; in these cases, the time of emergence was that time at which the aardvark left its position to begin foraging. During 0 to 30 minutes before emergence, or, occasionally, shortly after an aardvark's emergence, logger data showed a transition from multiple values < 5 % (resting) of the maximum activity to values ≥ 5 % (active). A similar but reversed pattern occurred following an aardvark's return to its burrow. For each activity data point, I calculated the median of six values before and six values after this data point (i.e., median activity over a duration of 65 minutes). If the median deviated from zero and reached a threshold of ≥ 5 % of the maximum activity for each individual, I considered the aardvark as 'active'; if not, it was considered as 'inactive'. I considered the time-stamp of the data point at which the 65-minute median changed from ‘inactive’ to ‘active’ to be the time of emergence, whereas the reverse change from ‘active’ to ‘inactive’ marked the time of the aardvark’s return to a burrow. Long periods of inactivity could be fragmented by short bouts of apparent activity, possibly as a result from short-duration intense movements (such as intense scratching or digging inside the burrow) while the aardvark was inside its burrow. Short bursts of intense activity ≤ 65 minutes could raise the entire 65-minute median to a value above the 5-% threshold for activity, and falsely indicate an aardvark’s time of emergence. Thus, I only considered activity bouts that lasted ≥ 65 minutes as an emergence to forage. Any inactive bout ≤ 65 minutes during foraging could have resulted from the aardvark moving very slowly, or not moving at all during the moment when the logger was recording locomotor activity, falsely indicating a return to a burrow. Thus, I considered an inactive bout of ≤ 65 minutes as part of the longer activity phase during which it occurred. To verify whether these calculations reliably represented time of emergence and return, I compared the resulting values with the results manually obtained from days and nights on which I had recorded time of emergence or return of aardvarks in the field (N = 176), and in each case, the recorded emergence or return of an aardvark occurred within the predicted 65-minute-period of the biologger data.

Because aardvarks are largely nocturnal, assigning the conventional 00:00-24:00 period to each day would have fragmented their activity phases at midnight. Thus, to match a date to an activity phase, I applied the following criteria: if an aardvark emerged between 00:00 and sunrise, the date of the last sunset was assigned to the emergence and to the return (i.e., if sunset occurred on 1 August at 18:00 and the aardvark only emerged after midnight on 2 August at 01:00, and returned to its burrow on 2 August at 06:00, the dates of emergence and return were classified as 1 August). I calculated maximum, total, and duration of activity between each time of emergence and return. Occasionally, an individual aardvark showed two or three activity bouts ≥ 70 minutes in the same night, interrupted by inactive bouts lasting between 70 to 180 minutes. Bouts registered as inactivity (activity < 5 % of maximum activity) during the 10-second interval over which the logger counted locomotor activity could have resulted from the aardvark standing still while preying on a termite colony or defecating, or from the aardvark moving very slowly.

All such short inactive bouts occurred during the same night between the aardvark's first emergence from a burrow and sunrise. Hence, I combined these bouts using the first emergence as the start of the active phase and the end of the last bout as the end of the active phase, and calculated total activity and maximum activity across the combined bouts of activity. In this way, I omitted a total of 43 short activity bouts of < 65 minutes from the dataset by merging each one with the inactive bout during which it had occurred. Rarely, aardvarks did not emerge from their burrows but remained inactive underground, and the loggers did not record activity bouts of > 65 minutes. In such cases, I assigned zero-values to foraging duration, total, and maximum activity of that day.

Once I had determined the time of emergence and return using the method described above, I calculated the duration of each active phase and the total activity and maximum activity per active phase. To obtain seasonal average values per 24-h period of total and maximum activity, duration of the active phase, time of emergence and return, and the proportion spent diurnal, I calculated the mean ± SD of these variables first per aardvark per season, then across all aardvarks per season. I calculated mean ± SD 24-h activity rhythms at 1-h intervals first per aardvark per month to obtain monthly average 24-h activity patterns, then averaged these across all aardvarks, and then over seasons (summer: December to February, autumn: March to May, winter: June to August, spring: September to November; see below for details) to obtain seasonal 24-h activity patterns of all study aardvarks throughout the study period.

I obtained air temperature at the time of emergence and at the time of return of each study aardvark per day. To obtain daily mean time of emergence and mean time of return for each 24-h period throughout the study, I averaged the time of emergence and time of return between all aardvarks for each 24-h period. For each aardvark, I also calculated the proportion of each active phase that occurred before sunset, to quantify diurnal activity of aardvarks across seasons and years.

I divided each year into four seasons of a consistent three-months duration across years, rather than selecting seasons depending on rainfall, because rainfall patterns were inconsistent in the different years. I defined the seasons as winter (June, July, August), spring (September, October, November), summer (December, January, February) and autumn (March, April, May). In a ‘good’ year, summer rain induced high vegetation productivity (high EVI) over the following months (e.g., summer rains in the growing season 2013-14 lasted from November 2013 until January 2014, resulting in EVI > 1.5 up until June 2014, at which stage grass was frost-killed), whereas in a ‘poor’, drought year with late and little rainfall, vegetation productivity was low, reflecting in low EVI (Chapter 3). High vegetation productivity at Tswalu coincided with high prey abundance, resulting in the aardvarks being in good condition, whereas during less productive years, resource scarcity caused poor aardvark condition (Chapter 3). Aardvark body condition positively correlated with EVI (Chapter 3). I thus used EVI as an indicator of aardvark body condition in the following analyses. I used general linear mixed-effect models (GLMM) to determine the effects of biotic and abiotic conditions on aardvark activity. I used each 24-h period as a sampling unit in the GLMMs, and aardvark identity as random effect. The dependent variable was either time of emergence, time of return, total duration of the active phase, total activity or maximum activity within each activity bout, or the proportion of diurnal activity. As independent variables, I chose mean 24-h air temperature, EVI (a proxy for aardvark body condition, see Chapter 3), photoperiod (time between sunrise and sunset), % lunar illumination (phase of the moon, with 100 % for full moon and 0 % for new moon; data obtained from Time and Date AS, Norway; http://staging.timeanddate.com). Photoperiod was correlated with mean air temperature, therefore, photoperiod was only included in GLMMs that were related to the timing of aardvark activity, but not in GLMMs of total and maximum activity. I did not include aardvark sex as a factor, because for some aardvarks, sex was unknown, and all other aardvarks included in the dataset were females. A repetition of these GLMMs with minimum air temperature replaced with maximum air temperature provided similar results, which I excluded from the results section for simplicity.

I used Excel 2016 and Prism 5 (GraphPad Software, Inc., USA) to prepare raw data for analyses and to create graphs. I used a script in Python 2.7.13 (Python Software Foundation, USA) to automatically perform calculations of the 65-minute median around each activity measurement to determine daily time of emergence and time of return of aardvarks from their burrows. I used the mixed-effects linear regression function in STATA SE10 (Quantec Research (Pty) Ltd., South Africa) to perform GLMM analyses. Unless otherwise stated, I present data as mean ± SD, and considered $P < 0.05$ to be statistically significant.

4.3 Results

4.3.1 Data summary

Between July 2012 and September 2015, ten aardvarks were implanted with data loggers for 2943 days in total. Once data loggers had been retrieved from the aardvarks, I retrieved 2574 complete days of activity records (735264 measurements in 5-minute intervals) between July 2012 and May 2015 (excluding capture periods) from nine of these aardvarks (Table 4.1). The longest activity record stemmed from aardvark 9, with 675 consecutive days during the period from July 2013 until May 2015 (Table 4.1).

On 2553 of 2574 total sampling days, aardvarks were active for ≥ 70 minutes, and the active phase had a median length of 8.2 h (range 0 to 19.7 h; Table 4.1). The proportion of diurnal activity differed considerably between aardvarks: while all study individuals reached a maximum diurnal proportion of 100 % at some point (except for aardvark 1 whose logger failed early on), some aardvarks also showed a large median proportion of diurnal activity (Table 4.1), indicating that their diurnal activity was not an exception but occurred often and extensively. Notably, all aardvarks that displayed such considerable diurnal activity died either during the summer drought 2012-13 (aardvarks 1, 2, and 5) or during the winter after the drought (aardvarks 10, 11, and 14).

On 21 out of 2574 sampling days, aardvarks remained inactive inside their burrows, effectively skipping an active phase. On two occasions, two individual aardvarks coincidentally remained inside their respective burrows on the same day: aardvarks 2 and 5 did not emerge on 17 August 2012; aardvarks 9 and 15 did not emerge on

Table 4.1 Overview of locomotor activity data recorded with biologgers in each aardvark at Tswalu Kalahari Reserve between July 2012 and May 2015. ID - aardvark identity; N days - number of days for which activity logger data exist; Period - time during which data were recorded; N days active - number of days the aardvark was active for ≥ 65 minutes; N days inactive - number of days the aardvark was inactive (activity < 65 minutes); median (range) of duration - median, minimum, and maximum duration (hours) of the active phase; median (range) of proportion diurnal - median, minimum, and maximum proportion (%) of the active phase an aardvark spent during daylight.

ID	Period	N days recorded	N days active	N days inactive	Median (range) duration of the active phase (h)	Median (range) proportion of activity diurnal (%)
1	Jul 2012 to Jan 2013	181	181	0	7.5 (1.3 to 17.8)	0.6 (0 to 66.5)
2	Aug 2012 to Mar 2013	227	225	2	7.8 (0 to 14.8)	53.0 (0 to 100)
5	Aug 2012 to Mar 2013	68	65	5	6.8 (0 to 19.7)	98.1 (0 to 100)
7	Aug 2012 to Mar 2013	227	225	2	8.3 (0 to 12.4)	0.0 (0 to 100)
8	Jul 2013 to Jul 2014	384	382	2	8.2 (0 to 11.8)	0.0 (0 to 100)
9	Jul 2013 to May 2015	672	672	0	8.5 (1.3 to 14.8)	0.0 (0 to 100)
14	Jul 2013 to Aug 2013	34	32	2	5.4 (0 to 8.8)	53.7 (0 to 100)
15	Jul 2013 to Oct 2014	478	470	8	7.7 (0 to 11.8)	0.0 (0 to 100)
17	Jul 2014 to May 2015	303	301	2	8.7 (0 to 11.8)	0.0 (0 to 100)

17 July 2014. It is unclear why the aardvark did not emerge since temperatures were not unusual on these days compared to the days before and after, and no rain or notable wind occurred on either day. Episodes of very short activity occurred during summer 2013-14 and winter 2014.

4.3.2 Seasonal patterns of activity

The long-term patterns of activity variables of aardvarks strongly varied between seasons and years (Figure 4.1 and Table 4.2). During warm seasons (spring, summer, autumn) except during drought years (see below), aardvarks were exclusively nocturnal, and their total 24-h activity was greater, maximum 24-h activity higher, and the duration of the active phase longer than during winter (Figure 4.1). During the hottest summer periods (e.g., February 2015), total and maximum 24-h activity declined, and the active phase shortened (Figure 4.1). During winter, total 24-h activity, maximum 24-h activity, and duration of the active phase declined, and aardvarks became partly diurnal (as shown for aardvark 9, Figure 4.1). This pattern of more intense and nocturnal activity in warm seasons compared with less intense and partly-diurnal activity during winter was repeated throughout the different years of the study (Table 4.2), except during the year of the drought summer (2012-13). In the drought periods spring 2012, summer 2012-13, and autumn 2013, aardvarks showed substantial diurnal activity (up to 50 % of their active phase occurring before sunset) while the duration of their active phases did not increase notably (Figure 4.1D and Table 4.2). During summer and autumn of the drought year (2012-2013), total and maximum 24-h activity were markedly lower than during the preceding winter and spring, and up to ~45 % lower than during summer and autumn in the following years (Table 4.2). During winter 2013 following the summer drought, aardvarks spent a greater proportion of their active phase diurnal (Table 4.2), and were diurnal for a longer period (Figure 4.1D) than during winters after normal summers.

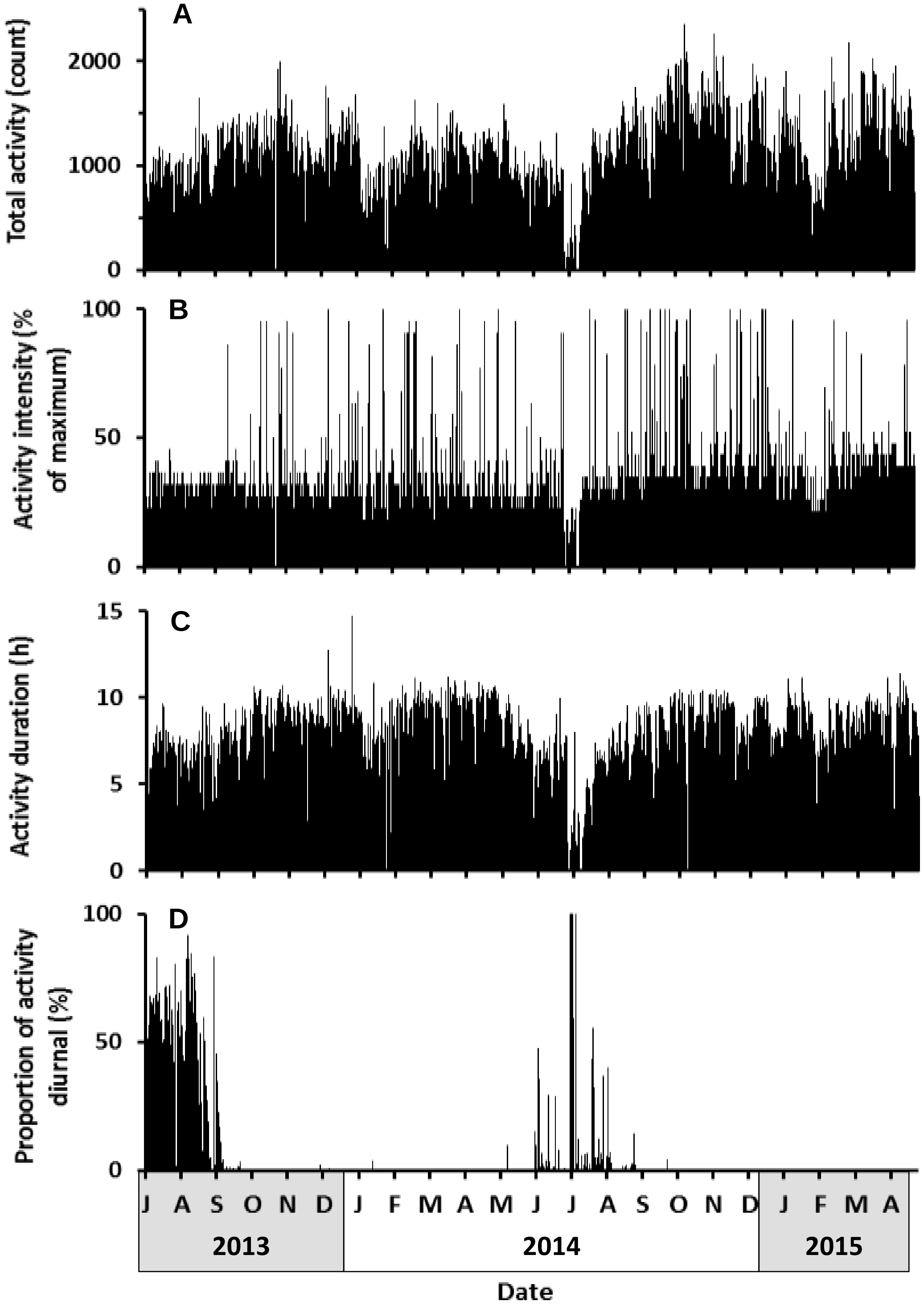

Figure 4.1 Activity dataset of aardvark 9 for the period July 2013 to May 2015 (N = 675 consecutive days excluding capture days). A) Total 24-h counts of activity logs; B) maximum 24-h activity, expressed as % of the maximum reached by this aardvark during instrumentation with the logger; C) duration (hours) of each active phase; D) proportion (%) of each active period that the aardvark was diurnal. Note that data from aardvark 9 were selected for display because this dataset is the longest continuous record of activity.

Table 4.2 Aardvark activity variables recorded with locomotor activity data loggers, summarised by season for each of the study years over the period of measurements from July 2012 to May 2015. Values are mean ± SD per 24-h period. The category 'veld condition' provides a coarse two-category index of the vegetation productivity at Tswalu based on the maximum EVI of that growing season.

Season	Veld condition	Total activity (count)	Maximum activity (% of maximum)	Active phase duration (h)	Proportion diurnal (%)	Time of emergence (h)	Time of return (h)	N days	n aard-varks
winter 2012	normal	1127.8 ± 741.0	42.3 ± 21.2	6.2 ± 2.9	23.9 ± 26.4	16:00 ± 3:48	22:41 ± 4:19	151	4
spring 2012	normal	1419.0 ± 631.1	48.1 ± 16.8	7.9 ± 2.3	31.0 ± 13.0	15:49 ± 1:44	23:49 ± 2:49	298	4
summer 2012-13	drought	882.9 ± 899.8	29.4 ± 11.3	8.2 ± 1.9	29.6 ± 8.8	16:37 ± 2:24	00:56 ± 3:05	224	3
autumn 2013	drought	712.1 ± 557.1	21.2 ± 2.4	7.6 ± 1.9	50.0 ± 0.0	12:20 ± 0:52	19:58 ± 1:55	30	2
winter 2013	drought	969.7 ± 340.0	35.0 ± 11.7	6.1 ± 1.8	53.9 ± 25.0	14:32 ±2:05	20:45 ± 2:04	208	4
spring 2013	drought	1295.3 ± 301.1	38.4 ± 12.5	8.3 ± 1.8	2.5 ± 8.3	19:10 ± 1:05	03:32 ± 2:05	273	3
summer 2013-14	normal	1155.3 ± 374.0	42.9 ± 20.1	8.3 ± 2.0	0.1 ± 0.4	20:24 ± 1:14	04:42 ± 1:46	270	3
autumn 2014	normal	1147.4 ± 272.4	38.7 ± 15.2	8.7 ± 1.8	0.8 ± 5.7	19:10 ± 1:32	03:52 ± 2:34	276	3
winter 2014	normal	995.6 ± 303.1	35.7 ± 16.9	6.3 ± 1.9	7.6 ± 16.8	17:44 ± 1:55	00:04 ± 2:55	278	4
spring 2014	normal	1371.5 ± 286.1	43.6 ± 19.3	8.6 ± 1.5	0.1 ± 0.9	19:33 ± 0:45	04:10 ± 1:25	242	3
summer 2014-15	drought	1147.5 ± 336.1	39.0 ± 16.8	8.3 ± 1.5	1.1 ± 7.4	20:51 ± 2:47	05:24 ± 2:08	180	2
autumn 2015	normal	1314.9 ± 275.5	37.8 ± 9.4	9.1 ± 1.3	0.0 ± 0.2	19:51 ± 1:11	04:55 ± 1:44	144	2

4.3.3 Timing of the active phase

Locomotor activity of aardvarks over 24-h periods was monophasic and aardvarks were active throughout the entire active phase, although their activity at a resolution of 5-minute intervals was interspersed with brief inactive bouts, and inactive phases were interspersed with brief active bouts (as shown for aardvark 9, Figure 4.2). Aardvark locomotor activity was usually restricted to night-time. During warm seasons, the onset of locomotor activity closely tracked the time of sunset and activity ceased around sunrise. However, during winters, locomotor activity shifted to earlier times of the day and occasionally began before sunset and ended up to several hours before sunrise. These shifts of the times of start and end of activity were not synchronised, as the start time became earlier sooner during the colder season than did the end of the active phase, resulting in a shortening of the active phase combined with a shift to diurnal activity (Figure 4.2). Generally, in winter, aardvarks became diurnal for brief periods only. However, a distinct shift to increased diurnal activity occurred in winter 2013 following the summer drought, with pronounced daytime activity from early July to late September.

Times of emergence and return derived from median locomotor activity over 65 minutes confirm the pattern of the 5-minute interval data that aardvarks generally emerged around sunset, and returned to their burrows shortly before sunrise (Figure 4.3). Times of emergence and return shifted to earlier times during winter, with aardvarks occasionally emerging in the late afternoon, and returning several hours before sunrise (Figure 4.3). Aardvarks emerged before sunset more often, and earlier, during a drought year (2012-13) than during a normal year (2014).

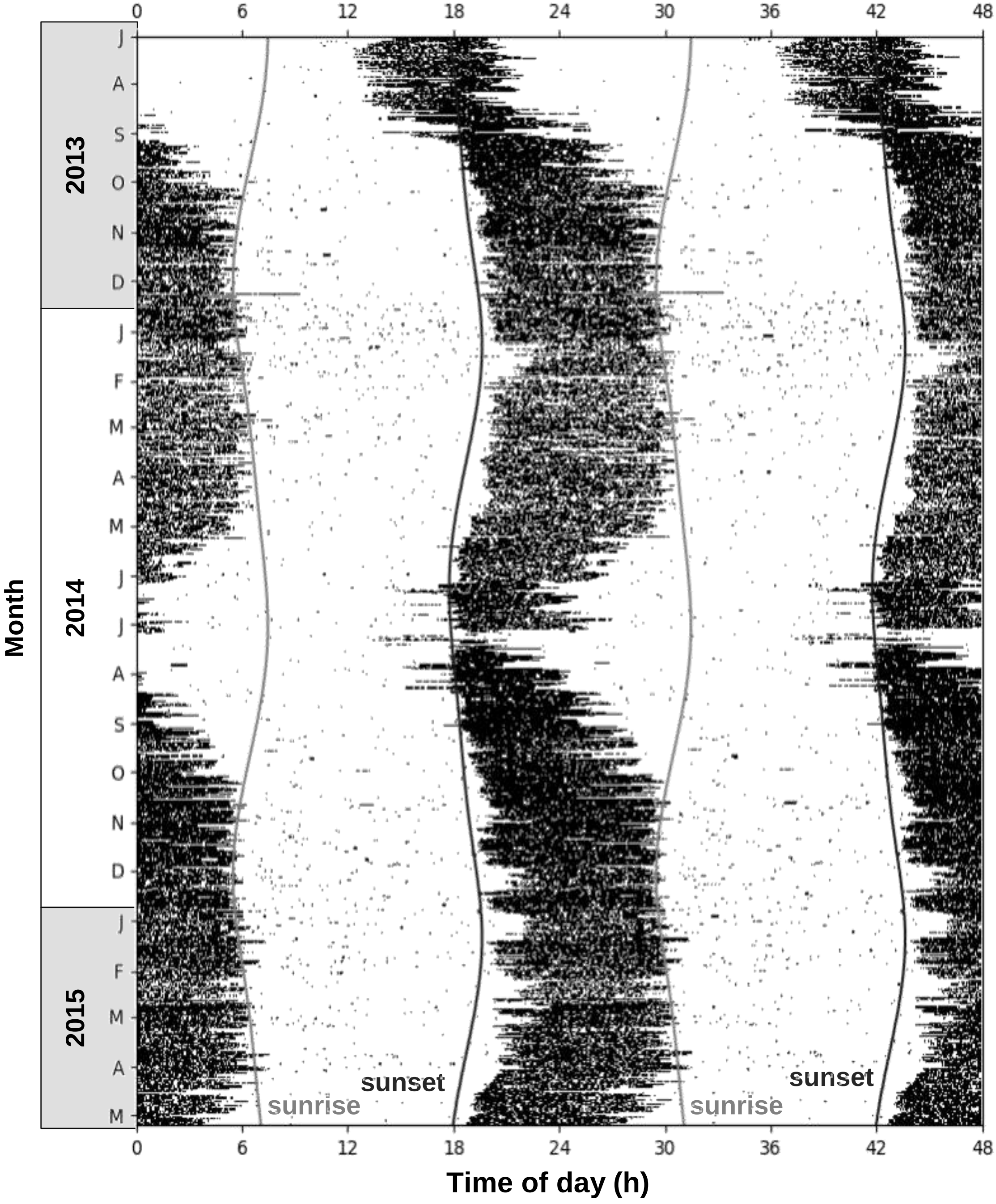

Figure 4.2 Actogram showing locomotor activity of aardvark 9 as a representative for all study aardvarks at Tswalu, free-ranging in its natural environment, for the period July 2013 to May 2015 (N = 675 consecutive days). Days are stacked vertically, data are displayed in 5-minute intervals. Black bars represent periods when the aardvark was active (≥ 5 % of maximum activity); white areas represent periods when the aardvark was inactive (< 5 % of maximum activity); dark grey line is the time of sunset; light grey line is the time of sunrise. For better visualisation of seasonal shifts in nychthemeral rhythms, activity is plotted over 48 hours, with two consecutive 24-h periods displayed beside each other. . Note that data from aardvark 9 were selected for display because this dataset is the longest continuous record of activity.

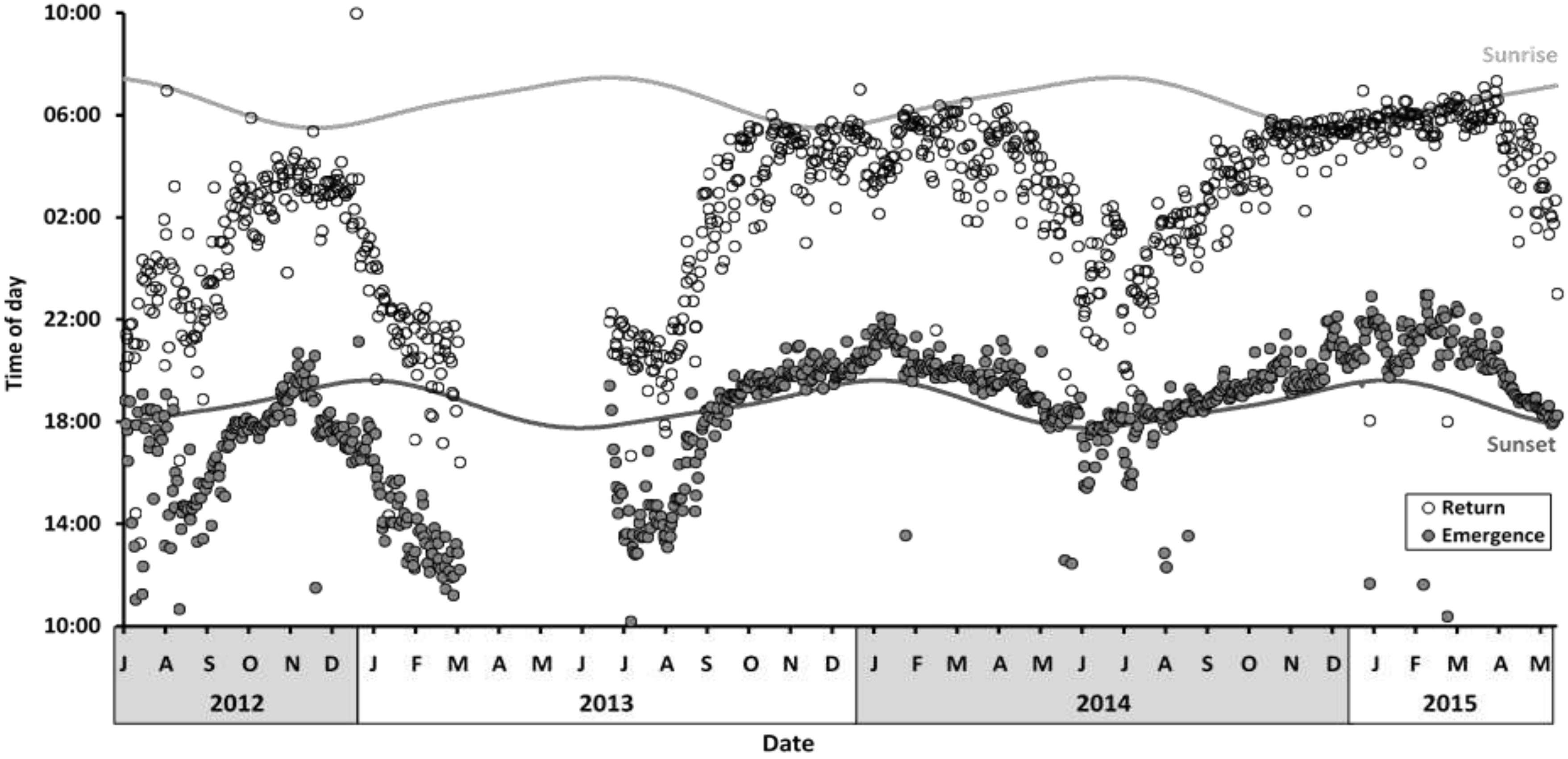

Figure 4.3 Daily activity patterns of all study aardvarks in relation to photoperiod between July 2012 and May 2015. Filled grey dots - time of emergence of aardvarks from a burrow, hollow circles - time of return to a burrow. Values are averages for all aardvarks per day (N = 1032). Dark-grey line - sunset, light-grey line - sunrise. Time-axis ranges from 10:00 in the morning until 10:00 the following morning. No data were available between March and July 2013, because all study aardvarks but one had died in March, and the logger in the only surviving aardvark stopped recording.

4.3.4 Seasonal 24-h locomotor activity patterns

Mean seasonal 24-h activity rhythms of aardvarks reveal several distinct patterns (Figure 4.4). In normal / good years, aardvarks were usually nocturnal during spring, summer and autumn, with activity between 18:00 and 06:00 in spring and autumn, and from 20:00 to 06:00 in summer but shifted their activity to earlier hours of the day in winter (Figure 4.4). The occurrence of diurnal activity in winter varied between years, with little diurnal activity in the winter of a productive year (2012, 2014), but pronounced diurnal activity in the winter of a drought year (2013). Moreover, an almost complete shift to diurnal activity occurred during the summer drought of 2012-13, with activity occurring during all hours of the daytime and peaking during mid-day. In the following autumn 2013, aardvark activity was greatest between morning and mid-day, with inactivity during the afternoon and little activity between sunset and sunrise.

Patterns of 24-h activity differed between individuals in response to drought. During normal, non-drought seasons, variation between individuals (as indicated by standard deviation) was small, but large inter-individual variation (large SD) of activity existed during the summer drought 2012-13 and the subsequent autumn 2013 (Figure 4.4). This variation was largely a result of some aardvarks becoming active in the daytime during the summer drought 2012-13, notably January to March 2013, when they would experience high daytime heat loads, while one remained nocturnal. In this case, the aardvarks that were diurnal during summer died in late March 2013 at the end of the drought, whereas the one that remained nocturnal throughout the summer drought survived. No activity data exist for the period after the drought summer, because most study aardvarks had died during the drought summer, and no data after the drought were available from the one survivor (aardvark 7). However, low inter-individual variation in activity (low SD) during the winter after the drought confirms the observation that all study aardvarks showed diurnal activity during the winter after the drought (Figure 4.4).

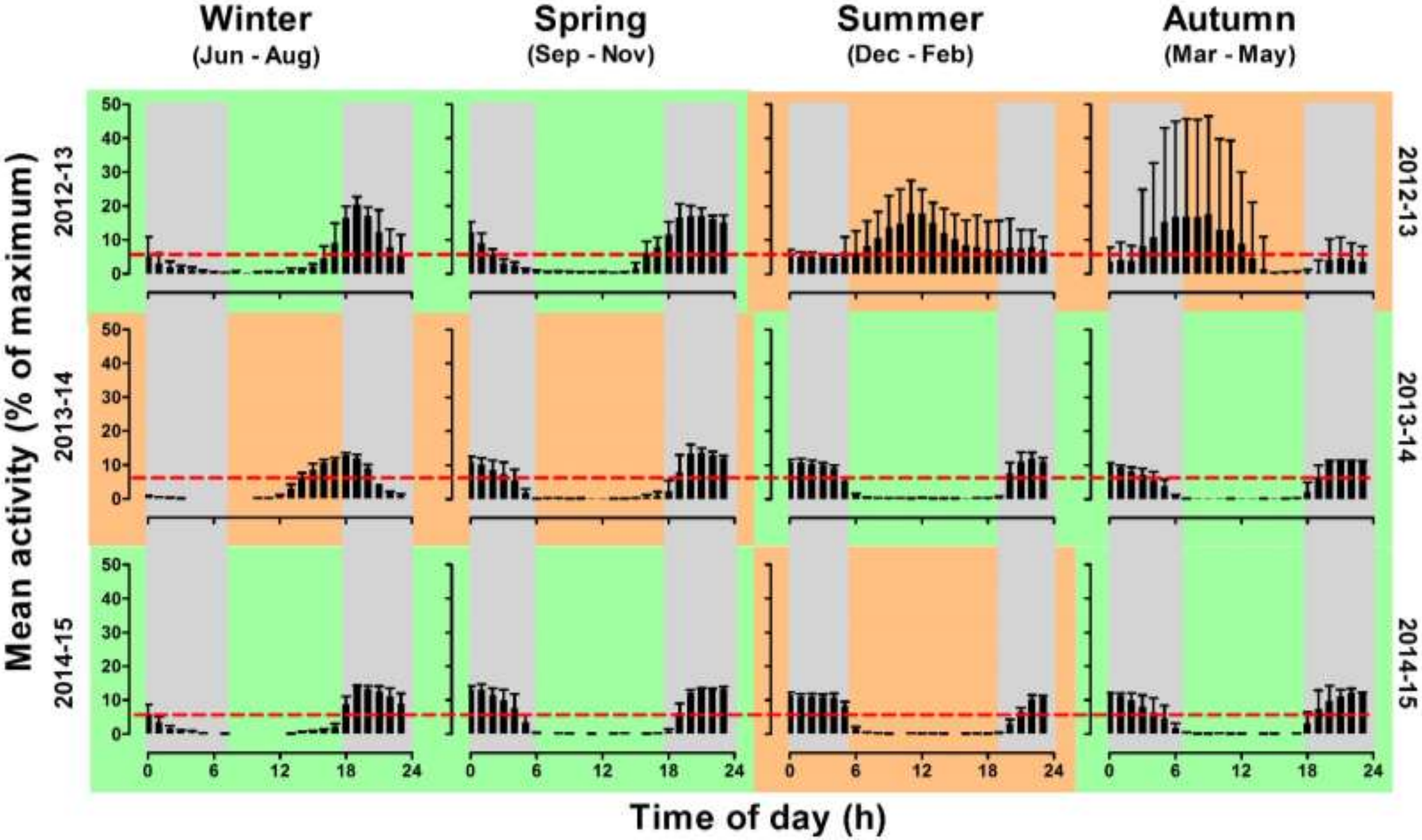

Figure 4.4 Mean seasonal 24-h activity patterns of all study aardvarks over 3-month-seasons at Tswalu between July 2012 and May 2015, based on data from activity biologgers. Each row is one year of the study; seasons are stacked vertically in columns; orange backgrounds indicate drought periods, green backgrounds indicate normal productivity; red dotted lines indicate 5%- threshold for activity, grey boxes indicate night-time, error bars represent SD between individuals.

4.3.5 Air temperature at time of emergence and return

The ranges of air temperatures at which aardvarks emerged (–3.2 to 36.9 °C) or returned (–2.4 to 39.4 °C °C) to burrows between 01 July 2012 and 31 May 2015 were variable, and only slightly narrower than the full range of air temperatures experienced at Tswalu (–4.4 to 39.9 °C). Air temperatures were usually higher at time of emergence than at time of return (Figure 4.5), except during the drought summer 2012-13; from January to March 2013, aardvarks returned to burrows at temperatures higher than those during emergence. The high maximum air temperatures at emergence and return during the drought summer 2012-13 (notably January to March 2013) were largely the result of aardvark 2 emerging during daytime. Aardvark 2 became entirely diurnal during the drought summer, and emerged in the morning and midday at temperatures that were lower than temperatures in the afternoon, when the aardvark returned to its burrow (Figure 4.5), until the aardvark died in March 2013 at the end of the drought. For comparison, during the same period, aardvark 7 (the only study aardvark that survived the drought) remained nocturnal and became active at cooler temperatures than did aardvark 2 (Figure 4.5).

4.3.6 Effect of environmental variables on different measures of activity

As indicated by the GLMM results, total 24-h locomotor activity of aardvarks during the active phase was positively associated with photoperiod, but not with mean air temperature, lunar illumination, or EVI (Table 4.3A). In other words, total 24-h activity was greater when days were longer.

Maximum 24-h locomotor activity during the active phase was positively associated with mean air temperature, photoperiod, and EVI, and not associated with lunar illumination (Table 4.3B). Thus, aardvarks tended to be more intensely active when days were warm, long, and productivity high (i.e., aardvarks had good body condition).

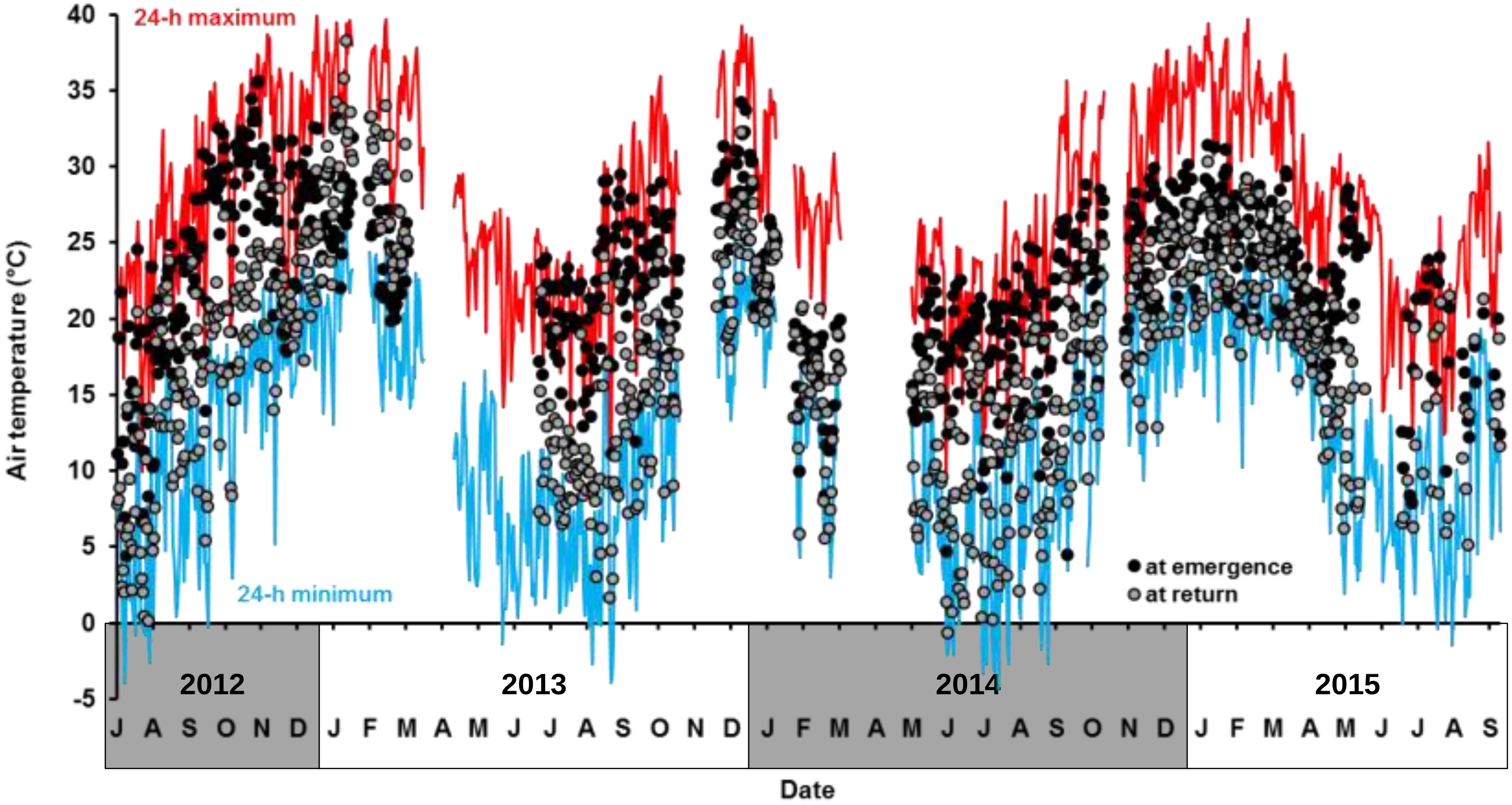

Figure 4.5 Air temperature at time of emergence and return of study aardvarks at Tswalu Kalahari Reserve between July 2012 and September 2015, averaged across all aardvarks per day. Black circles represent air temperature at time of emergence; grey circles represent air temperature at time of return; blue line represents daily minimum air temperature and the red line is daily maximum air temperature. No times of emergence and return were available during March to July 2013, because most study aardvarks had died, and the logger in the one survivor stopped in March. New aardvarks were added to the study in July 2013. Temperature data were not available for periods in February 2013, November 2013, January 2014 and April 2014 because of weather station failure.

The duration of the active phase of aardvarks associated positively with mean air temperature, photoperiod and EVI, but no association existed with lunar illumination (Table 4.3C), indicating that aardvarks were active for longer when days were warm, long and their body condition was good.

The diurnal proportion of activity was inversely associated with photoperiod and EVI, and not associated with mean air temperature and lunar illumination (Table 4.3D), indicating that aardvarks tended to spend a greater proportion of their active phase before sunset when days were short and productivity low (i.e., aardvark body condition was poor).

Time of emergence from a burrow was associated positively with photoperiod and EVI, but there was no association with mean air temperature and lunar illumination (Table 4.3E). In other words, aardvarks emerged later when days were long, and aardvarks were in good condition, whereas air temperature and phase of the moon had no effect on their emergence time.

Time of return to a burrow was associated positively with mean air temperature, photoperiod, and EVI, but not associated with lunar illumination (Table 4.3F), indicating that aardvarks returned to their burrows later when days were warm and long, and aardvarks in good condition.

Table 4.3 GLMM results showing effects of mean air temperature (°C), lunar illumination (%), photoperiod duration (hours between sunrise and sunset), and EVI (Gordonia duneveld vegetation) at Tswalu as an index of aardvark body condition, on A) total activity during the active phase, B) maximum daily activity during the active phase (% of maximum), C) duration of the active phase (hours), D) proportion of the daily active phase spent during daylight, E) time of emergence, and F) time of return for each 24-h period between August 2012 and September 2015. No activity data were available from March to June 2013. For time of emergence and return, camera trap data were included in the dataset on days on which no biologger data were recorded (May to September 2015). Aardvark 2 was omitted from the GLMMs on total and on maximum activity because of an error in its dataset. In all models, aardvark identity was included as a random factor. Significant *P*-values are italicised.

Activity	**Variable**	**β ± SE**	***Z***	***P***	**95 % CI**
A) Total activity	air temperature	1.31 ± 2.51	0.52	0.60	–3.61 to 6.23
	lunar illumination	–0.36 ± 0.26	–1.41	0.16	–0.86 to 0.14
N = 2441	photoperiod	894.39 ± 303.30	2.95	*0.003*	299.93 to 1488.85
	EVI	–315.45 ± 258.95	–1.22	0.22	–822.97 to 192.08
	constant (intercept)	808.19 ± 125.44	6.44	< *0.001*	562.34 to 1054.04
B) Maximum activity	air temperature	–0.40 ± 0.11	–3.82	< *0.001*	–0.61 to –0.20
	lunar illumination	< –0.01 ± 0.01	–0.55	0.58	–0.03 to 0.02
N = 2241	photoperiod	55.85 ± 12.73	4.39	< *0.001*	30.89 to 80.81
	EVI	25.56 ± 10.86	2.35	*0.019*	4.26 to 46.85
	constant (intercept)	16.29 ± 5.26	3.10	*0.002*	5.98 to 26.60
C) Duration of the active phase	air temperature	< 0.01 ± < 0.01	6.46	< *0.001*	< 0.01 to < 0.01
	lunar illumination	< 0.01 ± < 0.01	–1.57	0.90	< 0.01 to < 0.01
	photoperiod	0.22 ± 0.06	3.68	*0.001*	0.10 to 0.34
N = 2501	EVI	0.41 ± 0.05	7.74	< *0.001*	0.31 to 0.52
	constant (intercept)	0.09 ± 0.03	3.73	< *0.001*	0.04 to 0.14
D) Proportion of the active phase diurnal	air temperature	–0.19 ± 0.14	–1.39	0.16	–0.47 to 0.08
	lunar illumination	< 0.01 ± 0.01	0.12	0.90	–0.03 to 0.03
	photoperiod	–56.94 ± 17.13	–3.32	*0.001*	–90.51 to –23.36
N = 2460	EVI	–206.14 ± 15.05	–13.70	< *0.001*	–235.63 to –176.65
	constant (intercept)	79.87 ± 7.15	11.17	< *0.001*	65.85 to 93.89

Activity	**Variable**	**β ± SE**	***Z***	***P***	**95 % CI**
E) Time of emergence **N = 2556**	air temperature	< 0.01 ± < 0.01	0.52	0.61	< 0.01 to < 0.01
	lunar illumination	< 0.01 ± < 0.01	–0.08	0.94	< 0.01 to < 0.01
	photoperiod	0.70 ± 0.09	8.11	< *0.001*	0.53 to 0.87
	EVI	1.03 ± 0.08	13.36	< *0.001*	0.88 to 1.18
	constant (intercept)	0.23 ± 0.04	6.44	< *0.001*	0.16 to 0.30
F) Time of return **N = 2482**	air temperature	< 0.01 ± < 0.01	4.24	< *0.001*	< 0.01 to 0.01
	lunar illumination	< 0.01 ± < 0.01	–1.15	0.25	< 0.01 to < 0.01
	photoperiod	0.95 ± 0.10	9.29	< *0.001*	0.75 to 1.15
	EVI	1.41 ± 0.09	15.65	< *0.001*	1.23 to 1.59
	constant (intercept)	0.32 ± 0.04	7.43	< *0.001*	0.23 to 0.40

4.4 Discussion

With this study, I am the first to quantify activity patterns in free-living aardvarks and to show seasonal as well as inter-annual variability in their responses to climatic conditions and resource availability. As far as I am aware, I also present the longest records of locomotor activity in a large, free-living mammal to date. I show that the most important independent drivers of the timing and duration of the aardvarks' active phase, and of their total and maximum 24-h activity, were resource availability (as indexed by EVI, an indicator of aardvark body condition; see Chapter 3), day length (photoperiod, an index of season), and air temperature. Lunar illumination had no effect on aardvark activity.

During productive years with high resource availability, aardvarks emerged after sunset and always returned to their burrows shortly before sunrise. Aardvarks were active for at least ~8 hours per night in summer but shifted that activity by ~6 (rarely, up to 12) hours earlier in winter. Despite their earlier shift, aardvarks generally remained nocturnal due to earlier sunset times, apart from a few exceptions of late-afternoon foraging. During spring, summer, and autumn, aardvarks had a high total (up to ~1 400 counts per day) and maximum (up to ~48 %) locomotor activity, whereas during winter they had lower total (up to ~1 100 counts per day) and maximum (~ 35 to 42 %) locomotor activity. During the hottest summer periods, aardvarks occasionally showed low total and maximum locomotor activity and began foraging very late (several hours after sunset), with emergence after 23:00 resulting in active phases shorter than 6 hours as a result of the early sunrise time (~05:00).

During drought years, aardvarks reduced their active phases, an effect that was pronounced during cooler periods: when days were short, cold, and conditions poor, aardvarks returned to their burrows earlier but did not emerge earlier to the same extent, shortening their active phase durations from 8 hours to about 6 to 7 hours; the reduction in activity duration was most evident during autumn 2013 compared to the following autumns. Regardless of photoperiod and air temperature, aardvarks in poor condition were more diurnal, shifting activity by up to 12 hours earlier, resulting in diurnal activity both during the summer and winter of drought years. Aardvarks in poor condition also reduced maximum locomotor activity as daylength became shorter, with maximum activity no higher than ~21 % during autumn 2013. These reductions in maximum activity and active-phase length corresponded with lower total activity (~700 counts per day) when days were short. During the drought summer of 2012-13, study aardvarks completely shifted their activity to the daytime, thereby exposing themselves to intense heat (~40 °C in the shade). They died at the end of the drought in autumn (Chapter 3 and Rey et al. 2017), just before rains in late March 2013 increased vegetation productivity and prey abundance (Chapter 3). One study aardvark remained nocturnal throughout the drought summer and survived. In the winter that followed the 2012-13 drought, many aardvarks at Tswalu, including my study aardvarks, were diurnal and in poor condition (Chapter 3; pers. obs.), and all study aardvarks shifted from a pattern of nocturnal to diurnal activity, ceasing activity around sunset, with little nocturnal activity. On numerous drought winter mornings, study aardvarks emerged above ground but remained inactive, resting and basking (see Chapter 5) near to their burrow entrances before foraging.

Unfortunately, several study animals died during drought years, some aardvarks could not be located to remove loggers because of VHF tracker failures, and some of the retrieved loggers failed, which substantially reduced my original sample size. Nevertheless, I was able to detect seasonal and interannual variability in activity patterns of aardvarks which could not have been achieved based on traditional observational methods. Wild, unhabituated aardvarks are timid and skittish creatures, which makes behavioural observations challenging. I was able to observe aardvark behaviour for 36 hours, and obtained 408 times of burrow emergence and 107 times of return from camera trap footage. These records and the footage allowed me to validate the active and inactive phases of the aardvarks as recorded by the biologgers. Although the biologgers used here did not allow for differentiation of different types of behaviour (as do high-frequency tri-axial accelerometers, as for example in Shepard et al. 2008, my loggers did provide a reliable measure of activity levels based on a chosen threshold for activity of 5 %. The loggers used here allowed me to determine the time at which aardvarks emerged from their burrows and the time at which they returned after foraging, on 2574 sampling days for nine different aardvarks over a period of 34 consecutive months.

During the ~3 years of my activity records, Kalahari aardvarks were active every night, but there were a few exceptions when they remained inactive for a night, for unknown reasons. Similarly, Karoo aardvarks emerged every night to forage during one year of observations (Taylor, 1998). Both Karoo and Kalahari aardvarks emerged despite wind and rain, although they appeared more skittish during such conditions (this study and Taylor 1998), and on rare occasions on stormy nights, my Kalahari aardvarks sought shelter in burrows and resumed foraging once the strong winds had subsided. The lowest air temperature at which my study aardvarks were active (–3.2 °C) was substantially lower (by ~5 °C) than that reported (~2 °C) for aardvark activity in the Karoo; air temperatures in the Karoo dropped to as low –12 °C, compared to –4.4 °C during this study (Taylor, 1998; Taylor & Skinner, 2003). The possibility exists that Karoo aardvarks were indeed active at temperatures below 2 °C but that these occasions were not recorded as a result of the observation-dependent, lower sampling intensity, highlighting the advantage of biologgers for recording activity. In my study and in the Karoo, low temperatures at night limited foraging such that aardvarks returned to their burrows earlier (Taylor & Skinner, 2003). High thermal conductance of aardvarks associated with poor fur insulation (McNab, 2002) might limit aboveground activities in the cold, unless insulating subdermal body fat reserves reduce heat loss (see Chapter 5). At Tswalu, only study aardvarks in good body condition were nocturnally-active in winter, whereas those in poor condition became diurnal, avoiding extremely cold night-time temperatures. During drought winters, cold temperatures at night limited activity and caused aardvarks to return earlier to burrows. Nevertheless, the wide range of air temperatures at which aardvarks were active (–3.2 to 39.9 °C) indicates that temperature was not the key driver of activity timing.

Kalahari aardvarks' seasonal activity patterns during normal (non-drought) years resembled those of Karoo aardvarks in that when days were longer towards summer, the aardvarks were active for longer, exclusively nocturnal, and had high total and maximum 24-h activity. During winter, maximum and total activity of my study aardvarks declined, and active phases shortened. Similarly, Karoo aardvarks spent less time outside burrows during winter than during summer (Van Aarde et al., 1992; Taylor, 1998), and moved more slowly and for shorter durations during cold, dry winter months, proposedly because cold temperatures and wind make foraging conditions unfavourable (Van Aarde et al., 1992). Karoo aardvarks (Taylor, 1998) were, like Kalahari aardvarks, active for ~8 h during summer and 6 to 8 h during winter. They emerged and returned earlier when days were shorter in winter, resulting in more-diurnal activity. Shortened active phases of Kalahari and Karoo aardvarks during winter resulted from a more-pronounced shift of return than of emergence to earlier times. In the Kalahari, this pattern was exacerbated during drought periods, when aardvarks became entirely diurnal during summer and (at least the drought survivors) remained diurnal throughout winter, but for much-reduced periods. Aardvark activity in the Kalahari was also influenced by body condition such that well-nourished aardvarks were nocturnal, and those in poor condition become active diurnally regardless of season or air temperature. The Karoo aardvarks' body condition was not assessed, and so it remains unclear whether they emerged early as a result of poor body condition, or simply because cold-restrained earlier return-times made the aardvarks hungry earlier on the following day.

In general, aardvarks were rarely active at temperatures above ~30 °C, except for those aardvarks that became active in midday during the drought summer 2012-13 and experienced high daytime temperatures. During the hottest summer months, Kalahari aardvarks emerged only late at night when air temperatures had cooled to ~30 °C, and returned to their burrows around sunrise before air temperatures began to rise again. Despite the overall trend of active phase duration extending with warmer temperatures, such late emergences during hot periods caused a shortened active phase, effectively reducing the aardvarks' foraging time. During these brief periods, aardvarks decreased their total and maximum daily activity. Similarly, Karoo aardvarks became active later in the night during hotter seasons (Taylor, 1998). Another large myrmecophage mammal that adjusts its activity patterns and behaviour in response to air temperature is the giant anteater (De Sampaino et al., 2006). In the Brazilian Cerrado, where temperatures are similar to those of the Kalahari, the giant anteater shifts activity and selects different foraging habitats under different climatic conditions (De Sampaino et al., 2006). During summer, the giant anteater is predominantly nocturnal, active until sunrise and resting in canopy-covered habitats during the day and beginning its activity increasingly later with higher temperatures. In cooler seasons, the giant anteater remains nocturnal but no longer until sunrise, effectively shortening its active phase. On very cold days, the giant anteater may become entirely diurnal, and may bask in the warming sun. Utilising a cooler microclimate during the hottest periods of the year might have the advantage of preventing evaporative water loss to the environment. However, as in the giant anteater (De Sampaino et al., 2006), such behaviour may result in shortened foraging time for gathering energy and water from prey. Acquiring sufficient energy and water during the active phase to cover daily needs is crucial to survival, but may sometimes be impossible, for example during drought, when resources are particularly scarce in the Kalahari (Chapter 3). Lowered 24-h maximum activity of my aardvarks during unproductive periods could have been caused by aardvarks being weakened from malnutrition due to insufficient prey availability, an attempt to preserve energy instead of expending it on energy-costly digging, or a sign that there was too little prey available to make major digging efforts worthwhile.

Aardvarks have previously been proposed to avoid heat-producing activities such as intense digging (McNab, 2002) to prevent overheating at high air temperatures (Taylor & Skinner, 2004). My GLMM analyses showed an inverse relationship of maximum daily activity with mean air temperature, but a positive correlation of maximum activity with photoperiod and EVI (an index of body condition). These results suggest that aardvark maximum activity is indeed limited by heat, as well as by body condition (and thus likely body strength, which is required for intensive digging). Their sparse fur insulation and high thermal conductance (McNab, 1984) should enable aardvarks to lose excess metabolic heat from digging activity easily via evaporative and non-evaporative means. Evaporative cooling, the use of thermal windows (i.e., highly vascularised body surface areas), and vasodilation in response to changing ambient temperatures have not been investigated in aardvarks. Captive aardvarks frequently seek the warmth of infrared lamps, and they are also known to develop 'red ears' during hot summer days (A. Parys, Frankfurt Zoo, Germany, pers. comm.), pointing at the possible use of their large ears as thermal windows for heat loss. Captive aardvarks also show signs of discomfort such as arousal or restlessness when it is hot, and if available, may immerse themselves in water basins on hot days (A. Parys, Frankfurt Zoo, Germany, pers. comm.), suggesting skin-wetting as a mechanism for heat loss. However, while captive aardvarks have access to water, free-standing water is scarce in the semi-desert, thus body-wetting behaviour, or even drinking, is barely a reliable option for aardvarks in the Kalahari. Although aardvarks do drink water occasionally if it is available (see Chapter 3), free-living aardvarks in semi-arid regions must likely rely on their prey to cover their water requirements from their diet (Taylor et al. 2002; Taylor and Skinner 2004; Chapter 3). Therefore, when food is scarce during drought, so is water availability, and water-use efficiency becomes critical for survival. The diurnal activity of energy-deficient aardvarks in the drought summer of 2012-13 in the face of high environmental temperatures likely contributed to increased water stress, further jeopardising aardvark survival through the drought.

The theory of optimal foraging proposes that an animal should maximise energy intake while taking into account all potential costs and benefits of foraging (Krebs, 1980; Pyke, 1984), such that the animal would continue to forage as long as energetic benefits exceed foraging costs, including predation risk, energy costs of foraging, and interactions (Lima & Dill, 1990). When resources are abundant, an animal might increase its fitness by prioritising activities that enhance its energy intake (e.g., foraging), as well as its reproduction (e.g., mating behaviours, rearing of young;

reviewed in Bronson 2009) and its social status (e.g., grooming; McFarland et al., 2014). In turn, when resources become limited, an animal might either increase the duration or intensity of their foraging activities to locate sparse resources attempting to cover its energetic needs (Therrien et al., 2008; Clutton-Brock et al., 2009; Podolski et al., 2013), or decrease foraging effort and other activities to preserve energy (O’Donnell, 2000; Christian & Geiser, 2007). During a drought year, however, aardvarks did not attempt to compensate for reduced prey availability by foraging for longer but rather opted for reduced energy expenditure by shortening their active phases, and resting for longer.

Reduced maximum activity during poor conditions might reflect a reduction in energetically-costly digging activities (McNab, 2002). Indeed, during the dry winter of 2013 after the drought, when the aardvarks were in poor condition, I observed that aardvarks frequently re-used the same burrow for several consecutive nights or switched between the same two or three burrows over several weeks (Chapter 2). The longest period of consecutive use of the same burrow in one aardvark was 14 days (Chapter 2). During all other seasons and years, my study aardvarks changed burrows nearly every day, seldom re-used burrows on consecutive days, and barely ever refurbished older burrows (Chapter 2). In comparison, Karoo aardvarks re-used burrows for longer periods at a time than aardvarks (on average for 6.8 ± 7.2 consecutive days; ranging from 1 to 38 consecutive days; Taylor, 1998). Another large burrowing mammal, the giant armadillo uses the same burrow for about 3 consecutive nights in Brazilian Cerrado grasslands (Silveira et al., 2009) where it faces potential risk of predation from jaguars (*P. onca*), corroborating the argument that under increased predation risk, frequent burrow change may be an advantage.

Re-using one burrow over an extended period likely comes at a cost for an aardvark, or any other burrowing mammal. For example, it might become more predictable and thus vulnerable to predators if it continuously returns to the same location. While absence of large carnivores resulted in low predation risk at the study site, at sites where predators do pose an imminent threat, frequent moving of burrows with no predictable pattern for choosing the next resting location might aid aardvarks in maintaining crypticity. Moreover, parasite exposure risk might be greater when re-using the same burrow over extended periods. Use of a single burrow may also constrain the aardvark to feeding off the ant or termite colonies in a similar area each night, possibly contributing to colony depletion, especially when insect numbers are already compromised from the drought (Chapter 3). However, during spoor tracking, I noticed that aardvarks had often walked far (up to several kilometres) before the first feeding site of a night. Similarly, Karoo aardvarks did not necessarily burrow close to feeding grounds but often walked far to a burrow after feeding (Taylor, 1998). Lastly, by using only a section of its home range, an aardvark might miss out on interaction with conspecifics, such as mating opportunities or territorial behaviour. Energetically-challenged aardvarks potentially could reduce energy expenditure by renovating an old burrow rather than undertaking intense digging to excavate a new burrow.

To maximise energy intake, aardvarks would be expected to coordinate the timing of their foraging-activities with the times of the day at which their key prey in the Kalahari, the harvester termite *Hodotermes mossambicus* (Chapter 3), is most easily accessible. Harvester termites occur in deep (up to 7 m) underground hives (Hartwig, 1965), and emerge during day in winter and at night in summer to harvest grass (Nel & Hewitt, 1969b). These termites must undergo daily vertical migrations from the deep hive area and move to the upper soil levels during the day, to warm up in anticipation of their daily foraging. Thus, in winter, termites might aggregate nearer the surface several hours before emerging to forage during daytime, which might explain a shift in aardvark foraging to earlier times in winter. In summer, the termites would be expected to migrate towards the upper levels of the soil in the evening, in anticipation of their night-time foraging, which would match the nocturnal activity of the aardvarks in summer. However, aardvarks at Tswalu only became diurnal during drought winters but not during non-drought winters, thus an adaptation of their active phase to the timing of termite activity might not be the only explanation for the seasonal shift in aardvark activity. Similarly, in the Karoo, aardvark activity was independent of prey activity as the aardvarks were nocturnal but their predominant prey ants *Anoplolepis custodiens* (Taylor et al., 2002) were predominantly diurnal (Lindsey & Skinner, 2001). Moreover, harvester termites have also been reported to forage diurnally at high temperatures (Nel, 1970), substantiating the argument that aardvark activity is independent of that of their prey.

Aardvarks are thought to be temperature-sensitive, avoiding heat and cold (Taylor & Skinner, 2004). I found that aardvarks spent the coldest periods in their burrows and returned earlier to burrows when it was colder. As burrow temperatures generally fluctuate less than those outside (Chapter 2 and Taylor, 1998), burrow use likely decreases energy expenditure for thermoregulation in the cold. One also would expect an aardvark to avoid exposing itself to intense heat and solar radiation typical of summer days in the Kalahari semi-desert. Counterintuitively, however, I found that the aardvarks shifted to a diurnal activity pattern when prey was likely scarce during the drought summer. During periods of negative energy balance, some nocturnal animals shift activity to daytime, as reported for animals in the lab (Hut et al., 2011; Van der Vinne et al., 2014, 2015) and in the wild (Lockard, 1978; Boal & Giovanni, 2007). In combination with cold, the diurnal response to energy-deficiency is even more pronounced (Van der Vinne et al., 2014). This response is based on plasticity of the mammalian circadian system, and is thought to be an adaptive mechanism that allows nocturnal mammals to maintain energy balance when facing metabolic challenges; shifting activity from night to daytime can save up to 10 % of energy (Van der Vinne et al., 2015). While this mechanism is thought to help wild mammals save energy during winter by avoiding cold night temperatures (Van der Vinne et al., 2015), it also leads to diurnality in otherwise nocturnal animals when temperatures are high (Van der Vinne et al., 2014). Presuming that this adaptive mechanism is present in aardvarks and causes them to become diurnal in response to energy-deficiency, it would advantageously decrease their metabolic needs during winter by shifting activity to warmer daytime. However, energy-deficiency might then also have driven aardvarks to become diurnal during the drought summer. Consequently, aardvarks were exposed to intense daytime heat and aridity, likely further compromising their poor condition through increased body water loss. At the same time, a dearth of termites from which aardvarks normally obtain their water left no additional capacity to compensate for increased water loss likely experienced during hostile daytime conditions. As a result, aardvarks likely became dehydrated at the same time as they were energy-deficient. Such a mismatch between shifting activity to daytime to save energy while needing to avoid heat to save water likely contributed to the observed mass mortality of aardvarks during the summer drought.

Only one study aardvark survived the 2012-13 summer drought. In this aardvark, no diurnal activity was recorded during the summer drought until its activity logger stopped working in March 2013, although the aardvark was observed during late afternoon on two occasions in April 2013 (pers. obs.). No records of body condition exist for this aardvark during the drought. However, it is a possibility that this aardvark was in better condition prior to the drought summer compared to those study aardvarks that became diurnal during summer, and thus no response to become diurnal to preserve energy was triggered in this aardvark. As a result, the survivor aardvark did not expose itself to the high temperatures and intense solar radiation typical of summer daytime in the Kalahari, and possibly avoided dangerous dehydration effects superimposed on energy-deficiency during the drought. Avoiding diurnal exposure to high temperatures might have aided this aardvark to survive summer drought, but may only be an option for an aardvark that has not been compromised by other factors before a summer drought. Becoming diurnal during winter may aid the survival of famine periods by avoiding energy-costly conditions of cold nights. However, aardvarks at Tswalu only became expansively diurnal during winter after summer drought, and not (or to a much lesser extent) in winters after good summer productivity, indicating that diurnality must have some trade-offs, otherwise all aardvarks at Tswalu should become predominantly diurnal every winter. For aardvarks, remaining nocturnal may be advantageous for predator avoidance. However, to date, aardvark activity patterns have not been studied in areas with high predation risk, i.e., from lions or leopards.

When nocturnal, aardvarks were active whether nights were brightly moonlit or very dark, and moonlight had no effect on the aardvarks' activity at Tswalu, or elsewhere in southern Africa as reported by previous studies (Van Aarde et al., 1992; Taylor, 1998). In many prey animals, bright moonlight is associated with inactivity or shifts of activity to darker times of the night (reviewed in Kronfeld-Schor et al. 2013). Absence of an effect of moonlight on any of the aardvark activity variables, is, on the one hand, not surprising, since aardvarks are not visual hunters and do not need light to detect food, as do other nocturnal animals (Fernández-Duque et al., 2010; Smit et al., 2011; Cozzi et al., 2012). Instead, aardvarks rely on their sense of smell to detect prey (Taylor & Skinner, 2004). On the other hand, aardvarks could perhaps be expected to be less active during brighter moonlight to decrease the risk of themselves being detected by visually-hunting predators (Cozzi et al., 2012). However, aardvarks were unlikely to have been affected by predators (notably, lions and leopards) at my study site. Lions were absent from the specific section of Tswalu in which the study took place and the few leopards on Tswalu usually remained in more densely vegetated areas closer to the mountains (G. Van Dyk & D. Smith, pers comm.). Secondly, although other carnivores (cheetahs, brown hyenas (*Hyaena brunnea*), jackals (*Canis mesomelas*), and, from May 2014 onward, a pack of African wild dogs) roamed freely at Tswalu, aardvarks are not a common prey item in the diet of these carnivores (Mills, 1990; Hayward & Kerley, 2005; Hayward, 2006).

Under current conditions, aardvarks are employing diurnality to prevent energy losses during increased energy needs during cold periods, as well as during periods of low food abundance. This study shows that Kalahari aardvarks were able to display behavioural flexibility in response to environmental extremes such as drought, such that they reduced the duration and intensity of activity, and became more diurnal, during drought. However, these responses did not always lead to success, because nutritional compromise from drought-induced resource scarcity (Chapter 3) resulted in diurnal activity when it was likely detrimental to the aardvarks during hot summer conditions. Moreover, those aardvarks that survived the summer drought, as well as the following winter by employing diurnality during cold periods, needed several months to recover from their poor state (Chapter 3). With climate change, conditions in the Kalahari are becoming hotter and drier, and by the middle of this century, summer droughts will likely become the rule rather than the exception. I predict that aardvarks will be impacted by future increased drought frequency through insufficient food and dietary water and might not be able to survive sequential droughts (Chapter 3). Aardvarks are currently expressing plasticity in their behaviour and activity in response to environmental fluctuations, by changing the duration of their active phases and becoming diurnal during periods of resource shortage. However, these responses may not be sufficient to ensure the long-term survival of aardvarks through expected climatic scenarios in the Kalahari.

4.5 References

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Chapter 5 - Hypothermic heterothermy in aardvarks indicates drought-related energy-deficiency

5.1 Introduction

For endotherms, the maintenance of high, constant body temperatures within a narrow range over a 24-h period requires energy and water, and will thus be jeopardised if the supply of energy or water is inadequate. In large mammals, body temperature patterns fluctuate in response to extrinsic factors such as seasonal changes in resource abundance and environmental temperatures (Hetem et al., 2016). In highly seasonal habitats, a mammal might accumulate body fat reserves during summer which sustain it during winter, when food resources are scarce or buried under snow and the animal's energy budget is negative. During these stressful winter conditions, large mammals may reduce their activity levels and exhibit hypometabolism with low body temperatures (Signer et al., 2011) or subcutaneous temperatures (Arnold et al., 2004, 2006; Brinkmann et al., 2012) to save energy. Some smaller mammals (Brown & Downs, 2007) also employ basking as a means to preserve energy while maintaining high body temperature, but in large mammals, basking for this purpose has only been presumed a possibility in a single species, the alpine ibex (C*apra ibex ibex*) to date (Signer et al., 2011). Periods of energy deficits as a result of low food availability or increased energy expenditure are often associated with low minimum 24-h body core temperatures (i.e., the minimum body temperature within a 24-h period) even at high air temperatures (Fuller et al., 2014; Hetem et al., 2016). For example, western grey kangaroos reduced their minimum 24-h body temperatures in a hot period during nutritional challenge (Maloney et al., 2011). Similarly, Arabian oryx reduced minimum 24-h body core temperatures in periods of poor food quality and quantity compared with food-abundant periods at similar air temperatures (Hetem et al., 2010). In hot and dry environments, when access to water is limited, large mammals can exhibit high maximum 24-h body temperatures, thereby delaying the need for evaporative cooling and effectively saving body water (Mitchell et al., 2002). Both an increase in maximum 24-h body temperature or a decrease in minimum 24-h body temperature, or a combination of both, will result in an increased amplitude of 24-h body temperature rhythm, termed heterothermy (Hetem et al., 2016). For example, in the hot and dry Arabian desert, Arabian oryx displayed an amplitude of 24-h body temperature rhythm of 7.7 °C, the largest amplitudes ever reported to date in a free-living large mammal that survived this body temperature fluctuation (Hetem et al., 2010). The amplitude of 24-h body temperature rhythm may reflect the physiological welfare of a large mammal in its natural environment. Indeed, only healthy, undisturbed large mammals with sufficient access to food and water appear to display homeothermy (Hetem et al., 2016).

Similar drivers of thermoregulation have been proposed for aardvarks, with minimum 24-h body temperature being lowest during a drought summer in the Kalahari (Rey et al., 2017); however, this study did not quantify the resources available to aardvarks. In the South African Karoo, aardvarks maintained homeothermy (34.5 to 37.5 °C) in summer, and displayed a slightly lower minimum 24-h body temperature and thus wider range of body temperatures (33.5 to 37.5 °C) during winter (Taylor & Skinner, 2004). Karoo aardvarks also demonstrated a pronounced nychthemeral body temperature rhythm, with lower body temperature during times spent inactive inside burrows, and higher body temperatures during the active period (Taylor & Skinner, 2004). However, in their review paper, Taylor and Skinner (2004) reported aardvark body temperature records for only five consecutive days during winter and summer, and in only three individuals. The authors attributed the variability in body temperature to air temperatures and aardvark activity patterns because aardvark body temperature and activity fluctuated simultaneously, and because body temperature was slightly lower in winter than in summer. Digging for subterranean prey produces metabolic heat that must be dissipated efficiently (McNab, 2002), and might restrict aardvark foraging to night-times during the hot season to avoid overheating (Taylor & Skinner, 2004). Karoo aardvarks shifted their foraging activity toward daytime in the cold season and were not active at air temperatures below 2 °C, which the authors interpreted as sensitivity to cold temperatures (Taylor & Skinner, 2004). Aardvarks create burrows that provide a buffered environment in which they can avoid both extremely high temperatures during summer days, and low temperatures during winter nights (Taylor & Skinner, 2004). Thus, the temporal shift in my aardvarks’ activity patterns from nocturnal in productive/normal periods to diurnal during drought periods (Chapter 4) might reflect a response to energetic deficit.

Aardvark mortalities have occurred during a drought in Namibia in the 1980s (Nicholson 1993, Stuart & Stuart 2007), and during a drought in the South African Kalahari in the summer of 2012-13 (Rey et al., 2017). Aardvarks might be sensitive to drought either as a direct result from extreme heat and aridity or as a result of a decline in social insect availability associated with unfavourable climatic conditions. Throughout their distribution, aardvarks feed virtually exclusively on ants and termites (Melton, 1976; Melton & Daniels, 1986; Willis et al., 1992; Taylor et al., 2002). Drought and high temperatures can negatively impact populations of ants and termites (Tevis, 1958; Nel & Hewitt, 1969a) and alter their density, abundance and distribution (Botes et al., 2006; Barrow & Parr, 2008; Stuble et al., 2013), thereby ultimately influencing the nutritional physiology, behaviour, and survival of aardvarks and other myrmecophageous animals that rely on these social insects (McNab, 1984). The aardvark mortalities in the summer drought of 2012-13 in the Kalahari were attributed to starvation because aardvarks had low minimum 24-h body temperatures typical of mammals in nutritional deficit (Rey et al., 2017). Although low minimum 24-h body temperatures during resource-limited periods have been shown for large herbivores (Signer et al., 2011; Maloney et al., 2011; Brinkmann et al., 2012; Hetem et al., 2012b) and primates (Lubbe et al., 2014), it is unknown how body temperatures of myrmecophageous species, with their low metabolic rates (McNab, 1984), respond to periods of resource limitation. I have shown that during the summer drought of 2012-13 in the Kalahari, termites, the main prey item of aardvarks, likely became inaccessible to aardvarks, causing aardvarks to lose body condition (Chapter 3) and become more diurnal (Chapter 4). In the present chapter, I will assess the consequences of low resource availability on body temperature rhythms of aardvarks, and whether activity and possibly sun-basking influence that rhythm.

If a shift of activity patterns is not a sufficient response to buffer the aardvarks against changes in the environment, then I predict that the aardvarks will exhibit heterothermy.

I predict that periods during which aardvarks are in energy deficit will be associated with a decreased minimum 24-h body temperature, and that periods (particularly, hot periods) when the aardvarks obtain insufficient water will be associated with higher-than-normal maximum 24-h body temperatures. I therefore predict that the 24-h amplitude of the body temperature rhythm will be smallest in periods when resources are abundant and body condition of aardvarks is good, and largest when the aardvarks have insufficient resources, and are in poor body condition.

5.2 Methods and materials

5.2.1 Body temperature measurements

As detailed in Chapter 2, aardvark core body temperature was measured using data loggers (DST centi-T, Star-Oddi, Iceland; mass ~20 g; resolution 0.032 °C; accuracy 0.1 °C; range –1 °C to 45 °C) implanted into the abdominal cavity. Loggers were set to record body temperature at 5-minute intervals. As a result of unexpected deaths of a number of study aardvarks, as well as difficulties recapturing the shy and elusive aardvarks, body temperatures were recorded in different aardvarks during different years of the study, and for varying periods. I obtained a total of 874448 body temperature data points on 3882 measuring days in ten different study aardvarks. Body temperature data were obtained over 1135 consecutive days between August 2012 and September 2015. The longest consecutive number of measuring days in a single aardvark was 797 days (aardvark 9, July 2013 to September 2015 when the aardvark was captured for logger removal), and the shortest period was 34 days (aardvark 14, July to August 2013, when the aardvark died). I provide an overview of the calibrated but otherwise unmodified body temperature records of all study aardvarks between August 2012 and September 2015 (Figure 5.1 and Figure 5.2).

5.2.2 Environmental conditions

Air temperature and wind speed at the study site were recorded at 30-minute intervals (details in Chapter 2). I used the minimum, maximum, and mean 24-h air temperatures calculated from these data to explain variations in aardvark body temperature using GLMM (generalised linear mixed-effects model) analysis (see below).

Termites (notably harvester termites *H. mossambicus*) formed the main component of aardvark diet at Tswalu (Chapter 3). The abundance of these termites depends on grass availability, and consequently, aardvark body condition correlated with EVI (Enhanced Vegetation Index, data from Tokura, 2016), an index of vegetation productivity (Chapter 3). I therefore used EVI as an index of aardvark body condition.

5.2.3 Aardvark activity and behaviour

Using implanted accelerometric data loggers (Actical loggers: Mini-Mitter Corporation, USA during the first year 2012 to 2013; MLOG_AT1, Sigma Delta Technologies (Pty) Ltd., Australia during the following years; see Chapter 2), I obtained locomotor activity in 5-minute intervals (time-matched with body temperature recordings) over almost three years and nearly the entire study period (August 2012 to May 2015). Activity data analyses are detailed in Chapters 2 and 4. I used the start and end of each active phase within each 24-h period to calculate the duration of the active phase. I then determined the proportion of diurnal activity (proportion of each active phase that occurred during daylight before sunset), as well as the total activity count and the maximum activity reached by the aardvark during each active phase (Chapter 4). I confirmed activity of aardvarks using visual observations and camera trap footage obtained as described in Chapter 2. I observed aardvarks for a total of ~36 hours, and obtained 408 times of emergence and 107 times of return between July 2013 and September 2015.

During these field observations and camera trapping between July 2013 to September 2015, I serendipitously observed and recorded the study aardvarks basking, either before foraging or between periods of burrow-use. I obtained a total of 50 observations of basking in six different study aardvarks, including 18 camera trap records of an aardvark emerging from a burrow to bask. Of these 50 basking events, 47 bouts occurred during winter 2013, two bouts during winter 2014, and one attempted bout during autumn 2015 which the aardvark aborted after 3 minutes because something startled it, causing it to return into its burrow. This event, although noteworthy, was not included in further statistical evaluations. For 39 of the 50 basking events, corresponding body temperature data are available, and the exact start and end of the basking episode are known. To assess if basking affected body core temperature, I noted the start, end and duration of basking, body temperature at start and end of basking, as well as minimum body temperature during basking, since all aardvarks showed an initial dip in body temperatures upon their emergence to bask. I considered the change of body temperature from the start to the end of a basking bout to be the net body temperature change, and the change from the minimum body temperature to the body temperature at the end of the bout to be the total temperature change.

5.2.4 Data analyses

I excluded body temperature and activity data recorded on capture days and for two days after capture attempts (successful and unsuccessful) from all analyses. Using 5-minute recordings of body temperature, I calculated the mean, minimum, maximum, and amplitude (difference between maximum and minimum) of body temperature rhythm for each aardvark over each 24-h period. From these 24-h values per aardvark, I calculated average monthly and seasonal 24-h mean, 24-h minimum, 24-h maximum as well as 24-h amplitude of body temperature rhythm and its variability (SD) between aardvarks. To obtain seasonal 24-h body temperature rhythms, I averaged data points within each 5-minute interval across each season and averaged these for all aardvarks.

I used GLMM analysis to test the hypothesis that fluctuations in body temperature patterns serve as an indicator of physiological welfare in aardvarks. Specifically, I tested the effects of photoperiod as an index of season, of minimum 24-h air temperature, of maximum 24-h wind speed, of the proportion of time aardvarks spent active during daylight, and of EVI as an index of resource abundance and body condition (Chapter 3) on minimum 24-h body temperature of aardvarks. During hot summer months (notably Dec 2012, Dec 2013, Jan 2015), aardvarks had episodes of elevated body temperatures, with increased minimum, maximum and mean 24-h body temperature over several days, as is visible in the raw, calibrated body temperature of each aardvark (Figure 5.1 and Figure 5.2). I tested the effects of photoperiod as an index of season, of maximum 24-h air temperature, of EVI as proxy for resource abundance and thus water availability, and of total 24-h activity on maximum 24-h body temperature. I excluded maximum activity data of aardvark 2 from this analysis because the data logger was faulty and registered 100 % activity on nearly every measuring day.

I analysed my data and created graphs using Excel 2016 (Microsoft Windows, USA) and Prism 5 (GraphPad Software, Inc., USA), and performed GLMMs using the mixed-effects linear regression function in STATA SE10 (Quantec Research (Pty) Ltd., South Africa). I present data as mean ± SD, and considered $P < 0.05$ to be statistically significant.

5.3 Results

5.3.1 Environmental conditions

Air temperatures at Tswalu showed high seasonal variability, with high air temperatures over summer (up to 39.9 °C in the shade) and low air temperatures in winter (as low as -4.4 °C), but interannual differences were small (Figure 2.4). Interannual differences in the amount and timing of summer rainfall, the key driver of vegetation productivity in the Kalahari, resulted in interannual differences in EVI (Tokura 2016; see also Chapter 2, Chapter 3). In 2011 to 2012, the year before the start of this study, summer rainfall was within 25-year average and resulted in reasonable vegetation productivity during that summer and the following winter, in which this study started. In year 1 of the study (August 2012 to June 2013), summer rains were below average and only occurred at the end of March 2013, four months later than is common in the Kalahari. In addition, a heat wave occurred during February, and above-average, soil-drying winds during the summer, amplified the effects of drought (Rey et al., 2017). As a result, vegetation productivity was very low during the summer 2012-13 and the following winter 2013. In year 2 (July 2013 to June 2014), rainfall was above-average and the rainy season lasted five months, resulting in high vegetation productivity. In year 3 (July 2014 to June 2015), rainfall again was lower than the 25-year average and resulted in low vegetation productivity that prevailed until year 4 (July to September 2015, when the study ended). Although the summer of year 3 (notably February) was dry, and EVI low, there was not such an exaggerated heat wave and strong, drying winds compared to the drought in year 1.

5.3.2 Aardvarks that died, and similarities in their body temperature patterns

Of the 10 study aardvarks for which we retrieved body temperature records, six individuals (aardvarks 2, 5, 6, 13, 14, and 15) died of natural causes during the study. Aardvark 15 was an exception from the other individuals, as she died inside her burrow at the end of October 2014, likely of a snakebite (veterinary opinion, Dr Anna J. Haw). Aardvarks 2, 5, and 6 died during the drought in summer (February to March) 2013. Aardvark 14 died during winter (early August) 2013 after that summer drought, following a loss of body condition. Aardvark 13 died in winter 2015, after progressive loss of body condition following the dry summer 2015. All study aardvarks lost body condition and show heterothermy during the winter of 2013 (Figure 5.1 and Figure 5.2), associated with a gradual decline in 24-h mean body temperature (Figure 5.3). This decline in mean body temperature was a result of an exaggerated decrease in minimum 24-h body temperature. In heterothermic, moribund aardvarks, declining minimum body temperatures coincided with declining maximum body temperatures in the days leading up to their deaths.

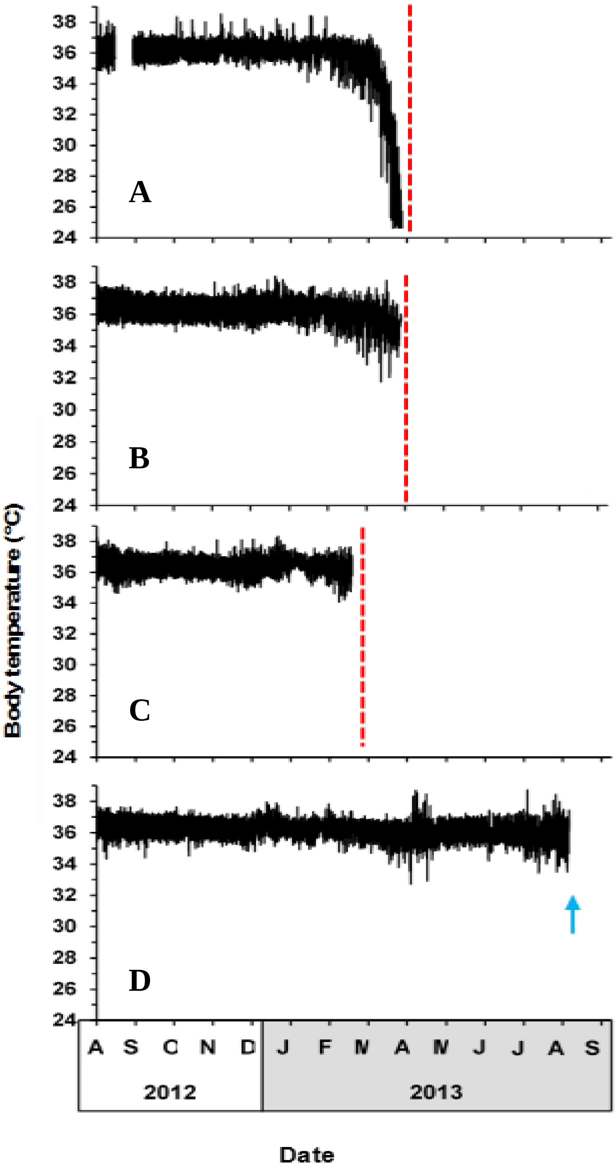

Figure 5.1 Body temperature records of individual study aardvarks at Tswalu during year 1 and early year 2 of the study (August 2012 to September 2013). Records of aardvark 2 (panel A) ended when the aardvark died after prolonged starvation. Aardvarks 5 (panel B) and 6 (panel C) also died following starvation but their logger data ended before their deaths. Aardvark 7 (panel D) was recaptured in September 2013 after 14 months. Each dataset begins three days after the first capture of each individual; blue arrows indicate recapture event; red dashed lines indicate deaths of aardvarks.

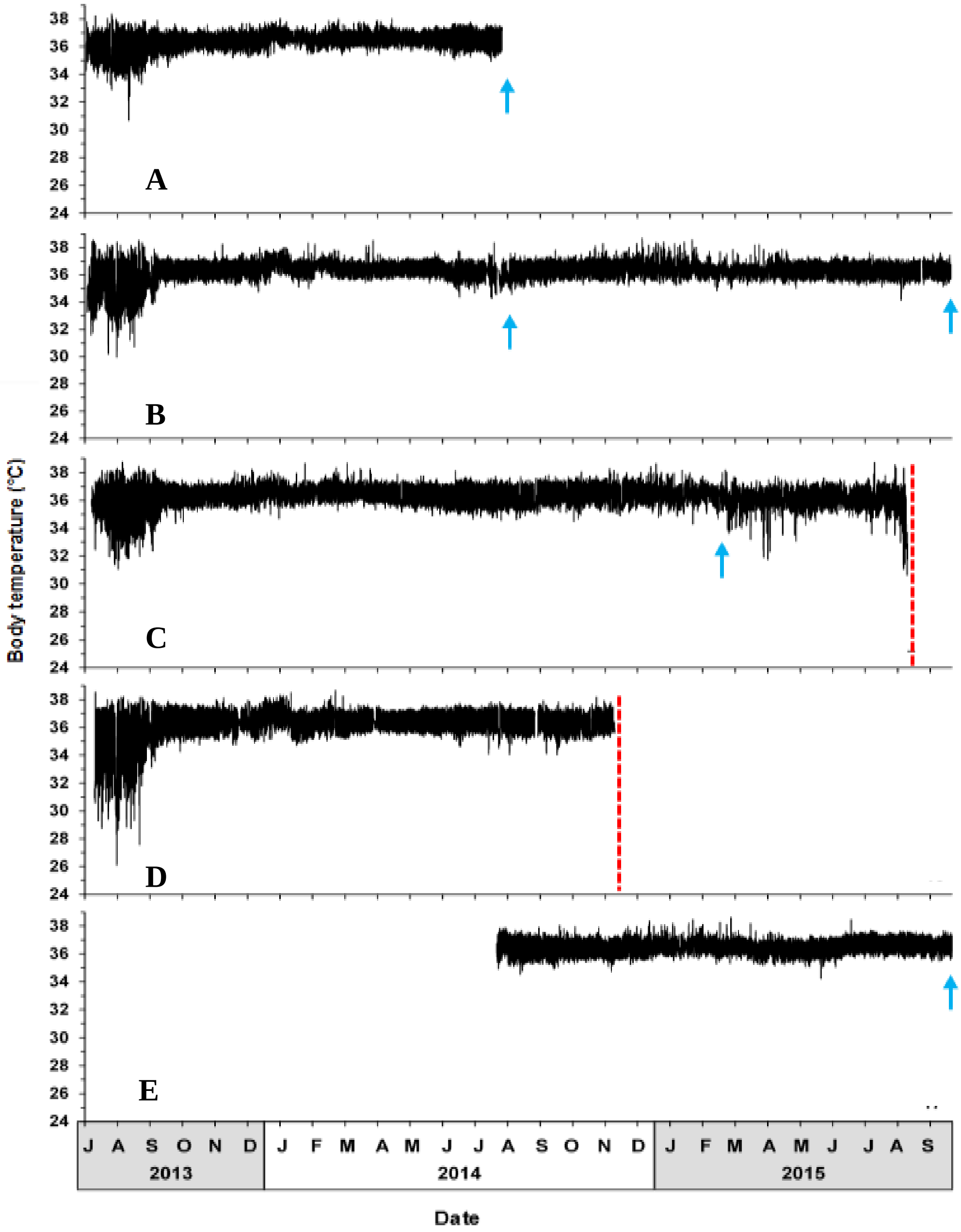

Figure 5.2 Body temperature records of individual study aardvarks at Tswalu during years 2 and 3 of the study (July 2013 to September 2015). Records of aardvark 8 (panel A) ended because when the aardvark's tracking device failed shortly after it had been exchanged after the first year, and the individual could not be located. Records of aardvark 13 (panel C) ended because the aardvark died in late July 2015 after a period of progressive body condition decline. Aardvark 15 (panel D) died unexpectedly in November 2014. Aardvark 9 (panel B) was recaptured and reimplanted in mid-2014, and recaptured for logger removal in September 2015. Aardvark 17 (panel E) was added to the study in July 2014 and recaptured in September 2015. Each dataset begins with the first capture of each individual; blue arrows indicate recapture events; red dashed lines indicate deaths of aardvarks.

5.3.3 Long-term patterns of body temperature

The original, calibrated body temperature recordings of all aardvarks in 5-minute intervals throughout the study period are displayed (Figure 5.1 and Figure 5.2). Mean 24-h body temperature of all aardvarks at Tswalu during the study period (July 2012 to September 2015) was 36.1 ± 0.6 °C. Body temperature in aardvarks ranged between a minimum of 24.7 °C and a maximum of 38.8 °C (Table 5.1). Maximum amplitude of 24-h body temperature was 11.7 °C, recorded in aardvark 15 on 30 July 2013, when her body temperature ranged from 26.1 to 37.8 °C within 24 hours. Although other study aardvarks reached similarly high amplitudes of body temperature (Table 5.1), the minimum 24-h body temperature of 26.1 °C in aardvark 15 during the winter 2013 following the summer drought 2012-13 was the lowest body temperature of aardvarks that survived, only surpassed during the summer drought by aardvark 2 (24.7 °C), which died shortly after this body temperature minimum occurred.

In year 1 of this study, body temperature records in all aardvarks remained between 35 and 37.5 °C until February 2013, when aardvarks showed a progressive decline in minimum body temperatures, concomitant with an increased body temperature amplitude, during the summer drought and heat wave. In aardvark 5, records ended in February 2013 as a result of logger failure, and aardvarks 2 and 6 were assumed to have died when logger temperatures tracked ambient temperature in March 2013. These three aardvarks were found dead in early April 2013, after the summer drought.

Of my study aardvarks, only aardvark 7 survived the drought in year 1. During the summer drought, its body temperature (Figure 5.1D) did not decline as much as that of the other three aardvarks which died (Figure 5.1 A to C). Its body temperature did not fall below 34 °C during the drought as it did for the three other aardvarks, but the aardvark did have an increased amplitude of 24-h body temperature rhythm as a result of reduced minimum body temperatures in late March/April and July/August 2013.

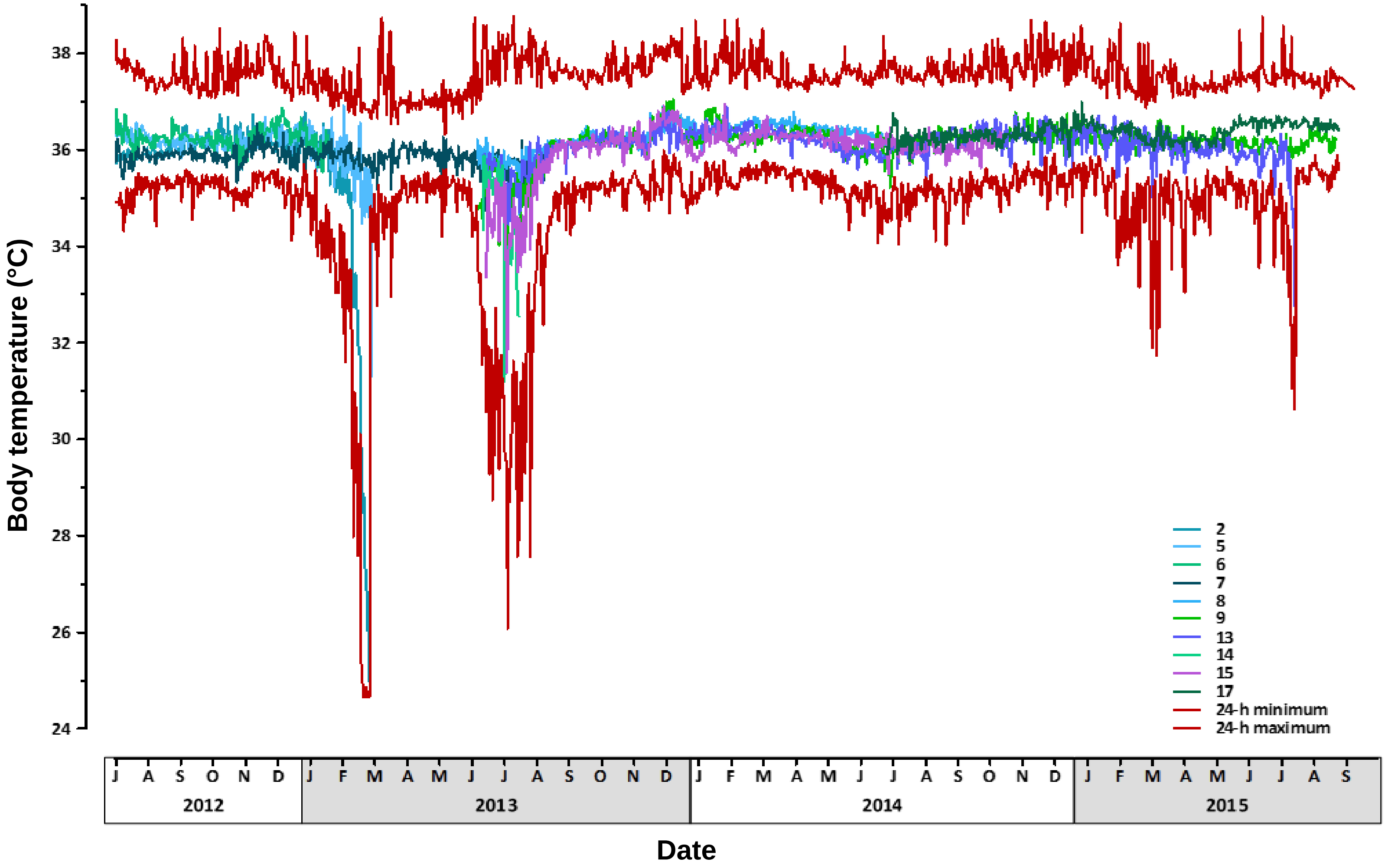

Figure 5.3 24-h body temperature of all study aardvarks at Tswalu from August 2012 to September 2015. Each colour line represents mean 24-h body temperature of a different individual. Upper and lower red lines display the absolute maximum and absolute minimum body temperature of all study aardvarks within each 24-h period to indicate the total range of body temperatures reached in aardvarks.

Table 5.1 Summary of 24-h body temperature data of all study aardvarks at Tswalu over the period August 2012 to September 2015. ID - aardvark identity, n - number of 24-h periods over which body temperature was recorded (excluding capture periods).

ID	24-h body temperature (°C)			n	died?	Circumstances of death
	minimum	maximum	maximum amplitude			
2	24.7	38.5	8.1	223	yes	drought
5	31.8	38.4	4.7	237	yes	drought
6	34.1	38.4	3.1	197	yes	drought
7	32.8	38.7	4.3	365	no	-
8	30.7	38.4	7.1	384	no	-
9	29.9	38.7	8.4	793	no	-
13	30.6	38.8	7.3	752	yes	winter after drought
14	27.6	38.3	9.3	34	yes	winter after drought
15	26.1	38.7	11.7	476	yes	snake bite?
17	34.2	38.6	3.0	420	no	-

Following the summer drought, all study aardvarks were heterothermic (as indexed by the amplitude of the 24-h body temperature rhythm), and showed episodes of high amplitudes of 24-h body temperature rhythms during winter and early spring 2013 (Figure 5.2, July to September 2013). Several individuals died during these months (aardvarks 10, 11, and 14). The surviving aardvarks resumed homeothermy in mid-spring (Figure 5.2, October 2013).

The heterothermy during winter 2013 was unlikely a consequence of the capture and implantation of data loggers, since aardvark 7, the survivor of the drought in year 1, showed similar heterothermic patterns (Figure 5.1D) as aardvarks 8, 9, 13, and 15 (Figure 5.2) despite not having undergone capture at the time. Moreover, study aardvarks did not show such decreased minimum body temperature after other capture events (Figure 5.1 and Figure 5.2). After winter 2013, study aardvarks maintained body temperatures within a narrow amplitude of ~2.5 °C (between ~ 35 and 37.5 °C) until the end of the study (Figure 5.2). An exception was aardvark 13 during the last year of the study, when her minimum body temperature declined to as low as 32 °C during a heat wave in late summer (February 2015). Although aardvark 13’s body temperature resumed near-normal patterns with narrow amplitude of 24-h body temperature rhythms throughout the autumn months (March to May 2015), minimum body temperature declined progressively from the beginning of winter (June 2015) until the aardvark’s death (late July 2015). Low body temperatures and heterothermy of aardvarks during and after drought are examined in more detail below.

Daily mean body temperatures of all study aardvarks over the ~3.5 years of the study show similar patterns of notable fluctuations in all study aardvarks during the summer drought 2012-13, as well as during the subsequent winter, with wide ranges between absolute minimum and maximum body temperatures (Figure 5.3). All study aardvarks that were heterothermic during the summer drought died. Aardvark 7 survived the summer drought and became heterothermic during the following winter, as did all other, additional study aardvarks. Body temperature patterns of those aardvarks that survived the winter recovered to homeothermic patterns during the spring months and all aardvarks were, and remained, homeothermic from October 2013 onward. An exception was aardvark 13, which became heterothermic during the dry summer in February 2015, and again in winter 2015, before she died in late July 2015.

5.3.4 Patterns of 24-h body temperature

Aardvark body temperature was generally lowest during the day, and highest at night, with a clear decline in body temperature around or before sunrise, and a steep increase in body temperature around or just after sunset resulting in a pronounced square shape of the curve (Figure 5.4). Nychthemeral rhythm of body temperature changed seasonally (Figure 5.4), becoming more cosinor in shape during late summer 2012-2013 to early autumn 2013 and winter 2013. This cosinor rhythm resulted from body temperature reaching a maximum around sunset, followed by a progressive decline throughout the remainder of the night and the morning hours toward a nadir during daytime (around early morning in summer months and late morning in winter), before increasing more or less steadily again in the afternoon. During most months in each season, the nychthemeral rhythm of body temperature had a small (~2.5 °C) amplitude within a range from ~ 35 °C to 37.5 °C. Aardvark 24-h body temperature patterns during winter 2013 differed from all other seasons and all other winters (Table 5.2), with a large mean amplitude of body temperature (7.3 °C, between 30.2 and 37.5 °C) in winter 2013 (Table 5.2).

5.3.5 Patterns of 24-h body temperature and activity

To investigate whether changes in the nychthemeral rhythm of body temperature during the drought period were associated with changes in activity patterns, I extracted body temperature and activity patterns of four representative aardvarks during the same periods in a drought summer and the following winter, as well as in a productive summer and a ‘normal’ winter following a productive summer (Figure 5.5).

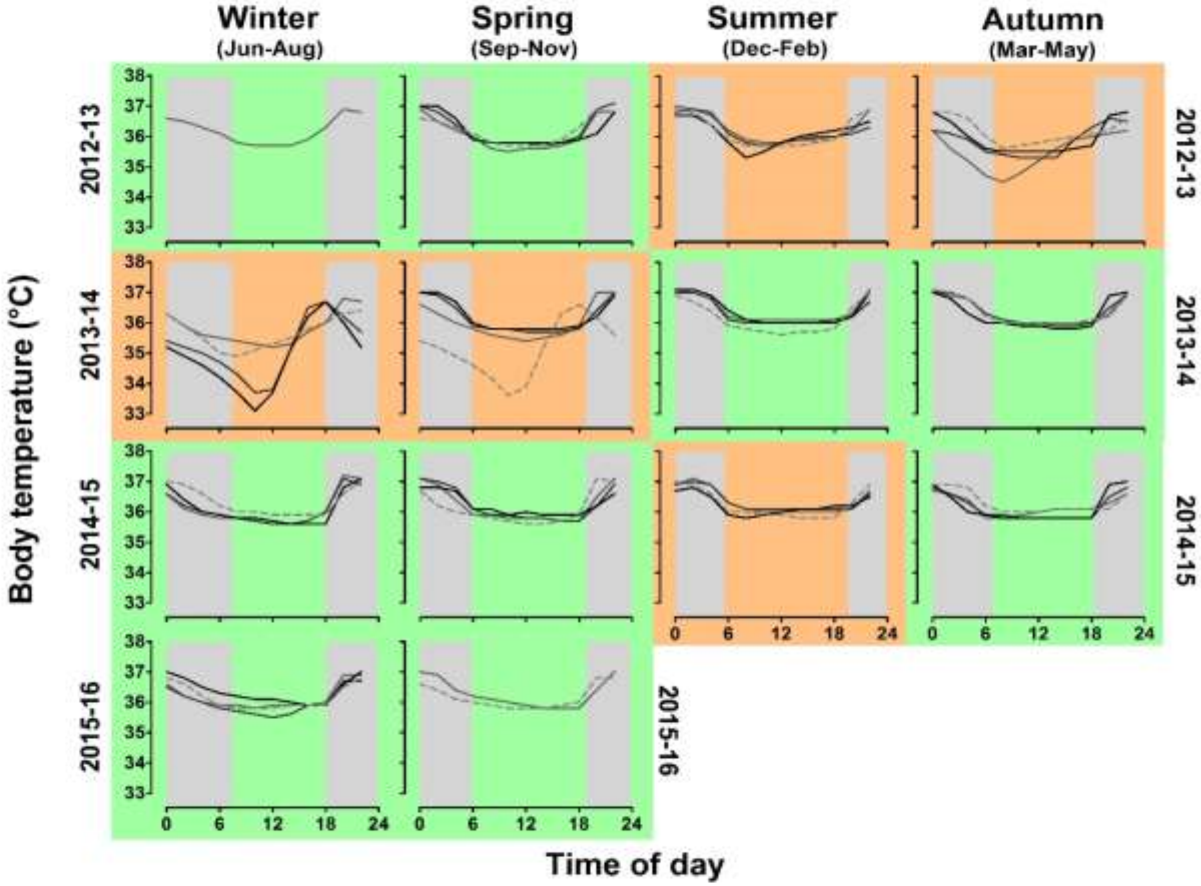

Figure 5.4 Monthly and seasonal 24-h body temperature rhythms of aardvarks over 38 months. Each line represents the body temperature rhythm averaged between all aardvarks for each month of that season; lightest shade is the first month of the season; darkest shade is the last month of the season, dashed line is the body temperature rhythm averaged over the previous season. Winter - June, July, August; spring - September, October, November; summer - December, January, February; autumn - March, April, May. Records lasted from August 2012 to September 2015, thus the first winter displays body temperature for August 2012 only and no indicator for a previous season, and the last spring only displays body temperature for September 2015 and the previous season. Grey areas indicate night time.

Table 5.2 Summary of body temperature over each season of the 3.5 year study period. Seasonal mean ± SD of mean, maximum, minimum, and amplitude of 24-h body temperature (°C) between all study aardvarks; year 1: August 2012 to May 2013, year 2: June 2013 to May 2014, year 3: June 2014 to May 2015, year 4: June 2015 to September 2015; winter: June to August, spring: September to November, summer: December to February, autumn: March to May; n indicates number of study aardvarks for which body temperature was available.

24-h body temperature	**Winter**	**Spring**	**Summer**	**Autumn**
mean				
Year 1	36.1 ± 0.2	36.1 ± 0.2	36.1 ± 0.3	33.3 ± 2.0
Year 2	35.2 ± 0.6	36.0 ± 0.1	36.4 ± 0.2	36.3 ± 0.1
Year 3	36.1 ± 0.2	36.2 ± 0.1	36.3 ± 0.2	36.2 ± 0.2
Year 4	36.1 ± 0.3	36.3 ± 0.1	NA	NA
minimum				
Year 1	35.3 ± 0.3	35.4 ± 0.2	35.3 ± 0.5	28.5 ± 4.7
Year 2	33.0 ± 1.2	35.1 ± 0.3	35.7 ± 0.3	35.7 ± 0.2
Year 3	35.3 ± 0.3	35.5 ± 0.2	35.6 ± 0.4	35.3 ± 0.4
Year 4	35.3 ± 0.5	35.6 ± 0.1	NA	NA
maximum				
Year 1	37.5 ± 0.3	37.2 ± 0.3	37.2 ± 0.3	35.3 ± 1.8
Year 2	37.4 ± 0.6	37.4 ± 0.3	37.5 ± 0.3	37.2 ± 0.2
Year 3	37.4 ± 0.2	37.4 ± 0.3	37.4 ± 0.4	37.2 ± 0.2
Year 4	37.2 ± 0.3	37.3 ± 0.1	NA	NA
amplitude				
Year 1	2.2 ± 0.4	1.8 ± 0.3	1.9 ± 0.6	6.8 ± 5.0
Year 2	4.4 ± 1.3	2.3 ± 0.5	1.8 ± 0.4	1.6 ± 0.3
Year 3	2.1 ± 0.3	2.0 ± 0.3	1.8 ± 0.5	1.9 ± 0.5
Year 4	1.9 ± 0.5	1.7 ± 0.2	NA	NA
n				
Year 1	4	4	4	3
Year 2	6	5	4	4
Year 3	5	4	3	3
Year 4	3	2	-	-

During the productive summer, elevated body temperatures coincided with periods when the aardvarks were active at night, and were lower when the aardvarks were inactive inside their burrows during the day (Figure 5.5, February 2014). During a ‘normal’ winter after a productive summer, aardvarks shifted their activity to slightly earlier times of day, becoming partly diurnal, and body temperature peaked earlier synchronously with the earlier onset of activity (Figure 5.5, August 2012).

When aardvark 2 was diurnal during the summer drought of 2012-13 (notably January to March 2013, before its death at the end of March), its body temperature was still highest at night even though the aardvark was inactive at night, and lowest while the aardvark was active in the morning, seemingly as the aardvark emerged from its burrow (Figure 5.5, February 2013). Such a dissociation of rhythms of body temperature and activity was not observed in aardvark 7, which remained nocturnal during this period and survived the summer drought, nor in any aardvarks that became diurnal during the winter that followed the drought (Figure 5.5, August 2013). During that winter, the aardvarks began activity in the afternoon. They became active earlier than during the ‘normal’ winter, yet not as early as aardvark 2 which was active in the morning during the drought summer, and their body temperature fluctuated simultaneously with their activity, unlike in aardvark 2. These aardvarks also survived the drought winter.

5.3.6 Effects of environmental variables and activity on body temperature

The GLMM results indicate that minimum 24-h body temperature was negatively associated with the proportion of the active phase that aardvarks were diurnal, and with maximum 24-h wind speed, and positively associated with photoperiod and EVI as a proxy for resource abundance (Table 5.3A), whereas minimum 24-h air temperature had no effect on minimum 24-h body temperature. In other words, minimum 24-h body temperatures were low when days were short in winter, body condition poor, wind speed high, and aardvarks were more diurnal.

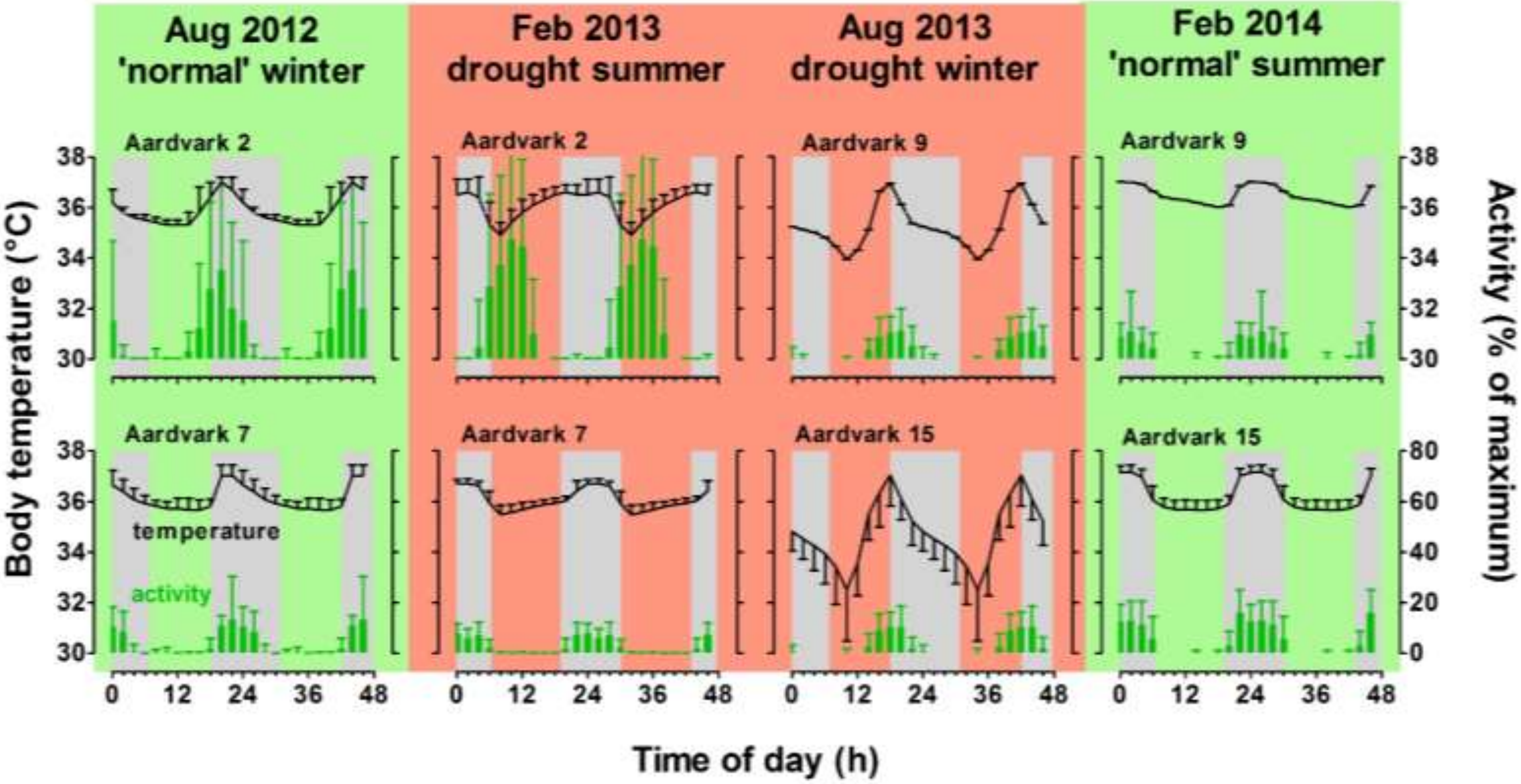

Figure 5.5 Nychthemeral patterns of activity and body temperature of four study aardvarks during winter and summer of a drought year (red background) between two productive years (green background), at Tswalu Kalahari Reserve. Grey areas - night time; green bars indicate mean aardvark locomotor activity for the month; black line indicates mean aardvark body temperature (°C). Error bars indicate SD between days of a month within one aardvark rather than between individuals as in other graphs of this chapter. Note that the high activity levels of aardvark 2 compared to the other individuals were likely a result of individual logger sensitivity rather than greater activity of the aardvark. Air temperatures (not displayed here) were similar during both summers and both winters (Figure 2.4).

Maximum 24-h body temperature of aardvarks was positively associated with photoperiod and with total 24-h activity, and negatively associated with maximum 24-h air temperature, but was not associated with EVI (Table 5.3B), indicating that aardvark maximum body temperature was higher when days were longer in summer and cooler, and when aardvarks were more active.

5.3.7 Basking

Aardvarks made use of basking predominantly during winter (49 of 50 observations), and most of these events occurred during winter 2013 (47 out of 50) following the summer drought. Body temperature records were retrieved for 39 of these basking events. Aardvarks generally basked within close proximity (0 to 5 m) of the burrow in which they had spent the previous night. The animals usually positioned themselves sternally and spread-out flat on the ground, with their head resting on their front legs (Figure 5.6).

The aardvarks' body temperature at the start of basking was 32.7 ± 1.5 °C (range 28.6 to 36.0 °C), increasing by 2.9 ± 2.0 °C over basking (range 0 to 8.5 °C). They basked, on average, for 3:51 ± 3:01 h, although the duration varied greatly from less than a half hour to nearly 14 hours on occasion, i.e., from before sunrise until sunset (Table 5.4). This particularly long basking event occurred in aardvark 14 on 1 August 2013, during which time its body temperature increased by 5.1 °C. The maximum increase of body temperature (8.5 °C) during a basking event also occurred in aardvark 14, on 9 August 2013; the aardvark died during the early morning hours of the following day after its body condition had severely deteriorated over the previous weeks. The lowest minimum body temperature, longest basking bout, lowest body temperature at the start of basking, and the greatest body temperature increase during basking all occurred in the month of August 2013 (Table 5.4).

Table 5.3 GLMM results showing effects of A) photoperiod (season), minimum 24-h air temperature (°C), proportion of diurnal activity, maximum 24-h wind speed (km h^{-1}), and EVI of Gordonia duneveld vegetation (an index of vegetation productivity which correlated with aardvark body condition) at Tswalu on minimum 24-h body temperature (°C); and B) photoperiod, total 24-h activity, maximum 24-h air temperature (°C), and EVI of Gordonia duneveld vegetation at Tswalu on maximum 24-h body temperature (°C); for each 24-h period between August 2012 and September 2015. Aardvark 2 was ommitted from GLMM B because of an error in its activity-count dataset. In all models, aardvark identity was included as a random factor. Significant *P*-values are italicised.

Body temperature	Variable	β ± SE	*Z*	*P*	95 % CI
A) 24-h minimum **n = 2220**	photoperiod	5.24 ± 0.53	9.80	*<0.001*	4.19 to 6.28
	EVI	3.22 ± 0.54	5.95	*<0.001*	2.16 to 4.28
	wind speed	–0.01 ± <0.01	–5.03	*<0.001*	–0.01 to –0.01
	minimum air temperature	0.01 ± <0.01	1.34	0.18	<–0.01 to 0.01
	proportion of diurnal activity	–0.02 ± <0.01	–23.32	*<0.001*	–0.02 to –0.01
	constant (intercept)	32.43 ± 0.26	127.13	*<0.001*	31.93 to 32.93
B) 24-h maximum **n = 2002**	photoperiod	1.67 ± 0.23	7.19	*<0.001*	1.21 to 2.12
	EVI	–0.16 ± 0.21	–0.77	0.44	–0.57 to 0.25
	maximum air temperature	–0.01 ± <0.01	–7.14	*<0.001*	–0.02 to –0.01
	total activity	<0.01 ± <0.01	5.19	*<0.001*	<0.01 to <0.01
	constant (intercept)	36.84 ± 0.09	409.07	*<0.001*	36.67 to 37.02

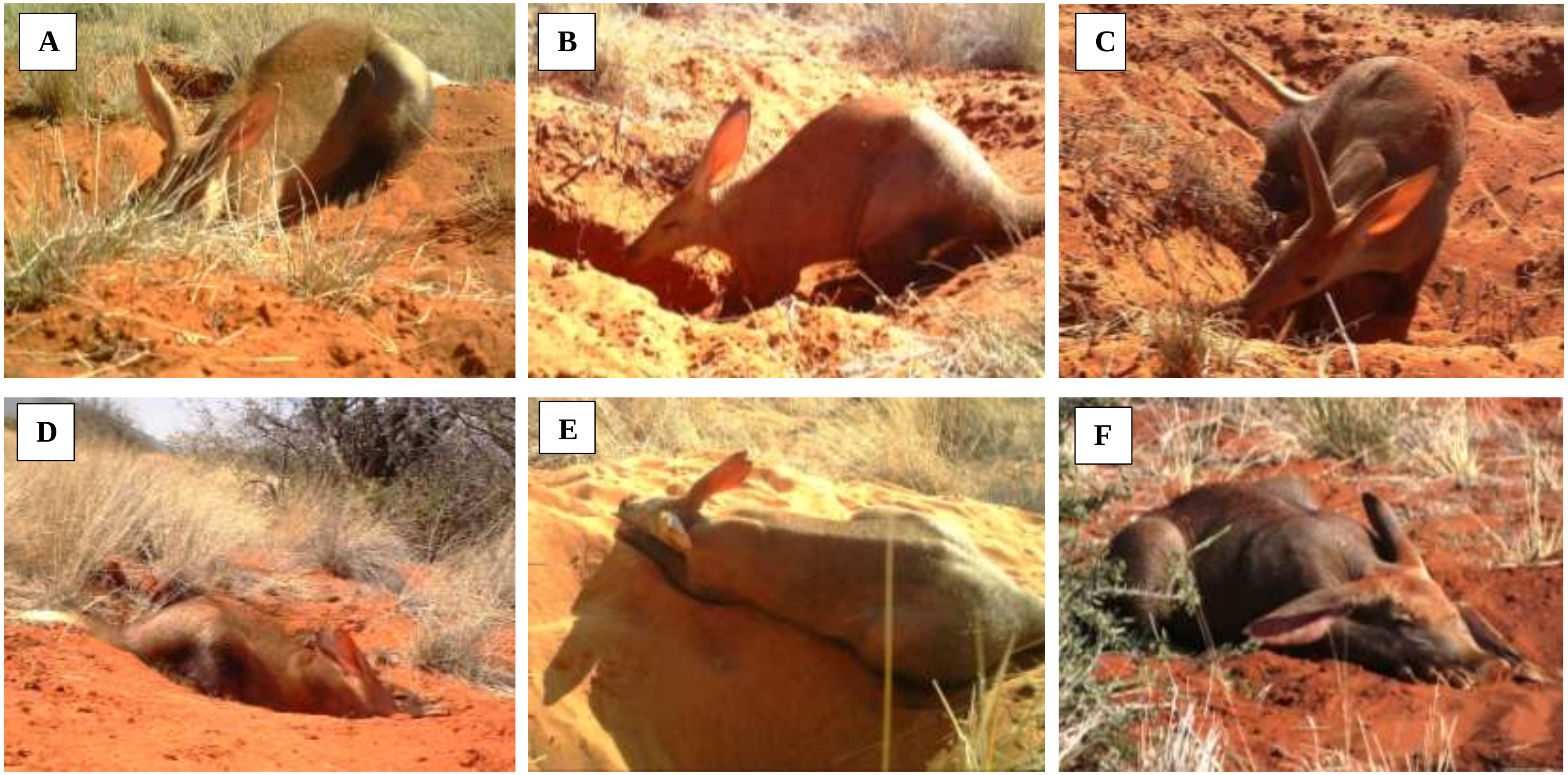

Figure 5.6 Basking study aardvarks at Tswalu, captured on camera traps during winter 2013 after a summer drought. All study aardvarks were observed basking during the winter 2013, generally at entrances to their respective burrows during the morning or mid-day hours. Aardvarks 8 (panel A), 9 (panel B), 12 (panel C), 13 (panel D), and 15 (panel F) survived the winter; aardvark 14 (panel E) died before the end of winter (August) 2013. (Photo credit: N. Weyer).

Visual evaluation of body temperature changes during basking events in winter 2013 revealed a typical pattern (Figure 5.7, data from aardvark 9 as a representative of all study aardvarks): while the aardvark was inactive and inside a burrow, its body temperature gradually declined. When the aardvark emerged, its body temperature dropped slightly to a minimum before showing a notable increase during basking in the sun. When the aardvark returned to the burrow, its body temperature declined again, whereas foraging (or another bout of basking) led to further increase in body temperature (Figure 5.7). The increase in body temperature when foraging after basking occurred during daylight hours occasionally resulted in a body temperature overshoot, with the resulting maximum body temperature being higher, and amplitude of body temperature greater (heterothermy), than body temperature during nocturnal foraging in a year in which aardvarks remained in good condition. The aardvark was partly diurnal during winter 2013, ceasing activity before or around midnight.

While air temperatures were lower in August 2014 than during the same month in 2013, no basking was observed in this or any other study aardvark in that period in winter 2014 nor in winter 2015. The aardvark was exclusively nocturnal in 2014 and 2015, and its body temperature remained homeothermic within a narrow range between 35.5 and 37.5 °C.

Table 5.4 Summary of basking events between July 2013 and September 2015 during which body temperature was recorded in aardvarks (N = 5 aardvarks). Basking duration - time an aardvark spent basking between emergence from and return to a burrow, or before leaving the position to forage; start body temperature - body temperature of the aardvark at the time they initiated a bask; min body temperature - lowest body temperature during the basking bout; Δ body temperature - net change in body temperature during the basking bout, calculated as the difference between body temperature at the start and end of the basking bout; n - number of basking events recorded during behavioural observations or on camera traps.

		basking duration (hh:mm)			**start body temperature (°C)**			**min body temperature (°C)**			**Δ body temperature (°C)**		
	n	**mean ± SD**	**min**	**max**	**mean ± SD**	**min**	**max**	**mean ± SD**	**min**	**max**	**mean ± SD**	**min**	**max**
Jul	8	05:45 ± 03:19	03:00	11:16	32.3 ± 0.9	31.2	33.6	31.0 ± 1.4	28.6	32.71	3.2 ± 2.1	0.4	6.2
Aug	27	03:34 ± 02:50	01:05	13:37	32.5 ± 1.4	28.6	33.8	31.5 ± 1.9	27.6	33.59	3.1 ± 2.1	0.0	8.5
Sep	2	01:43 ± 00:24	01:26	02:00	34.3 ± 0.2	34.2	34.5	34.0 ± 0.2	33.9	34.16	2.0 ± 0.8	1.4	2.6
2013	37	04:01 ± 03:01	01:05	13:37	32.5 ± 1.4	28.6	34.5	31.5 ± 1.9	27.6	34.16	3.0 ± 2.0	0.0	8.5
Jun	1	00:24			36.0			35.8			0.0		
Jul	1	01:09			34.8			34.5			1.1		
2014	2	00:46 ± 00:31	00:24	01:09	35.4 ± 0.8	34.8	36.0	35.2 ± 0.9	34.5	35.81	0.5 ± 0.8	0.0	1.1
Total	39	03:51 ± 03:01	00:24	13:37	32.7 ± 1.5	28.6	36.0	31.7 ± 2.0	27.6	35.81	2.9 ± 2.0	0.0	8.5

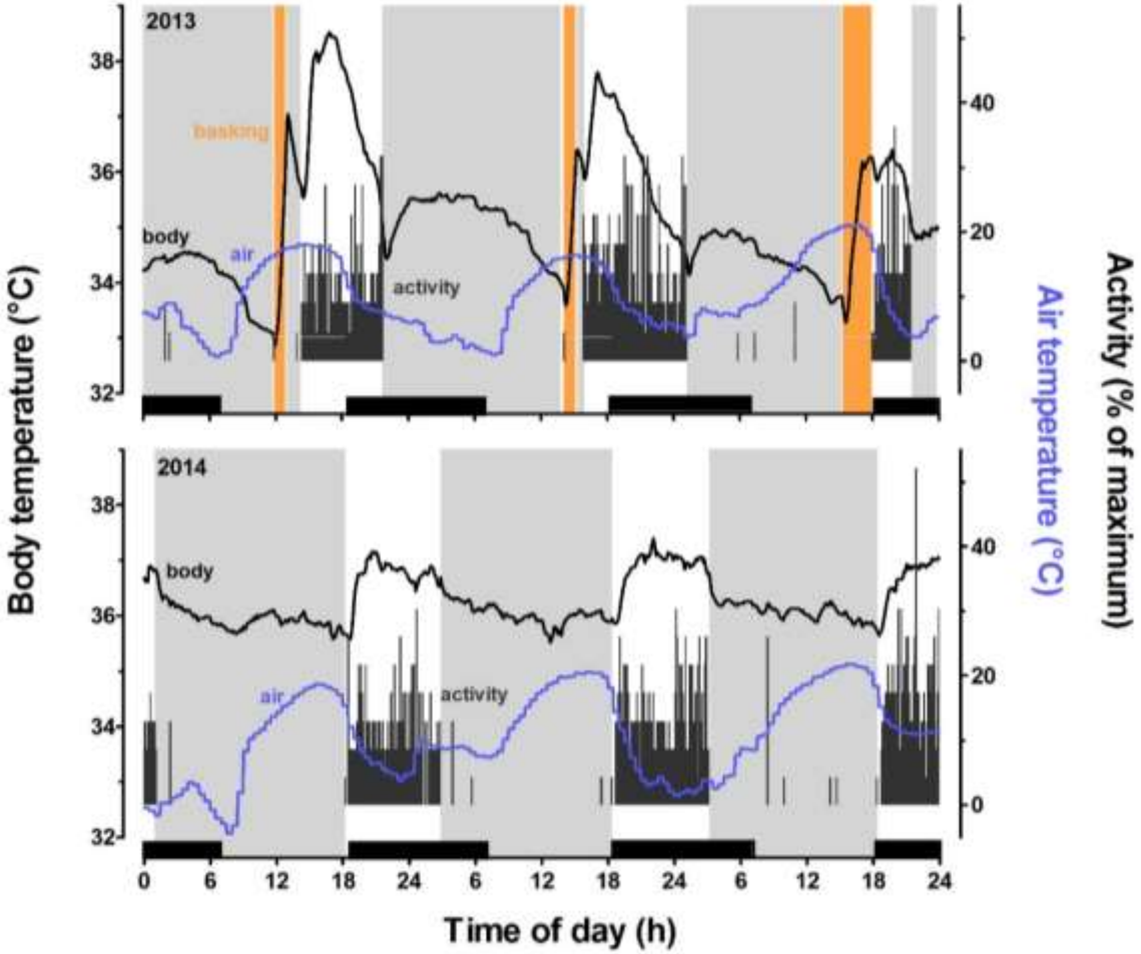

Figure 5.7 Body temperature and locomotor activity in aardvark 9 over three days (19 to 21 August) during two subsequent winters with similar air temperatures but different resource abundance at Tswalu. During winter 2013 (drought year), the aardvark was in poor body condition and often basked in the sun before foraging, occasionally re-entering a burrow before foraging. Black lines represent body temperature (left y-axis), blue lines represent air temperature (right y-axis), grey bars represent locomotor activity (right y-axis); different background colours indicate when the aardvark was basking (orange), foraging (white), or inactive inside the burrow (grey); black horizontal bars indicate night time. During winter 2014 (arid but non-drought year), the aardvark was in good condition and was not observed basking. Data from 2015 closely resembled those of 2014 and are not displayed here.

5.4 Discussion

As far as I am aware, the present study on body temperature patterns in Kalahari aardvarks has resulted in the longest continuous record of body temperature in any species of large, free-living terrestrial mammal in its natural habitat to date. In a single individual, the 797 consecutive days from July 2013 to September 2015 recorded in study aardvark 9 represent the longest continuous record of body temperature. Across all individuals in my study, 1135 consecutive days of body temperature were recorded between July 2012 and September 2015. Body temperature of aardvarks varied considerably over time (Figure 5.1 and Figure 5.2). I have shown that irrespective of the season, when aardvarks were in good condition during periods of resource abundance (Chapter 3) they were exclusively nocturnal (Chapter 4), and maintained homeothermy, with small amplitudes of 24-h body temperature of ~2.5 °C (between 35 and 37.5 °C). Aardvarks in poor body condition became partly diurnal (Chapter 4), and showed declining minimum 24-h body temperatures which often caused exaggerated heterothermy, with an amplitude of 24-h body temperature of up to 11.7 °C in one individual (which survived) and an overall body temperature range between 24 and 38 °C. This large amplitude of 24-h body temperature rhythm is the largest recorded in a large, free-living mammal to date, larger than that previously reported for aardvarks during the summer drought (8.6 °C; Rey et al., 2017) or for Arabian oryx (7.7 °C; Hetem et al., 2010). Such fluctuations in body temperature with large amplitude of 24-h body temperature rhythms were proposed to be a result of reduced resource abundance during summer drought (Rey et al., 2017). With this study, for the first time, I provide a quantifiable association of aardvark minimum 24-h body temperature with poor resource availability (as indexed by EVI) during and after a summer drought.

A mass-mortality occurred during the summer drought in 2012-13, proposedly due to low resource abundance (Rey et al., 2017), and more aardvarks died during the following winter (Chapter 3). Another aardvark lost body condition, showed increased heterothermy and declining minimum body temperature during autumn and winter of

2014-15, and died in winter of 2015. Elevated body temperatures occurred temporarily during particularly hot periods, also resulting in heterothermy, though to a lesser extent than low minimum body temperatures. With this study, I have also shown that aardvarks were not only adversely affected during the drought itself, but surviving aardvarks also needed a long time to recover from the loss of body condition (Chapter 3), reflected in the slow return to homeothermy several months after the drought. Only one study aardvark survived the summer drought, with body temperatures recovering during the autumn months (April, May) after the late summer rains fell. During the following winter, all eight study aardvarks exhibited heterothermy as a result of minimum body temperature declining to as low as 26.1 °C. At the same time, they showed pronounced diurnal activity. Another three individuals died during this winter. The winter heterothermy of the surviving individuals resolved over the spring months as temperatures got warmer and rainfall caused increased vegetation productivity and likely associated prey availability in late October, and all study aardvarks were homeothermic by October 2013. When aardvarks were homeothermic, they were exclusively nocturnal, and their body condition had recovered to “good” or “very good” scores (Chapter 3). Nocturnal activity and good body condition continued throughout the following summer, during which summer rainfall started early in the season and was high, resulting in high vegetation productivity and abundant prey availability that allowed aardvarks to maintain good nutritional state (Chapter 3).

Aardvark 24-h rhythms of body temperature and activity usually fluctuated simultaneously, such that body temperatures increased when aardvarks began activity, and decreased when aardvarks were inactive in their burrows. When aardvarks in poor condition showed a pronounced shift of their active period into daytime, starting foraging in the afternoon, particularly during a winter after a summer drought (Chapter 4), their 24-h body temperature rhythm fluctuated synchronously with activity, thus 24-h body temperature peaked at an earlier time of day. In an extreme case during the summer drought of 2012-13, one individual completely shifted its activity into daytime, beginning to forage early in the morning (Chapter 4), and displayed a dissociation of

24-h rhythms of body temperature and activity in the days leading up to its death: its body temperature was highest when the aardvark was inactive at night, and lowest when it was foraging during the morning hours. Although the aardvarks that survived the drought and following winter resumed nocturnal activity after that winter as soon as night-time air temperatures became warmer, their body temperatures only slowly returned to homeothermic patterns over several months after that winter, matching the slow recovery of body condition (Chapter 3).

This study provided the most comprehensive dataset of aardvark body temperature records, despite several unforeseen events that limited my sample size. In addition to the challenges of working on an elusive, nocturnal and shy animal that was exceptionally challenging to capture, several study aardvarks died during drought, and some tracking devices failed which prevented retrieval of all implanted data loggers. Despite these limitations I was able to demonstrate fascinating responses of aardvarks to interannual variability in environmental conditions. Body temperatures were recorded over different periods in individual aardvarks. This challenge was overcome by using GLMMs for analyses, which provide an overall response for all aardvarks taking into account different measurement periods for different individuals. The long-term records of individual aardvark body temperature patterns encompassed a range of environmental conditions between years.

The range of body temperatures (~ 35 to 37.5 °C) of study aardvarks when in good condition during productive (i.e., non-drought) years was within the range of previous short-term (5 days) records of temperatures of free-living aardvarks in the South African Karoo, which were 34.5 to 37.5 °C in summer, and 33.5 to 37.5 °C in winter (Taylor & Skinner, 2004). Rectal temperatures of healthy captive aardvarks ranged between 34.5 and 36 °C in a zoo (McNab, 1984), and between 35 and 36.4 °C in an experimental laboratory (Vanderplank, 1941; Burtt, 1946), showing a narrower range and slightly lower maximum values than free-living aardvarks. Aardvark body temperature was slightly lower than expected for a similarly-sized mammal (Hetem et al., 2016), most likely due to their low metabolic rate, and possibly to the high thermal conductance of aardvarks which is likely a result of their sparse fur (McNab, 1984).

In many free-living large mammals, the amplitude of 24-h body temperature appears to reflect mainly the energy and water balance of an individual animal, rather than its activity (Mitchell et al., 2002). Maximum 24-h body temperature in large mammals can be elevated during low water availability in hot periods to preserve body water, whereas lower minimum body temperatures are associated with energy deficit (Fuller et al., 2014; Hetem et al., 2016). Intense digging activity has also been suggested to increase body temperature in aardvarks (Taylor & Skinner, 2004). When animals have insufficient food and water, homeothermy may be relaxed, as demonstrated by 24-h variations of body temperature of as much as 8 °C in Arabian oryx antelope in hot, dry periods (Hetem et al., 2010). Indeed, during the drought summer 2012-13 (January to March) in this study, some aardvarks displayed diurnal activity (Chapter 4), with body temperature ranging from as low as 26 to 37 °C. Although these aardvarks were exposed to air temperatures as high as ~40 °C, the lowest body temperature of 26 °C occurred during the day, thus being lower than air temperatures. In free-living grey kangaroos, minimum 24-h body temperatures were 2.2 °C lower in summer when they were presumably nutritionally challenged, than at the end of the wet season in spring, despite maximum daily ambient temperatures being 15 °C higher in summer than they were in spring (Maloney et al., 2011). Body temperature is linked to metabolism and daily energy expenditure in endotherms, thus lower body core temperatures in the kangaroos during summer likely allowed for considerable energy savings of up to 7 % (Maloney et al., 2011). The lowered body temperatures likely decreased the aardvark's daily energy expenditure for maintaining high body temperature. However, in aardvark 2, decreased body temperatures and becoming diurnal during summer were not sufficient in saving enough energy to survive the summer drought, as it died in March 2013, before the delayed summer rains finally arrived at the end of that month.

5.4.1 Body temperature and activity

During periods when resources were abundant, aardvarks were exclusively nocturnal (Chapter 4) and their body temperature patterns showed a tightly controlled nychthemeral rhythm. The body temperature rhythm of my aardvarks was similar to aardvarks in the Karoo, with lower body temperature during daytime when the aardvarks were inside burrows, and higher body temperatures at night when they were actively foraging (Taylor & Skinner, 2004). The authors suggested that body temperature peaks in active aardvarks resulted from intensive digging action (Taylor & Skinner, 2004), which produces metabolic heat (McNab 2002). It was proposed that the endogenous heat produced by intense digging might restrict aardvark foraging to the cooler night-time during hot seasons to avoid hyperthermia (Taylor & Skinner, 2004). In contrast, aardvarks were suggested to shift their foraging activity towards daytime because they are sensitive to low (2 °C and less) ambient temperatures (Taylor & Skinner, 2004).

Rather than avoiding the cold, my study suggests that aardvarks became diurnal when they struggled to maintain their energy balance. They became diurnal when their body condition had declined, and they exhibited increased heterothermy (largely as a result of reduced minimum body temperature). Indeed, aardvarks at Tswalu did not only become diurnal when it was cold but also during a summer marked by a severe drought, displaying low body temperatures during the day compared to at night, and pronounced heterothermy, and many aardvarks died during and after the drought. The aardvarks also showed increased body temperature during diurnal activity in winter 2013 after the drought, compared with when they were active nocturnally at the same time of a non-drought year (Figure 5.7), when temperatures were the same as during the drought, but productivity was higher, and aardvarks were in better condition. When solar radiation was absent after sunset in the winter following the drought, the body temperature of the aardvarks immediately declined (Figure 5.7). However, body temperature then did not just decline to the levels of an active aardvark during a non-drought year (~37 °C), but progressively and rapidly declined to as low as 35 °C during activity (Figure 5.5 and Figure 5.7). Once a burrow had been re-entered, body temperature continued to decline, but appeared to do so less rapidly than out in the open (Figure 5.7). I suggest that when resources were abundant, and aardvarks were in good condition, they had sufficient energy to sustain energetically costly homeothermy, even when active in cold nights during winter. In contrast, when aardvarks were in poor condition after the drought, they did not have enough energy to sustain homeothermy. Thus, when exposed to cold temperatures during winter evenings after sunset, they were unable to defend high body temperatures, often ended their active phase soon after sunset, and shifted to diurnal activity.

Aardvark body temperatures were impacted by solar radiation in that foraging in broad sunlight raised their body temperatures from nocturnal hypothermia of as low as 33 °C to as high as 38.5 °C within one active phase. The resulting amplitude of body temperature of 5.5 °C was more than twice as large as during a winter when aardvarks were in good condition. I propose that the aardvarks adjusted their activity pattern to diurnality in an attempt to reduce the metabolic costs of maintaining a high body temperature. In addition to aardvarks, this response has previously been observed in energy-deficient in rodents in the lab (Hut et al., 2011; Van der Vinne et al., 2014, 2015) and in the field (Lockard, 1978; Boal & Giovanni, 2007), and might be a common, widespread response to energy-deficiency in nocturnal mammals. This adjustment might have been driven by a circadian mechanism found in nocturnal mammals that become diurnal when starving, thereby saving energy by exploiting warmer daytimes in winter (Van der Vinne et al., 2015). Pronounced diurnal activity in otherwise nocturnal mammals might allow them to save considerable amounts of energy and possibly avoid further body temperature declines, especially when it is cold (Van der Vinne et al., 2015). The reduced body mass of aardvarks in poor condition likely contributed to more rapid increases in body temperature, reflected in the intense effects of solar radiation and low air temperature on the body temperature. In addition, the ratio of body surface to body volume was much greater in starved compared to well-nourished aardvarks, increasing their thermal lability. Thus, in addition to inadequate water for evaporative cooling and insufficient food abundance for heat generation, starved aardvarks likely also had greater heat exchange with the environment than aardvarks in good condition, resulting in body temperature rapidly increasing in sunlight and decreasing at night when the effects of solar radiation were absent, and air temperatures were low.

During periods of resource scarcity, minimum body temperature of inactive aardvarks progressively declined toward the end of their resting phase, an effect which was reversed when activity was resumed. Although this pattern of declining minimum 24-h body temperature occurred to some extent during all winters, accompanied by slight activity shifts toward diurnality, the resulting heterothermy was most pronounced during winter 2013 following the summer drought and also during the summer drought, when aardvarks were largely diurnal. I therefore propose that temporal shifts in aardvark activity patterns from nocturnality in productive periods to diurnality in drought and thus resource-restricted periods reflected a response of aardvarks to energy deficiency.

My study aardvarks showed diurnal behaviour when resources were scarce, and the resulting exposure to high air temperatures during mid-day and afternoon foraging bouts as observed during the summer drought, as well as in the winter after the drought, likely resulted in a greater heat load on the aardvarks. Body temperature in large mammals can be elevated during low water availability in hot periods to preserve body water (Hetem et al., 2016); however, the aardvarks' body temperatures were greatest at night. The exposure to heat did not appear to increase the body temperature of diurnal aardvarks in summer; moreover, their body temperature was not highest during active foraging in the morning, but during the inactive phase at night. Thus, I propose that intense activity, such as digging to access prey or construct burrows, might lead to a slight, short-term increase of body temperature, but does not increase body temperature in a way that metabolic heat would become a limitation for aardvark activity both at night when their high thermal conductance probably supports heat loss, nor during the day, provided that sufficient prey is available to cover the water needs of aardvarks for potential evaporative cooling. Whether and how aardvarks make use of evaporative cooling is not known, but remaining inside a burrow might not only shelter aardvarks from predators and extreme temperatures: burrow air temperatures (Taylor, 1998) are likely low enough that evaporative cooling might not be required, and provide higher air moisture, possibly minimising passive, uncontrolled evaporative water loss. While aardvarks are known to make use of water if it is available (Chapter 3 and Kerley & Tompkins, 2017), water access is limited in the Kalahari, and aardvarks must rely on their termite diet to obtain water. A starving aardvark that becomes diurnal during summer in pursuit of food can thus perhaps save energy by exposing itself to elevated temperatures, but at the same time might risk dehydration, thereby amplifying its already poor nutritional state during times of prey scarcity. The reduced termite availability during and after the drought likely limited the water intake, and thus the capacity for evaporative cooling, resulting in elevated body temperatures during daytime foraging.

5.4.2 Minimum body temperatures

During the summer drought, aardvarks (notably aardvark 2) had remarkably low (~25 °C) minimum body temperatures, occurring whilst the animals were active and feeding in the morning and midday. To my best knowledge, these are the lowest core body temperatures ever reported in a large mammal that was actively foraging, and lower than body temperatures in large mammals during hibernation. For comparison, hibernating brown bears (*U. americanus*) reduce body temperatures to ~29 °C while inactive inside a den (Tøien et al., 2011). Minimum body temperatures of aardvarks during drought reached levels of those predicted for torpid mammals (28.3 °C minimum body temperature predicted for a mammal of 40 kg body mass, Ruf & Geiser, 2015). However, unlike torpor, which represents a controlled downregulation of body temperature, my study aardvarks showed a progressive lowering of minimum 24-h body temperature over several weeks, and a progressive decline of body temperature during resting phases. The lowest body temperature (14.6 °C) at which a mammal has shown directed movement was recorded in the small (10 g) Australian fat-tailed dunnart (*Sminthopsis crassicaudata*), a daily heterotherm which during arousal from daily torpor often crawls to a basking spot to gain exogenous heat during rewarming (Warnecke et al., 2008). However, such low body temperatures are likely to be unsustainable in a large mammal. In humans, core body temperatures below ~33 °C are considered severe hypothermia, and lead to an inability to spontaneously recover (Mitchell & Laburn, 1985). In free-living large non-hibernating mammals such as Arabian sand gazelle and blue wildebeest, low minimum 24-h body temperatures, and resulting hypothermic heterothermy, were observed during periods of inadequate energy supply, and were pronounced in individuals that died (Hetem et al., 2016). Indeed, the study aardvarks in which low body temperatures and large amplitudes of 24-h body temperature occurred during the summer drought died (this study and Rey et al., 2017). Moreover, during the winter following the drought, all aardvarks that were hypothermic were also in poor condition, and some individuals died. However, some aardvarks that were hypothermic during the winter survived, and the body temperature amplitude of a surviving aardvark in winter 2013 was larger than that of a moribund aardvark during summer 2012-13. The increased heterothermy in winter compared to summer was likely enhanced by lower ambient temperatures.

I propose that the pronounced heterothermy in poorly-nutritioned aardvarks reflected an inability to sustain high body temperature that are well-controlled within a narrow range when energetically challenged. In the Kalahari, resource abundance and environmental conditions fluctuated strongly within and between years during this study (Chapter 3). The presented long-term records of the magnitude of heterothermy provided a valuable index of stress within aardvarks in the Kalahari, as has been proposed for free-living, undisturbed large mammals (Fuller et al., 2014). In addition, I propose that in the generally nocturnal aardvark, a shift to diurnal activity might indicate that the animals are in negative energy balance.

5.4.3 Basking

During winter 2013 following the summer drought, numerous aardvarks were in poor condition, many died, and many were partially or completely diurnal and often basked from early morning onward. Basking events resulted in pronounced rapid short-term increases of body temperature, accompanied by an overshoot in body temperature (slight hyperthermia) once the aardvark started foraging during daylight that contributed to greater amplitude in 24-h body temperature (heterothermy). Basking was evident only when study aardvarks exhibited lower-than-normal minimum body temperatures, indicating that they were likely energy-deficient. Hetem et al. (2016) proposed that the low minimum body temperatures reported for energy deprived mammals were likely an inability to maintain high body temperatures rather than a controlled downregulation of body temperature as is the case for torpor. My basking observations and simultaneous body temperature records provide support for this hypothesis: if aardvarks had downregulated their body temperature set-point to save energy (as is the case in torpor), they should have been able to uphold their body temperature at a lower set-point, instead of having to bask, during the inactive phase. Moreover, aardvarks in good condition showed steep declines of body temperature at the start of resting, and controlled, tightly regulated body temperature which was slightly lower during the resting phase compared to the active phase. Contrarily, body temperature of aardvarks in poor condition continuously declined throughout the inactive period, with no evidence of a controlled, endogenous regulation at a lower temperature. These arguments, and the fact that so many aardvarks displayed hypothermia before their deaths, provide the best support to date that low minimum body temperature indicates a period of struggle with energy deficiency in a large mammal rather than an actively-regulated response, and that heterothermy is an index of wellbeing in large mammals.

Many smaller endotherms (birds and mammals) commonly use basking to save energy when rewarming from daily torpor and returning to high body temperatures (Geiser et al., 2004; Geiser & Körtner, 2010) or when sustaining high body temperatures during cold periods (Brown & Downs, 2007; Signer et al., 2011). The only other large terrestrial mammal in which basking has been proposed as an energy-saving mechanism is the alpine ibex. Alpine ibex become hypometabolic during winter, and likely bask to save body fat reserves that they need to survive through winter (Signer et al., 2011). However, ibex are predominantly diurnal, and basking was not observed but was indirectly inferred from biologger records of metabolic rate, activity, and body temperature (Signer et al., 2011). I provide the first quantitative evidence of a large, nocturnal terrestrial mammal, typically thought to be confined to a burrow in the morning, using basking to increase body temperature. This increase in body temperature helped aardvarks to avoid uncontrolledly declining body temperatures, thereby preventing aardvarks from succumbing to hypothermic death sooner than if they had not basked.

In addition, basking likely reduced the cost of defending high body temperature during the inactive phase, thereby ameliorating the energy deficits caused by reduced prey availability. Aardvarks increased their body temperatures by 2.9 ± 2.0 °C during basking, and had a mean body mass of 35 kg (between 29 to 42 kg) at capture. Based on the specific heat capacity of protoplasm (3.436 kJ kg^{-1} K^{-1}, see Bartholomew & Rainy, 1971), the warming of 35 kg of tissue by 3 °C (Table 5.4) would have required 360.8 kJ. In Chapter 2, I estimated that the daily energy requirements of Tswalu aardvarks with a body mass of 35 kg would be ~11 700 kJ in 24 hours (range of the 95 % confidence interval for this prediction: ~4 700 to ~29 100 kJ in 24 hours, based on Nagy 1987; Nagy et al. 1999), and that the actual daily energy intake of the aardvarks was ~2 865 kJ in 24 hours, only 61 % of the predicted ideal energy intake. In saving 7.7 % of their ideal daily energy needs, basking thus contributed considerably to the daily energy budget of aardvarks, and may, in fact, have been critical for survival of aardvarks through winter 2013 after the drought, when they were energy-deficient and unable to sustain high body temperatures during the cold season.

Nevertheless, a trade-off of basking compared to resting inside a burrow must exist for the aardvarks that prevents them from opportunistically making use of basking extensively during every winter. Basking and foraging in daylight might put aardvarks at higher predation risk than they would be inside their burrows as they become more easily detected by diurnal predators. At the same time, exposure to daylight may impair their already poor sense of sight; they have only rod cells for nocturnal vision but no cone cells (Franz, 1908; Sonntag & Woollard, 1925) and thus no colour vision and poor spatial perception. Diurnal activity might put them at a disadvantage because they rely only on their ears for predator detection (Taylor & Skinner, 2004), while a predator would potentially be able to see as well as hear an aardvark that is active in daylight. Additionally, aardvarks have only sparse pelage, directly exposing much of their skin to solar radiation during diurnal activity. Aardvarks also reportedly are at risk of intense sunburn when exposed to solar radiation for extended periods (E. de Jager, veterinarian at ZURI Wildlife Orphanage, Namibia, pers. comm.). In this study, I have shown that only energetically-compromised aardvarks that were heterothermic exposed themselves to sunlight at Tswalu, while aardvarks that were able to maintain homeothermy remained exclusively nocturnal and did not bask, even during winter.

In all aardvarks in poor condition, body temperature progressively declined throughout the inactive phase. Interestingly, a sharp, transient fall in body temperature was superimposed on the overall decline when aardvarks emerged from their burrows. Similar observations have been reported for kangaroos (Brown & Dawson, 1977) as well as some ungulates such as elands (*Tragelaphus oryx*; Fuller et al., 1999) and camels (*Camelus dromedarius*; Schmidt-Nielsen et al., 1956). The drop in body temperature may result from vasodilation of cutaneous blood vessels when the skin is warmed by solar radiation, or by cooler blood from the body periphery and previously inactive skeletal muscle returning to the core during initial movements, i.e., emergence to bask (Mitchell et al., 2002). Indeed, the sharp decline was generally reversed once aardvark body temperature started rising during basking or activity.

Basking in aardvarks has not previously been reported in the scientific literature, but only in few anecdotes (summarised by Knöthig, 2005), without notes on the body condition of these aardvarks. However, in recent years, growing ecotourism to remote places of southern Africa and the popularity of photograph-sharing on social media platforms have contributed to ample online-footage of wild, diurnally foraging or basking aardvarks, often described as “sleeping” or “lazy” aardvarks, particularly in semi-arid regions of South Africa such as the Kalahari and Karoo, as well as in the Limpopo province (Figure 5.8). Upon closer examination of such footage I noticed that the aardvarks on such photographs were usually in poor condition, and that images of skinny aardvarks were generally taken during winter, when conditions were dry and resources likely scarce. Moreover, most photos of basking aardvarks coincided with years during which droughts had occurred over extensive regions of South Africa. These droughts likely resulted in adventitious reductions in prey availability and thus energy intake, which aardvarks attempted to compensate for by basking. The photographic footage is in line with the present study, where study aardvarks basked only when their condition had declined during periods of resource scarcity and increased energetic demand during winter.

5.4.4 Conclusion

Aardvarks in the Kalahari used a number of energy-saving responses available to them such as basking, shifting their temporal niche, and reductions of their minimum body temperature. During a year with average, semi-arid conditions and normal resource abundance during summer but reduced availability in winter, these mechanisms likely allowed the aardvarks to preserve sufficient energy to survive through winter, when low temperatures increased energy expenditure.

However, during a drought year in the Kalahari with low and late rainfall causing low resource availability during summer which had likely not recovered by winter, the plastic responses of aardvarks were exhausted and did not suffice to preserve enough energy to survive a drought summer. The deaths of aardvarks at Tswalu during the summer drought and the following winter were not limited to the study aardvarks. In addition to the five dead study aardvarks in summer, 11 other aardvarks were found dead within the central region of the reserve (Rey et al., 2017).

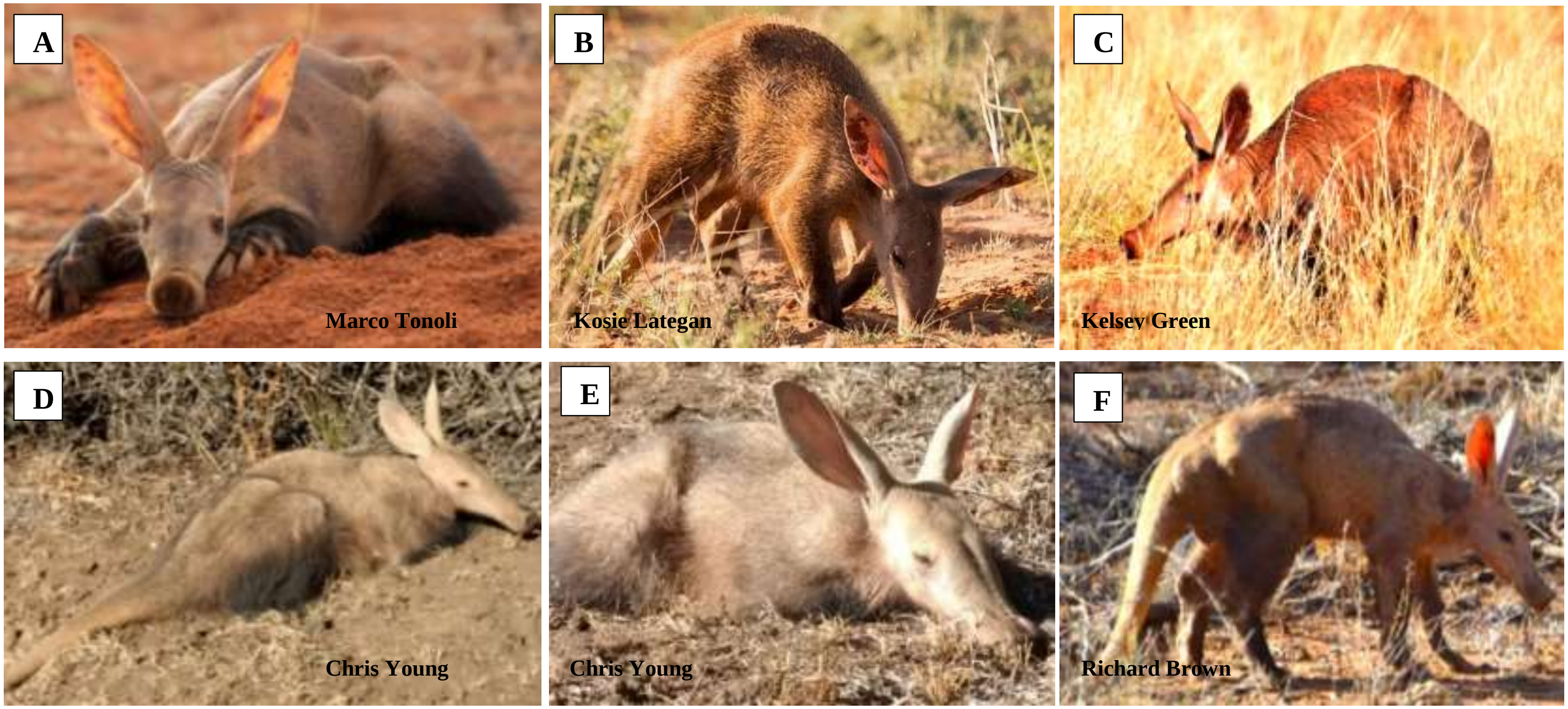

Figure 5.8 Image collection of aardvarks basking or foraging during daytime while in poor condition, from social media platforms, photographed in different regions of South Africa. A) Aardvark basking at Tswalu in August 2013 (https://goondwan.com/animals/ant-eaters/#jp-carousel-13381). B) Aardvark foraging in daylight at Tswalu in July 2016 (https://www.tswalu.com/media/blog-article/aardvarks-by-field-guide-kosie-lategan). C) Aardvark basking at Tswalu during winter 2015 (K. Green, pers. comm.). D, E) Basking aardvarks at Samara Game Reserve, Eastern Cape in July 2016 (C. Young, pers. comm.). F) Aardvark foraging at 16:00 on 11 August 2016 at Raptor's View Wildlife Estate, Limpopo (http://raptorsview.co.za/wp-content/uploads/2016/08/Raptor-News-26web.html). Note that droughts had occurred over extensive regions of South Africa during 2012 to 2013, and 2015 to 2017.

During the winter after the drought, the aardvarks that had survived the drought summer were then challenged by the high energy demands of defending high body temperatures during the cold season. This challenge was likely amplified in many aardvarks by failure to recover fully from the summer drought adversities or because their main prey remained limited, again rendering the thermoregulatory responses of aardvarks insufficient to survive the cold season that followed the drought. During winter, when three more study aardvarks died, five additional dead aardvarks were found. During both periods, numerous sightings occurred of emaciated, weak aardvarks foraging in daylight. According to the reserve management, such high numbers of mortalities and weak aardvarks had never previously been observed at Tswalu since the reserve’s establishment in the 1990s (Gus van Dyk, Manager at Tswalu Kalahari Reserve, pers. comm.).

In semi-arid zones with summer rainfall, such as the Kalahari, resources are primarily dictated by the timing and amount of rainfall, and delayed onset of annual rains results in low vegetation productivity at a time when conditions are heating up. Summer droughts combined with heat waves, as observed at Tswalu in the summer of 2012-13, will occur increasingly regularly in future as a result of global climate change, and might severely impact the persistence of aardvarks in this increasingly arid environment by pushing them beyond their physiological limits. Although increasing environmental temperatures and a decline in the number and intensity of cold days and nights might ease the energy deficits experienced from cold temperatures during winter, this effect will likely be overshadowed by lack of resources induced by summer drought. Consequential extirpation of aardvarks, key ecosystem engineers that provide thermal refugia to dozens of animals, might have severe knock-on effects on biodiversity in the Kalahari ecosystem.

5.5 References

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Chapter 6 - Conclusion

6.1 Summary of my research

I examined body temperature rhythms, activity patterns, body condition, and diet of aardvarks in response to seasonal fluctuations in environmental conditions and food resources over ~3.5 years in the semi-arid Tswalu Kalahari Reserve. This long-term study has resulted in the longest and most comprehensive study on the ecophysiology of free-living aardvarks to date, allowing me to investigate plasticity in aardvarks' physiological responses to seasonal and interannual environmental variability. Ongoing climate change is bringing about more frequent, more intense, and more extensive droughts combined with less predictable rainfall patterns in the Kalahari and throughout much of the aardvark's range (Figure 1.2; Rouault & Richard, 2005; Niang et al., 2014; Gemeda & Sima, 2015). Studies investigating the physiological plasticity of a species currently inhabiting hot and dry climates, with superimposed extreme events such as droughts and heat waves, can provide a current analogue for the conditions likely to become prevalent in Africa in the future, as was the case with the current study.

Diet of aardvarks in the Kalahari consisted largely of termites (notably harvester termites *H. mossambicus*) throughout the year, and the remainder was comprised of ants (Chapter 3). This composition contrasts with the diet of aardvarks in less arid habitats, which has greater ant components throughout the year (Melton & Daniels, 1986; Willis et al., 1992; Taylor et al., 2002). The Kalahari is the most arid environment currently inhabited by aardvarks, which are excluded from truly arid zones such as the neighbouring Namib Desert, or the Sahara Desert (Figure 1.2). Under normal circumstances, the reliance of Kalahari aardvarks on harvester termites as prey might have advantages in this dry environment, because harvester termites are large in size, abundant, and most importantly provide more than eight times as much water and twice as much energy per individual as any other prey item at Tswalu (Chapter 3). Ants contain up to one third more energy per mass unit than termites and are thus a better energy provider, but provide less water, and comprised the smaller fraction of the diet (Chapter 3). While aardvarks occasionally access standing water (Chapter 3 and Kerley & Tompkins, 2017), they generally do so only rarely, even in semi-arid habitats (Chapter 3 and Taylor & Skinner, 2004). During the study, I never observed my animals drinking, and none had drinking water source within their home range area. Therefore, the high water content of harvester termites might ultimately be the key that enables aardvarks to survive in an environment as hot and dry as the Kalahari.

The presence of termites, however, is dependent on the availability of dietary plant material, typically dry grass (Nel & Hewitt, 1969a). Despite their ability to store grass, harvester termites are known to decline during extended periods of summer drought and low vegetation cover, and recover only slowly (over multiple years), if at all, from drought-related population crashes (Nel & Hewitt, 1969a). Drought can also affect ant species (Marsh, 1987), especially those that harvest seeds and other plant matter, such as *Ocymyrmex* sp., *Messor* sp., *Pheidole* sp., which also occur, to varying extents, in the aardvark's diet (Chapter 3 and Willis et al., 1992; Lindsey, 1999; Taylor et al., 2002). Levels of annual vegetation productivity in the Kalahari are affected by summer drought, and the intense and frequent droughts expected in southern Africa under climate change (Niang et al., 2014) will likely have long-term impacts on termites.

In the Kalahari, seasonal changes in vegetation productivity (notably grass cover) occur throughout the year, with productivity generally highest between October and March. During my study, inter-annual rainfall variability was high; two good rainfall years occurred which had high amounts of early rainfall, and high vegetation productivity (as indexed by EVI; Chapter 3 and Tokura, 2016). During these years, ant (largely in summer) and termite abundances were high, thus aardvarks obtained sufficient prey to cover their minimum daily energy and water requirements, and were in good body condition (Chapter 3). Irrespective of the season, aardvarks in good condition remained nocturnal (Chapter 4), and were homeothermic, with a low 24-h amplitude of body temperature (~2.5 °C; varying from 35 to 37.5 °C; Chapter 5). Their 24-h rhythm of body temperature closely tracked that of activity, with body temperature increasing at the beginning of the active phase, and declining at the end of the active phase, resulting in a square-shaped 24-h pattern of body temperature (Chapter 5).

During drought years, especially during 2012-13, vegetation productivity was markedly low (Chapter 3 and Tokura, 2016), likely impacting harvester termite colonies which rapidly and permanently respond negatively to drought-related vegetation shortage (Nel & Hewitt, 1969a). It is possible that rather than having been killed by the drought immediately, termites and ants at Tswalu ceased activity in the superficial soil layers during the summer drought, remaining inside their deep (~7 m) underground nests and surviving on stored plant matter. In either scenario, the summer drought at Tswalu likely reduced the availability of termites and ants to aardvarks such that aardvarks were unable to meet their energetic and water needs (Chapter 3). A mass mortality of aardvarks occurred at the end of the summer drought, and surviving aardvarks were in poor condition. During the summer drought, many aardvarks became partly diurnal, some shifting activity entirely to the daytime in the weeks leading up to their deaths (Chapter 4; see also Rey et al., 2017).

The diurnal shift in aardvark activity is likely attributable to a circadian response that drives nocturnal mammals to become diurnal during periods of energy-deficit to reduce the energetic cost of thermoregulation (Van der Vinne et al., 2015). This postulate is corroborated by the observation that the diurnal aardvarks simultaneously became increasingly heterothermic, with amplitudes of 24-h body temperature of up to 11.7 °C, largely due to declining minimum 24-h body temperature (Chapter 5; see also Rey et al., 2017), an effect termed hypothermic heterothermy (Hetem et al., 2016). The progressively declining body temperature in starving aardvarks during the resting phase resulted in a more cosinor shape of the 24-h body temperature curve, compared to the square shape of the curve when in good body condition. On the days shortly before death, maximum 24-h body temperature declined as well; however, the amplitude of 24-h body temperature remained larger than usual until death (Chapter 5). The increased amplitude, as well as the declining minimum, mean, and maximum of 24-h body temperature, were likely a result of failure of the starving aardvarks to sustain energetically-costly thermoregulation. In addition, some aardvarks showed a dissociation of the 24-h rhythms of body temperature and activity such that body temperature was highest at night during inactivity, and lowest in the morning during activity (Chapter 5). The only study aardvark that survived the summer drought had not become diurnal and displayed less pronounced heterothermy and less of a decline of minimum 24-h body temperature during summer than its conspecifics that died (Chapter 5), suggesting that it was better nourished and hydrated than the other aardvarks. Such intra-individual variation in susceptibility to starvation might have been due to age difference, body condition before the drought, or reproductive state; however, these factors could not be assessed within the scope of this study. Nonetheless, the observed contrast of pronounced hypothermic heterothermy in moribund, emaciated aardvarks during drought compared to homeothermy in well-nutritioned aardvarks provided solid evidence for the concept (Hetem et al., 2016) that body temperature variability is indicative of inadequate energy supply in large mammals.

By the winter that followed the summer drought, the late and poor summer rains had not sufficed to ensure a complete recovery of the termite and ant populations at Tswalu (Chapter 3). Termite colonies that had survived the drought on underground grass stores had likely depleted those stores by the winter, negatively impacting their populations and preventing aardvarks from meeting their energetic needs. All study aardvarks were in poor condition during this winter, and again, many individuals died. EVI was a robust indicator of prey availability and body condition of aardvarks, and implicated the drought event as the indirect cause of aardvark mortalities. All study aardvarks displayed diurnal activity (Chapter 4) simultaneously with heterothermy and reduced minimum 24-h body temperature (Chapter 5). Although body temperature increased and decreased synchronously with the start and end of the active phase, it also declined progressively during the inactive phase (Chapter 5). During winter after drought, the body temperature of aardvarks in poor condition was higher when they were active during the day than when they were active at night. This effect likely helped to save energy of thermoregulation (Van der Vinne et al., 2015). In addition, many poorly-nutritioned aardvarks often basked in the sun for extended periods in the daytime during their resting phases (Chapter 5). Basking prevented body temperature of poorly-nutritioned aardvarks from declining while resting, compared to resting inside burrows, and allowed the aardvarks to passively rewarm before becoming active (Chapter 5). Basking potentially allowed energy savings of up to 7 % of daily energy needs (Chapter 5). However, the energy saved by employing diurnal activity combined with basking was not sufficient in all study aardvarks in preventing death from starvation during periods of low resource abundance.

6.2 Monitoring methods

During my study, monthly EVI correlated with harvester termite activity as indexed by soil-surface termite signs (Chapter 3). However, all current methods for termite population assessments are indirect, laborious, often physically demanding, and require an investigator to be based on site continuously. Thus, improved, more efficient, and spatially and temporally more highly resolved methods of termite population assessments are needed to perform extensive long-term monitoring of population size fluctuations. These could include monthly or even weekly observations of foraging intensity, and numbers of foragers at fixed sites. However, due to the cryptic lifestyle of termites, these methods will likely remain indirect, unless techniques are developed to assess termite hive activity underground. If responses of termite populations to plant matter availability could be assessed for different sites and areas, and their responses correlated with local remote-sensing data (e.g., EVI), the latter could be upscaled to monitor and predict termite population fluctuations on a regional scale without the necessity of on-site ground truthing, especially in remote places.

EVI also correlated with aardvark body condition during this study (Chapter 3). However, the assessment of body condition was limited to my study individuals and depended on regularly tracking these individuals to observe them or obtain camera trap footage. Improved methods of assessing body condition of aardvarks could include mass-arrays of camera traps, as well as photogrammetric setups as used for other large animals including primates (Kurita et al., 2012) and marine mammals (Waite et al., 2007; Postma et al., 2013). Photogrammetry is a method by which three-dimensional models of animals are constructed based on photographs, for indirect determination of body mass without manipulation or capture of the animal (de Bruyn et al., 2009). Aardvarks could be an excellent candidate for photogrammetry, because their surface is not concealed by dense pelage, allowing for accurate assessments of their body volume and condition. Indeed, attempts to conduct photogrammetric measurements to assess mass variation of my study aardvarks using a mobile automated photogrammetry camera-trap system were promising (Postma et al., 2015). However, such setups are costly, and still require further refinement before they can be widely implemented for long-term assessments of body volume (and thus body condition) changes in free-living aardvarks, and other species.

In this study, biologging allowed the quantification of physiological and behavioural responses of aardvarks to drought-related resource scarcity. The resulting records of body temperature and activity patterns were a good indicator of aardvark well-being in the Kalahari. Long-term records of body temperature have also been shown to reflect welfare in other large mammal species (reviewed in Hetem et al., 2016). Therefore, the approach of linking EVI with activity and body temperature patterns has great potential as a relevant assessment and monitoring method to investigate the well-being of aardvarks and other free-living large mammals in their natural habitats, particularly in the light of ongoing climate change. Although the capture of aardvarks is challenging, biologgers are relatively easy to implant and can be used to investigate aardvark ecophysiology in other areas. Importantly, physiological responses of aardvarks to drought would should be investigated in other habitats where ants, as opposed to termites, are the preferred prey of aardvarks. The ecophysiology of aardvarks in the Kalahari and in other hot and dry parts of their geographical distribution, such as south of the Sahara, could be compared to that of aardvarks from non-arid (including tropical, i.e., hot but non-arid) regions, to examine their sensitivity to heat in different aridity regimes. Citizen science, such as reporting instances of diurnal activity as well as body condition of aardvarks to an online platform (e.g., a dedicated social media page), could augment biologging data, providing long-term ecophysiological information on how drought and climate change are impacting aardvark populations. Public records and images of aardvarks that are diurnal and/or in poor condition could aid in assessing and monitoring aardvark condition and serve to detect periods of sub-optimal conditions for aardvarks, and thereby indirectly their prey. A combination of such studies, conducted across wider conservation zones, could be used to map the future distribution of aardvarks under different climate change scenarios, where a certain decline in rainfall has a known negative effect on aardvark body condition and survival.

6.3 Ecological significance of aardvarks

Starvation-related declines or extirpations of aardvarks might severely impact the species reliant on aardvark burrows in many African habitats, with cascading effects on biodiversity in local communities, and thus on ecosystem functioning. As aardvarks generate large numbers of underground burrows co-used by dozens of other animal species (Whittington-Jones et al., 2011), they are considered key ecosystem engineers in many African habitats (Cilliers, 2002). Being the only such proliferously burrowing species in Africa, aardvarks cannot be functionally replaced by any other African species.

Aardvark burrows are important structures that offer numerous benefits. Firstly, aardvark burrows have considerable thermal buffering capacity. For example, during early summer 2013-14 at Tswalu, air temperatures inside vacant aardvark burrows at a depth of ~1 m varied between 25 and 32 °C, while those outside ranged from 15° to 40 °C (Chapter 2). As climate change imposes growing heat loads on animals, the importance of thermal refuges will increase (Pike & Mitchell, 2013). Secondly, aardvark burrows offer protection, for example from predation, and for reproduction, denning and raising young for numerous mammals, birds, and reptiles (listed in Whittington-Jones et al., 2011; Taylor, 2013). Some animals are already dependent on aardvark burrows for shelter under current environmental conditions, for example warthogs which do not excavate their own burrows (Cumming, 1975; Melton, 1976). Porcupines can excavate their own burrows, but often use burrows originally excavated by aardvarks (Whittington-Jones et al., 2011; pers. obs.), and could thus be considered secondary burrow providers while aardvarks are primary burrow producers.

Aardvarks also provide additional ecosystem functions in semi-arid habitats. Their foraging pits facilitate access to insect prey for various opportunistic feeders such as bat-eared foxes, aardwolves, and several bird species (Taylor & Skinner, 2000, 2009; Taylor, 2013). These species have limited digging abilities, and are thus otherwise incapable of reaching deeper soil levels where ants and termites are abundant. This food source is especially important during winter, when the surface-foraging activity of ants is reduced, and when aardvarks often forage during daylight hours (Cilliers, 2002; Taylor, 2013). Being ‘prime-movers’ of soil, aardvarks’ digging activities contribute to soil nutrient redistribution and provide important seed germination sites (Dean & Milton, 1991). Therefore, the disappearance of aardvarks especially from dry habitats may have considerable impacts on opportunistic co-feeders and on composition and stability of plant communities.

Other key species that provide burrows for numerous co-users in regions becoming hotter and drier with climate change include wombats in Australia and giant armadillos in South America (Silveira et al., 2009; Pike & Mitchell, 2013). Wombats are reportedly sensitive to drought (see below; Gaughwin et al., 1984), and are thus among the many native mammals sensitive to increasingly hot and dry conditions predicted for much of the Australian continent under climate change (Steffen et al., 2009). The main threat for the giant armadillo of South America is habitat loss, and impacts of land-use change and of climate change will likely exacerbate its population decline (Zimbres et al., 2012; Anacleto et al., 2014). The loss of such important ecosystem engineers from hot regions could reduce biodiversity and impact the functioning of ecosystems (Pike & Mitchell, 2013). Indeed, in Australia, deteriorated ecosystem functionality has been attributed to a decline in digging and burrowing mammals (Steffen et al., 2009; Fleming et al., 2014), which fulfil many important roles such as soil turnover, nutrient distribution and seed germination improvement (Eldridge & James, 2009; James et al., 2009).

Research on the responses of keystone animals, especially of those whose key services are becoming increasingly important under climate change (e.g., providing of food, microclimates, and other ecosystem services), should be emphasized. Large-scale studies, for example using extensive camera-trap setups, could provide an estimate of population densities of burrow-providing species such as aardvarks in different habitats, and how these densities might fluctuate with environmental conditions and resource availability. Moreover, a better understanding is needed of the degree of reliance on burrows as thermal shelters by burrow-co-using animal species via field-based monitoring and extensive camera trapping. Automated technology for species identification (Yu et al., 2013; Gomez Villa et al., 2017) could be used to distinguish species using burrows. Current algorithms for estimating microclimates (e.g., Kearney et al., 2014) are not applicable to underground microhabitats. Hence, on-site measurements of burrow microhabitats could serve to develop mechanistic models that project the persistence of these species through different scenarios (e.g., in the presence and absence of aardvark burrows, under varying climate change projections). The inclusion of species interactions would greatly improve the quality of models for species' responses under different climate change scenarios, but is often difficult because of the complexity of ecosystems and a general lack of understanding of species interactions in the wild. More field data are required to elucidate these interactions.

6.4 Possible consequences for other myrmecophages in Africa and globally

Termite and ant populations are a key prey resource for numerous mammalian myrmecophages other than aardvarks in Africa and worldwide (Redford, 1987), and their possible demise under future increased heat and aridity will likely impact many of these species. These include several highly specialised myrmecophageous mammals such as the aardwolf (Cooper & Skinner, 1979; Richardson, 1987; Matsebula et al., 2009) and the four African pangolin species (Richer et al., 1997; Swart et al., 1999), as well as more-opportunistic species such as the bat-eared fox (Kok & Nel, 1992; Klare et al., 2011). In addition, a large number of small species of mammals and birds commonly consume ants and termites (especially *H. mossambicus* in African habitats; Kok & Hewitt, 1990). The inability of aardvarks to shift to ants sufficiently to compensate for the lack of termites during the drought manifested in their deteriorating body condition, which was likely exacerbated by synergistic effects of starvation and dehydration.

Like aardvarks, many myrmecophageous mammals in arid habitats of southern Africa are reportedly independent of free-standing water, meeting their water requirements with their termite or ant prey, such as the termitivorous aardwolf (Anderson, 2013; Green, 2015) and Temminck's ground pangolin (Pietersen et al., 2014c). These mammals will likely also be prevented from covering both their energy and their water needs during drought-related insect declines, with potential impacts on their physiological condition.

Some myrmecophages face additional population pressures from capture for illegal trade, and from loss or degradation of habitats, notably the pangolins of Africa (Pietersen et al., 2014a; Boakye et al., 2015; Durojaye & Olufemi, 2015) and Asia (Pantel & Chin, 2009; Nash et al., 2016). Moreover, extensive use of insecticides in farming targeted at ants and termites, which are often seen as a pest (albeit wrongfully so, see Nel, 1968), likely reduces their availability as prey to myrmecophages (Cilliers, 2002). Assessments of the precise dietary compositions of myrmecophages across different habitats in Africa, and the abundance of their prey, would be required to estimate the impacts of ant and termite population reductions on their predators. Since *H. mossambicus* is such an abundant and dominant termite species in African grasslands, any factors that impact its populations are likely to have negative impacts on trophic cascades. Resource scarcity under future climates might not only affect African myrmecophages: in Australia, myrmecophageous mammals (Redford, 1987) including the numbat (*Myrmecobius fasciatus*) and echidna (*Tachyglossus aculeatus*) will possibly face prey declines as climate change increases heat and aridity over the continent. Desertification of landscapes in Central and South America, such as the South American Cerrado and Amazon, might impact on myrmecophageous specialists such as the giant anteater and several species of tamandua. These regions are subject to high degrees of land-use change including deforestation and growing infrastructure, and deforestation in the Amazon itself causes higher drought probability (Baidya Roy & Avissar, 2002; Andreae et al., 2004; Cochrane & Laurance, 2008; Malhi et al., 2008). While these mammals are increasingly facing the risk of population declines (Miranda et al., 2014b; Ortega Reyes et al., 2014; Quiroga et al., 2016), the additive impacts of land-use change and climate change on populations of their ant and termite prey remain to be investigated.

6.5 Effect of drought on trophic cascades

Termites play invaluable roles in many ecosystems worldwide: they release nutrients from decomposing vegetation into soils, their symbiotic gut microorganisms enrich their waste products with atmospheric nitrogen, and their tunnelling activity improves water infiltration as well as topsoil retention (Prestwich et al., 1980; Elkins et al., 1986; Jones, 1990; Fox-Dobbs et al., 2010). Termites are also relevant for nutrient turnover in soil (De Bruyn & Conacher, 1990; Jouquet et al., 2011), and as a prey item to numerous animals (Redford, 1987; Kok & Hewitt, 1990). While termites might even increase the ability of arid ecosystems to withstand climate change impacts (Bonachela et al., 2015), their population demise under climate change could have severe ramifications for ecosystems (Shiday et al., 2011). However, the expected reductions in rainfall and consequently reduced plant forage availability will not only affect vegetation-harvesting insects such as ants and termites but all grazers, including antelope and many smaller mammals. Potential declines in populations of herbivorous prey animals will, in turn, impact carnivore species through disruptions of trophic cascades. Even if termite colonies do recover after drought, populations of their predators will unlikely bounce back to sustainable numbers quickly, especially for mammals that reproduce as slowly as do aardvarks. Low vegetation productivity has been predicted to amplify impacts of climate change on biodiversity through extinction cascades from plants to animals in ecosystems (Schleuning et al., 2016). However, the impacts of low vegetation quality and quantity during drought have not been included in many models for future species distribution or investigated in field studies. Long-term biologging of body temperature and activity could serve as a basis for large-scale studies on ecological and physiological responses of multiple species in the same habitat, and of populations of the same species in different habitats. Once the correlation of body condition with parameters such as body temperature and locomotor activity measured in this study, and with resource abundance, has been validated for a range of species, body condition would be a robust, inexpensive, and non-invasive index of animal well-being. The downsides of such an approach are that animals must either be observed in the field or recorded on camera trap (e.g., using photogrammetry as mentioned above) which can be costly. Moreover, it can be challenging to keep track of and record individual free-living wild animals unequipped with tracking devices, especially in the case of cryptic and nocturnal species. Remote sensing methods such as EVI, in addition to field-based studies, could be useful to monitor vegetation resource availability under climate change not only for termite herbivory but for a multitude of mammalian grazers. Such studies could serve to investigate the sensitivity of key ecosystem engineers to current and future environmental conditions.

Indirect negative effects of climate change on vegetation productivity might result in poor body condition and reduced reproduction in various herbivorous large and small mammals. In a semi-arid steppe habitat in North America, drought-reduced grass availability and caused a decline in body condition and reproduction of Townsend's ground squirrels (*Spermophilus townsendii*; Van Horne et al., 1998). In Australia, Koalas are sensitive to extreme weather events, and drought combined with heat wave resulted in koala deaths, followed by reproduction failure after drought (Gaughwin et al., 1984; Gordon et al., 1988). These specialist feeders might also be severely affected by future increased heat and aridity (Steffen et al., 2009; Black et al., 2014), as they obtain their food and water from eucalyptus foliage, the quality of which deteriorates during drought (Gordon et al., 1988). Wombat body condition deteriorated simultaneously with food quality and quantity during drought (Gaughwin et al., 1984), blood values changed (Gaughwin & Judson, 1980), and reproduction ceased for several years (Taggart & Temple-Smith, 2008; Woinarski & Burbidge, 2016). This long-term cessation in reproduction might be an adaptive response mechanism to life in habitats that undergo drought periods regularly. At Tswalu, my study aardvarks did not reproduce during the drought years, and while it is possible that aardvarks are capable of delaying reproduction to productive periods, it is more likely that starving aardvarks had a pathological inability to reproduce. However, reproduction of aardvarks in the wild remains to be thoroughly investigated.

6.6 Practical considerations for conservationists

Future ecosystems will likely differ from those we know today in terms of species' composition, competition, and other interactions (discussed in Chapter 1). Due to the elusiveness and nocturnal habits of aardvarks, their actual population size and trends in the wild remain unquantified, and the IUCN currently categorises aardvarks as a species of 'Least Concern' (Taylor & Lehmann, 2015). A recent study suggests that many mammal populations categorised as 'Least Concern' by the IUCN have indeed undergone population declines recently, and that these might be the precursor for large-scale extinctions (Ceballos et al., 2017). Being a keystone species in African habitats, extirpation of aardvarks could influence the entire community of species that are dependent on aardvarks (burrows, feeding opportunities, germination of seed). Conservation of keystone species has been proposed to make entire communities more resilient to the effects of climate change, as in the case of wolves, the top predators serving as controllers of intact communities in Yellowstone National Park, USA (Tylianakis et al., 2008). Numerous tools for species conservation management exist which can be adopted in conservation protocols aimed at coping with expected ecological changes and to ameliorating climate change impacts (Mawdsley et al., 2009; Watson et al., 2012). Examples of such tools include habitat preservation, species translocation, captive breeding, in-situ monitoring, natural resource planning, and improved legislation (Mawdsley et al., 2009). One strategy specifically targeted at species conservation through climate change is managed relocation, also termed assisted colonisation (Hoegh-Guldberg et al., 2008; Seddon, 2010; Lunt et al., 2013). However, imbalances may occur in prioritising conservation of species that are charismatic or have keystone status at the expense of those considered less relevant or popular (Lunt et al., 2013). Moreover, translocation of species bears risks, such as detrimental impacts including disease transmission or a translocated species becoming invasive and displacing resident species (Ricciardi & Simberloff, 2009; Corlett & Westcott, 2013). However, assisted colonisation strategies could be successful if the physiology of species to be translocated is taken into consideration (Tarszisz et al., 2014).

An option that could possibly benefit termites and other herbivores and thus maintain the functionality of ecosystems would be to promote drought-tolerant plant species, notably species of grasses (Craine et al., 2013), in regions expected to become hotter and drier with climate change. Molecular engineering could become an option to enhance the resistance of plants to physical stress such as heat, aridity, and soil salinization (Denby & Gehring, 2005; Ahuja et al., 2010). However, such methods need yet to be developed and successfully implemented.

To date, no effective option seems available for mitigating the negative effects of climate change on aardvarks through resource management. In the case of aardvarks, artificial water sources are of questionable value since aardvarks rarely drink even if water is accessible. Colonies of ants and termites take long to establish, and require vegetation productivity, which will be a limiting factor in future climates. However, southern African farmers have been asked to contribute to the conservation of the ecologically important aardvark by reducing the use of insecticides on their properties to maintain aardvark carrying capacity (Cilliers, 2002). Moreover, when aardvarks are weakened and diurnal during periods of resource-deficiency, they would likely be much more vulnerable to predation pressure, thus one option for aardvark conservation in managed fenced reserved could be to exclude large carnivores.

Under the fatalistic notion that aardvarks might become locally extinct, a pragmatic option could then involve the construction of artificial burrows as thermal refuges for burrow-dependent animals. However, even if used by burrow-dependent species, artificial burrows might reduce the impacts of increased heat load on such species but would not remove the issue of resource depletion. Providing artificial sources of water and food has often been suggested, for example, providing water to koalas (Mella et al., 2017; Reiner, 2017), which are dehydration-sensitive (Gordon et al., 1988), to prevent fatalities during climate change related summer drought and heat waves. However, despite best intentions, artificial provisioning might backfire. The spatial distribution of water in the landscape can determine the landscape use by large herbivores (Smit et al., 2007), which can, in turn, severely impact the vegetation in the proximity of the water source (Landman et al., 2012). Excessive installation of artificial waterpoints can have severe negative impacts. These impacts can include the destabilisation in ecosystem functionality and biodiversity decline as consequences of imbalanced benefits of the water source for herbivores, increased predation pressures, and extensive vegetation degradation (Owen-Smith, 1996). For example, rapid decline of rare antelope species (roan (*Hippotragus equinus*), sable (*Hippotragus niger*), and tsessebe (*Damaliscus lunatus*)) in the northern section of Kruger National Park in South Africa was attributed to the establishment of artificial watering holes, because they were exposed to increasing competition from invading water-dependent herbivore species, followed by increased predation pressure (Harrington et al., 1999). Thus, manipulating ecosystems that are not yet fully understood might lead to unforeseen complications. Indeed, mitigating the effects of global climate change through stringent management of global emissions as advocated by the Intergovernmental Panel on Climate Change since the 1980s (Pachauri et al., 2014) is the best hope for large-scale reduction of survival pressure on species free-living in their natural habitats.

6.7 Conclusion

Nocturnal large mammals and dietary specialists were predicted to be among the first to be affected by rapid climate change (McCain & King, 2014; Pacifici et al., 2017), and indeed, aardvarks will likely be affected by the rapidly increasing heat and aridity over Africa. Aardvarks in the Kalahari depended strongly on the termite *H. mossambicus* for energy and likely also water, and differed in this way from aardvarks in less-arid regions which relied predominantly on ants, and consumed termites mostly to compensate for low ant availability during winter. At Tswalu, compensation for a possible lack of termites did not appear possible (or only insufficiently so) during drought, when termite abundance was likely low due to lack of standing crop. The flexibility in activity patterns (manifesting as diurnal activity, extended active phases, and lower intensity of activity) and body temperature (notably hypothermic heterothermy) during periods of scarcity were not always sufficient to allow for adequate energy savings during resource scarcity. Aardvark mortalities in the Kalahari coincided with drought periods in summer and winter, and surviving aardvarks recovered slowly, over several months. Future increased drought frequency in southern Africa and other, extensive parts of aardvark distribution will likely have severe implications on aardvark survival. Aardvarks in the Kalahari semi-desert present an ideal model to continue to study climate change impacts as they are specialists uniquely positioned at the edge of their 'tolerance' range, and they seldom make use of water sources. Hence, aardvarks are likely one of the first large mammal species in which impacts of climate change could be detected. Using this aardvark study as a case example, research could also focus on other termitivorous animals in the same region to predict how the species composition of an entire community could be transformed under climate change.

Studying a specialist species as the aardvark at the edge of its range provided an excellent model for evaluating the first impacts of climate change on mammals in Africa. My findings indicate aardvark vulnerability to drought in this marginal habitat, where synergistic impacts of starvation and dehydration following summer droughts result in high mortality, and possibly local extinction, as climate change related droughts in the Kalahari become more frequent and intense.

6.8 References

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APPENDIX: ETHICAL CLEARANCE CERTIFICATES

STRICTLY CONFIDENTIAL

ANIMAL ETHICS SCREENING COMMITTEE (AESC)

CLEARANCE CERTIFICATE NO. 2013/29/05

APPLICANT:	Ms NM Weyer
SCHOOL:	Physiology
PROJECT TITLE:	Physiological plasticity of free-living Aardvark (Orysceropus afer) Ground Pangolin (Manis temminckii) and Common Warthog (Phacochoerus africanus) during changes in climate and resource

Number and Species

10 Aardvark
10 Common warthog
10 Ground pangolin

Approval was given for to the use of animals for the project described above at an AESC meeting held on 28/05/2013. This approval remains valid until 16/07/2015.

The use of these animals is subject to AESC guidelines for the use and care of animals, is limited to the procedures described in the application form and is subject to any additional conditions listed below:

None.

Signed: ______________________ (Chairperson, AESC) Date: 22/7/2013

I am satisfied that the persons listed in this application are competent to perform the procedures therein, in terms of Section 23 (1) (c) of the Veterinary and Para-Veterinary Professions Act (19 of 1982)

Signed: ______________________ (Registered Veterinarian) Date: 23/7/2013

cc: Supervisor: Prof A Fuller
Director: CAS

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