The activity and foraging patterns of the western rock elephant shrew (*Elephantulus rupestris)*

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By

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Preface

The experimental work described in this thesis was carried out at Farm Wellington in the Eastern Cape, South Africa, between March 2021 and May 2022. The study was conducted under the supervision of Professor Ben Smit.

This study presents original work by the author and has not been submitted in any other form for any other degree or diploma to any other university. Where use has been made of the work of others, it has been duly acknowledged in the text.

All procedures related to the use of animals in this study was approved by the Animal Ethics Committee of Rhodes University (ethics no. 2022-4873-6908).

Abstract

The increase, and prolonged periods, of high ambient temperatures are cause for concern for small mammals living in arid areas of Southern Africa. In this study, I aimed to determine the effect of high environmental temperatures on the activity, body temperature maintenance and foraging behaviour in a population of Western rock elephant shrew, *Elephantulus rupestris*, in the Eastern Cape, South Africa. I found that *E. rupestris* maintained stable body temperatures (T_b = 37.31 °C ± 0.64) over a range of environmental temperatures (T_{air} = 5° to 33.9 °C), indicating their ability to remain normothermic during the heat of the day. Under cool, mild and hot air temperatures, *E. rupestris* were predominantly active in the morning and night, being the least active during midday. This shift in activity time, known as polyphasic activity, is common amongst Macroscelidea species and is a mechanism for escaping thermal extremes. To determine the effect of temperature on foraging behaviour, I ran giving-up density (GUD) experiments on *E. rupestris* under a range of environmental conditions. GUD experiments yielded no conclusive results as animals did not show a significant preference for foraging under certain thermal conditions, and rather foraged under a variety of air temperatures. Overall, *E. rupestris* showed risk adverse behaviour, trading-off thermoregulation with foraging and activity for self-preservation during hot periods of the day.

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After a lengthy and challenging process, such as an MSc, it is only likely that I will have multiple parties to thank for their help and contribution which has gotten me this far. I would like to start out thanking Wimpie Bosch, the owner of Farm Wellington, on which my study was carried out. Thank you for permitting me to stay in your house and run experiments for lengthy periods of time on your land. Thank you for keeping me company on the days that you were around and always offering good words of advice. I also owe a few thanks to the staff on the farm for the help in organising wheelbarrows and keys for transporting heavy equipment.

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I owe an especially big thank you to Gary Kyle Nicolau, my partner, for his continued support and help throughout this MSc process. Not only has he had to deal with my

fluctuating stress levels and absence while in the field, but he has also had to endure the hard task of helping me move very heavy equipment across multiple sites. I am talking 20kg batteries, solar panels and lengths of receiver cord – all of which I struggle to even lift. Thank you for staying on the farm with me, helping me set up traps and just being the best support system a girl could ask for. I appreciate your contribution in helping me get this far, and I am very grateful to have you as such an invested partner. I cannot wait to return the favour when you embark on your own MSc journey.

Although I did not get to share my fieldwork experience with many family members, I still have my mom and dad to thank. They pushed me from a young age to persevere in sports and academics, teaching me the values of teamwork and education. Mom, thank you for being my biggest supporter throughout my schooling career. You were the one that always pushed me to do better and aim higher. If it wasn’t for your persistence I don’t think I would have made it into tertiary education. I doubt I would be the persistent and committed person I am today without you, so thank you Mom. Dad, I owe you quite a big thank you for instilling your love for nature and animals in me. From a young age my dad would walk me to school, teaching me about all the trees and birds that we saw along the way. You sparked an interest in me that I have carried into a career and hope to spend the rest of my life pursuing. I hope in the future you will be able to help me in the field and let me teach you that a marsupial is in fact, not a rat.

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Table of Contents

Introduction

Global change

Climate has the potential to affect living organisms in multiple capacities; including yet not limited to, their fitness, distribution, phenology, and physiology (Parmesan and Yohe 2003; Humphries et al. 2002; Boyles et al. 2011; Moses et al. 2012). Climate change has become an increasingly pressing issue, causing extreme fluctuations in weather events, with a dramatic increase in the duration, frequency and intensity predicted of heatwaves, drought, and flooding (Meehl and Tabaldi 2004; Welbergen et al. 2008; Buchholz et al. 2019). Extreme weather events threaten many species, as the rate of climate change is much faster than that of an animals' physiological ability to adjust, or to adequately disperse to areas with more suitable conditions (Scheffers et al. 2014). The most prevalent effects of climate change are increasing environmental temperatures, which are fluctuating and rising at a faster than natural rate (IPCC 2007), thus increasing the thermal stress experienced by organisms (Terrien et al. 2011; Bondarenco et al. 2014; Scheffers et al. 2014).

The extent to which organisms will be affected are dependent on an individual or population's ability to respond and adapt (Visser 2008; Williams et al. 2008). Thus, the interspecific effects will differ, as some species are more adaptable than others (Beever et al. 2017). A species' vulnerability to climate change is complex, dependant on multiple variables, and includes the alterations that climate change has on species' interactions within an ecosystem (Creel et al. 2016). Adapting to change requires either a physiological or behavioural response, or both (Hetem et al. 2014). Organisms that exhibit behavioural flexibility—having the ability to alter behaviour in response to environmental stimuli (Hadfield and Strathmann 1996)—are likely to be less effected by climate change as they have the capacity to mitigate the negative aspects associated with a warming world (Van Buskirk 2012; Hetem et al. 2014; Hall and Chalfoun 2018). Behaviour is seen as one of the most important responses to change as it tends to yield the shortest reaction time (Huey et al. 2012; Beever et al. 2017; Buchholz et al. 2019), thus allowing organisms to adapt faster.

Decision making – costs and benefits

When there is a choice, a decision must be made. Animals faced with environmental or intrinsic stressors will need to decide on the best route for mediation, by weighing the costs and benefits of each option (Lima and Dill 1990; Walton et al. 2006; Dylda and Wang 2022). When making a decision, an animal should almost always choose the option where the benefits outweigh the costs to achieve a positive outcome that maximises fitness and survival (McFarland 1977; Ha 2010). Although a choice may be beneficial overall, costs can be incurred simultaneously, and the benefit will be traded off against the costs (Ha 2010). The cost-benefit analysis is used to model the optimal cost to benefit ratio, stating that individuals should maximise the benefit of a behaviour while also minimising the costs associated with such behaviour (Ha 2010).

An animals time and energy are important “currencies” playing a role in their fitness and survival, and if used efficiently, they are a primary criterion for natural selection (Ydenberg et al. 1994; Speakman 1999). These currencies are used to evaluate the costs and benefits of behavioural traits (Piersma et al. 2003). The energy balance of individuals is ultimately governed by foraging decisions and influences the animals' reproductive success, body mass and overall survival (Searle et al. 2006). Therefore, an animal should choose the feeding strategy that maximises the net total energy gain (Houston 1987). Optimal decision making is often constrained by environmental and intrinsic factors, such as weather, resource fluctuation, morphology, competition and predation risk (Blumstein and Bouskila 1996; Abu Baker and Brown 2010; Ha 2010). Changes in environmental conditions can alter the availability of resources and therefore the costs involved with acquiring them (Sotillo et al. 2019).

Temperature as an important driver of decisions

Endothermic animals, like mammals and birds, have the ability to maintain a stable and constant body temperature (T_b), through metabolic heat production, over a range of environmental temperatures (T_e) (Rezende and Bacigalupe 2015). Temperature shapes the landscape and the ecological processes on multiple scales across space and time (Carroll et al. 2016), making it an invaluable factor to study and understand. A literature review by Beever et al. 2017 identified temperature as the aspect of climate most responsible for behavioural changes in animals. Exposure to extreme air temperatures (T_{air}), both low and high, is stressful for animals as it places them at risk of hypo- or hyperthermia (Terrien et al. 2011). When air temperatures (T_{air}) are extreme, surpassing an animals thermal neutral zone (the range of environmental temperatures where metabolic heat production is minimal) (TNZ), endotherms will respond by either increasing their thermoregulatory effort or by increasing their body temperature (T_b), in an effort to maintain homeostasis within a preferred range while simultaneously avoiding hyperthermia (Boyles et al. 2011). Animals such as certain birds and antelope are known to raise their T_b when active and foraging (Smit et al. 2013), allowing for passive heat loss (Williams and Tieleman 2005), while reducing the demand for evaporative cooling (Gerson et al. 2019). Alternatively, animals' experiencing $T_b > T_{air}$ will likely use evaporative cooling as a thermoregulatory mechanism (Mitchell et al. 2018; Fuller et al. 2014, 2021). Maintaining a stable T_b is essential for an endothermic animal's survival (Cunningham et al. 2021). Endotherms can behaviourally and physiologically adjust/maintain their body temperature within a safe limit by reducing activity, shade seeking or evaporative cooling (Wolf 2000; du Plessis et al. 2012; Cunningham et al. 2013).

Heat exposure is costly to animals, as environmental temperature is the primary constraint on an organism's time and energy budget (Bozinovic et al. 2000; Bacigalupe et al. 2003; Boyles et al. 2011). By using behavioural thermoregulatory mechanisms such as shade seeking and foregoing activity, animals reduce the more costly route of maintaining a stable T_b through physiological thermoregulation (Briscoe et al. 2014; Cunningham et al. 2021).

Behavioural thermoregulation requires less energy (and body water) than physiological thermoregulation, and can be sustained for extended periods (Maloney et al. 2005). Even though behavioural thermoregulation is less costly, it still comes with incurred costs in the form of missed opportunities. These missed opportunities are often important activities such as foraging, provisioning young, and mating (Mason et al. 2017; Cunningham et al. 2021), and can lead to decreased fitness (Cunningham et al. 2013; van de Ven et al. 2019).

Over prolonged periods of chronic exposure to extreme heat, animals are likely to incur sublethal fitness costs due to thermoregulatory and foraging trade-offs (du Plessis et al. 2012, van de Ven et al. 2019). Exposure to environmental temperatures $> T_b$ are also likely to result in a decline in an animal's overall performance (Cunningham et al. 2021), as the time that environmental conditions are best suited to essential activities, such as foraging, are reduced (Hall and Chalfoun 2018). The increase in temperature, coupled with fluctuations in other environmental variables (e.g. humidity), can compromise the reproductive and additional productive parameters of animals, such as fertility, nutrient intake, and weight gain (Sanin et al. 2015).

Giving- up density

Giving-up density (GUD) is a way to quantify and understand foraging decisions and outcomes of animals based on a selection of external pressures and the use of artificial feeding patches (Brown 1988). Giving-up density can be measured by the amount of food remaining after a foraging bout, and indicates the perceived risks, costs, and benefits, of foraging at a specific point (Brown 1988; Brown et al. 1997; Yahnke et al. 2020). An animal is expected to quit foraging or “give-up” when the cost of foraging start to equal the benefits (Carthey and Banks 2015). The outcomes of GUD, which are a measure of feeding intensity, are classified as high or low, with low indicating a low perceived risk and cost of foraging, whereas high indicates a high perceived risk and costs of foraging (Bedoya-Perez et al. 2013). High GUD’s indicate foragers quit the patch and left a large proportion of the food reward behind (low feeding intensity), and low GUD’s indicate that foragers exploited a patch and consumed a large portion of the food reward (high feeding intensity).

The GUD framework includes an equation to calculate the costs of foraging (Brown 1988), and includes harvest rate (H), predation risk (P), thermoregulatory costs (C), and missed opportunities (MOC):

$$H = C + P + MOC$$

There are several aspects of a forager that need to be taken into consideration before GUD experiments can take place. These aspects include food densities, patch location, resource availability, and forager state (Nguyen 2004; Cozzoli et al. 2018). The patch is an integral part of GUD experiments, as it can have an impact on foraging and a forager’s perception, based on location (exposed or sheltered), substrate used (Bedoya-Perez et al. 2013), and food type provided (Brown 2000; Abu Baker and Brown 2011). Patches that are open or exposed, may yield higher GUD’s as foragers are aware of the heightened predation risk due to less cover (Brown et al. 1994; Howe and Brown 1999; Druce et al. 2006, 2009; Abu Baker and Brown 2010), while patches that are covered or sheltered may yield lower

GUD’s as foragers feel a lower predation risk (Oyugi and Brown 2003; Brown and Kotler 2004; Abu Baker and Brown 2010). Patches with harder to move substrate may also yield higher GUD’s based on the increase amount of effort required to acquire a small reward - cost outweighs benefit, while patches with easier to move substrate may yield lower GUD’s as less effort is required to acquire a small reward—benefits outweigh costs (Kotler et al. 2001).

The substrate used within a patch should be one that requires work to be done to receive a reward, but it should also not be too easy nor too hard to move by the forager. The artificial feeding patch should be set up in a way that the food is evenly distributed within the substrate and that as the forager depletes the food reward, the reward thereafter becomes harder to find (Carthey and Banks 2015). The nutrient content or quality of food offered in the feeding patches is an important factor that contributes to a foragers perception of the patch. Nutrient rich foods will yield lower GUD’s, and nutrient poor food will yield higher GUD’s (Kotler et al. 1994; Brown and Morgan 1995). It is, therefore, important to understand a species' food preference before setting up GUD experiments, as low reward food sources may yield poor results.

The energetic state of a forager will determine the individuals perception of the patch (Sánchez et al. 2008; Bedoya-Perez et al. 2013), with state pertaining to an animal’s hunger, hydration and overall health. Foragers that have already consumed food will not perceive the patch in the same way that a hungry forager in a poor energetic state would. A forager’s energetic state would also influence the amount of risk they would be willing to take to forage, based on need, and therefore may lead to a trade-off between foraging and predation to avoid starvation (Brown 1992; Bedoya-Perez et al. 2013). A forager’s energetic state can also include size, sex and age, and the needs that come with them, such as growth rate, resource requirements and offspring provisioning (Ritchie 1998; Kotler et al. 2004; Randall et al. 2002; Cozzoli et al. 2018).

Even though giving-up density studies are a relatively new methodological framework, they prove to be a plausible way in which to better understand different components contributing to an animal’s overall foraging behaviour and their decision making process (Bedoya-Perez et al. 2013).

Arid environments as a model

The arid environments of South Africa, such as the Nama-Karoo, are characterised by large seasonal fluctuations in temperatures, with hot summers and cool dry winters (Mucina et al. 2006). This region experiences low rainfall, and droughts can be unpredictable and prolonged (Booysen and Rowswell 1983). The harsh temperatures, often exceeding 40 °C (Mucina et al. 2006), coupled with unpredictable rainfall, make water and food resources a scarce commodity. The conditions of arid regions impose great costs and energetic demands on small endotherms, making them ideal areas to study heat related stress, activity and decision making in animals.

Animals living in arid environments are already exposed to high environmental temperatures, low water availability, and reduced food resources, while living at the edge of their physiological tolerances, making them especially vulnerable to further warming as a result of climate change (Williams and Tieleman 2005; Speakman and Król 2010; Moses et al. 2012). The harsh conditions of this environment, coupled with further increasing temperatures, leave the organisms within at risk of lethal hyperthermia and dehydration (Cunningham et al. 2013). To avoid such risks, animals will have to use thermoregulatory mechanisms, and in doing so, trade-off this self-preservation activity with other important daily activities (du Plessis et al. 2012).

Many animals living in arid regions commonly have to trade-off self-preservation with daily activities, due to exposure to high environmental temperatures and prolonged heatwaves (du Plessis et al. 2012; McKechnie and Wolf 2019). Studies have shown that birds living in the Kalahari Desert of southern Africa that were exposed to high temperature extremes, use behavioural and physiological thermoregulation to avoid lethal hyperthermia (du Plessis et al. 2012; Whitfield et al. 2015; Smit et al. 2016; Conradie et al. 2019; van de Ven et al. 2019). The time animals spend thermoregulating or defending their T_b, results in time lost for other day-to-day activities, such as foraging, mating and offspring provisioning (Bacigalupe et al. 2003; Cunningham et al. 2013; Mason et al. 2017). Animals that reduce activity or seek shelter to avoid lethal hyperthermia, are trading-off thermoregulation with foraging. Without foraging and adequate resource acquisition, animals are likely to lose body mass and condition (du Plessis et al. 2012; van de Ven et al. 2019), and will result in decreased reproductive fitness (Cunningham et al. 2013; van de Ven et al. 2020).

Elephant shrews as model species

Elephant shrews (also known as sengis) are small mammals belonging to the group Afrotheria, endemic to the African continent (Corbet and Hanks 1968; Springer et al. 1997). They occupy a variety of habitats, including rocky outcrops, deserts, mesic forests and savanna, with the smaller species (Macroscelidinae; including genera *Elephantulus*, *Galegeeska*, *Macroscelides*, *Petrodromus and Petrosaltator*) occupying open semi-arid to arid habitats (Rathbun 1979), and larger ones (Rhynchocyoninae: *Rhynchocyon*) occupying forests (Kingdon 1974; Perrin 1995; Heritage et al. 2020). These small mammals display omnivorous diets, feeding on both plant matter and insects (Smithers 1983; McNab 1984), with the ability for dietary shifts based on resource availability and seasonality (Kerley 1995; Lawes and Perrin 1995). A small body size also offers the opportunity for additional thermoregulatory opportunities through the use of microsites such as burrows, rock crevices and patches of shade (Lawes and Perrin 1995; McKechnie and Wolf 2010; Cunningham et al. 2021).

Due to their flexibility, elephant shrews are suitable model species for understanding the effects of temperature on foraging and activity. They display the ability to (1) maintain a stable body temperature over extreme environmental fluctuations (Perrin 1995); (2) reduce their metabolic rate and body temperature through the use of torpor (Lovegrove et al. 1999, 2001); (3) shift their diet based on season and resource abundance (Kerley 1995; Lawes and Perrin 1995); and, (4) be active during both the day and night through polyphasic activity patterns (Woodall et al. 1989; Roxburgh and Perrin 1994). Due to their plasticity in both behaviour and physiology, the decisions that they make are of great interest and importance in understanding responses to environmental stressors.

In a laboratory-based study by Lawes and Perrin (1995), on *Macroscelides proboscideus*, the authors aimed to investigate and determine the effect of food supply on foraging behaviour sensitivity. This study found that *Macroscelides proboscideus* displayed risk-averse foraging behaviour when deprived of food and exposed to mild temperatures, choosing to visit more reliable food patches as opposed to variable ones. Additionally, food deprivation resulted in individuals losing weight, reiterating that small endotherms have a limited capacity to deal with energy shortfalls (Lawes and Perrin 1995).

Previous studies have focused on the effects that lower temperatures have on elephant shrews and their ability to enter into torpor (Lovegrove et al. 1999, 2001$_a$; Oelkrug et al. 2012). However, in my study, I will focus on the effects of high environmental temperatures on physiological and behavioural decisions made by the Western rock elephant shrew (*Elephantulus rupestris*). With risk-averse behaviour being found in *Macroscelides proboscideus* (Lawes and Perrin 1995), it is likely that animals experiencing higher temperatures over longer periods may experience energy shortfalls while trading-off foraging with thermoregulation. Thus, it is likely that animals experiencing hotter conditions (and potential heat stress) may expand or shift their activity and foraging times to compensate for such shortfalls and forage at reliable patches rather than variable ones.

Aims, objectives and hypotheses

In this study, I aimed to determine the effects of temperature on the foraging behaviour of *Elephantulus rupestris* living in an arid landscape.

(1) Body temperature

The first objective of this study was to determine the relationship between air temperature and body temperature. I aimed to determine if the body temperature of *Elephantulus rupestris* would increase when foraging on hot days, similar to patterns of body temperature regulation observed in birds when active during the heat of the day (Smit et al. 2013; Thompson et al. 2018). An increase in T_b will represent a physiological trade-off when foraging under hot conditions. Alternatively, a reduction in activity and foraging on hot days will result in no increase in T_b, allowing animals to avoid the risk of hyperthermia (Wolf 2000).

I predicted that *E. rupestris* would exhibit heterothermic body temperatures, that remain relatively stable across average environmental air temperatures, and drop slightly when air temperatures are low, given their tendency to use torpor (Boyles et al. 2011; Oelkrug et al. 2012). Under hotter conditions, body temperatures will likely fluctuate as activity under higher T_{air} is metabolically costly, and animals may show bouts of hyperthermia, as observed in birds foraging in the heat, and in *E. rupestris* exposed to the heat under laboratory conditions (Chalwin-Milton et al. 2022, unpublished data).

(2) Visitation Activity

The second objective of my study was to determine the effect of temperature on the visitation to stations of *E. rupestris*, by using camera traps to monitor their activity around feeding stations over time, under an array of environmental conditions (maximum daily temperatures). If activity patterns around stations are structured around the thermal environment, I can assess if the species is choosing to avoid certain extremes and actively trading-off activity/foraging with avoiding thermoregulatory stress.

I predicted that *E. rupestris* would reduce or alter visitation rates to feeding stations under high air temperatures, avoiding heat stress during the hottest parts of the day and compensating for lost time by increasing visitation during periods of cooler air temperatures. Air temperatures usually reach their highest at midday, however high temperatures exceeding normothermic body temperatures of elephant shrews (> 37 °C) are not restricted to this period, and those recorded outside of midday are just as likely to influence the activity of *E. rupestris*. I predicted that *E. rupestris* would alter or structure their visitation times around the thermal environment.

(3) Foraging/Giving-up Densities

The third objective of the study was to determine the effect of temperature on the foraging decision outcomes of *E. rupestris* by using GUD experiments, where environmental factors (air temperature) are the main changing variable. These experiments aimed to establish if thermoregulatory and foraging trade-offs are likely to occur in a natural wild population of *E. rupestris*. By identifying such trade-offs, I could subsequently predict the effect of future environmental temperature fluctuations on the species foraging behaviour. Thus allowing for the foraging behaviour of *E. rupestris* under thermal stress to be understood, and for understanding the implications of climate change on small arid-zone mammals.

I predicted that *E. rupestris* foraging under higher air temperatures would yield higher GUD’s as a result of self-preservation and forgoing foraging in an attempt to avoid heat stress. *Elephantulus rupestris* would yield lower GUD’s under cooler conditions when thermoregulatory costs are at their lowest, allowing them to maintain a stable T_b while acquiring a food reward.

Methods

Study site

The study was conducted on Wellington private livestock farm, 20 km west-northwest of Riebeek East, Eastern Cape, South Africa (33,15833° S, 25,95971° E), at an elevation of ~600 m above sea level. The site lies within the Nama-Karoo biome and is primarily composed of Albany broken veld vegetation type (NKI 4 - SANBI Vegetation Map 2018). The Albany broken veld is characterised by hills and lowland mountain ridges with scattered low trees, dwarf shrubs and grasses (Mucina et al. 2006). The vegetation at the site is presently dominated by succulent species (family Aizoaceae and genus *Aloe*) and a diversity of mixed shrubs and small trees (*Vachelia karoo, Papea capensis* and *Boscia oleoides*) that can tolerate arid conditions. This area has a hot and dry climate with seasonal extremes of very hot summers and cold winters (irregular frost), and irregular rainfall throughout the year, with slight peaks in the Austral summer and autumn (Mucina et al. 2006). Since 2015, the site has experienced a drought with lower than average annual rainfall, of less than 300 mm per annum (personal communication with W. Bosch, farm owner), instead of the usual annual 400-500 mm of rainfall received by the area (Fabricius et al. 2003; Clarke et al. 2012). The experiments were conducted along a single, large rocky sandstone/quartzite outcrop (3 x 1 km) on the western boundary of the farm, where the habitat was predominantly rocky with patches of shrubs, grasses, and aloes.

Study species

The Western rock elephant shrew *Elephantulus rupestris* is a small rupicolous mammal of the Afrotheria group (Smit et al. 2008), with a widespread distribution through western South Africa, western parts of Namibia, and southern parts of Angola and Botswana (Smithers 1971; Corbet and Hanks 1968; Rathbun 2005). *Elephantulus rupestris* is an arid-zone species occupying multiple habitat types, including arid Savanna, and shrublands on rocky substrates (Smit et al. 2010). They are active during the day and night (Woodall et al. 1989) and display an omnivorous diet of invertebrates and plant materials (Skinner and Chimimba 2005; Kingdon 2015), showing flexibility in both activity and foraging structure.

Study set up

Initially, seven camera traps (Spypoint, SolarDark) were placed at ground level, along the length of the study site, with a similar distance between them (70 to 100 m), to record the presence and activity of the target species *Elephantulus rupestris*. In the first three months that camera traps were set out, they were baited with peanut butter and rolled oat balls and set to record five photos (five seconds apart) when triggered, with a ten minute delay time between triggers. Camera trigger sensors were set to “optimal” to ensure minimal activity was missed due to missed triggers, and each photo was marked with a date, time and temperature. Camera locations were changed every week for four weeks, allowing the sites with the highest recorded *E. rupestris* activity to be identified.

Once sites with regular activity were identified, I selected four sites with the highest activity to be the sites for feeding stations and giving-up density (GUD) experiments. These sites were equipped with a permanently placed camera trap, a feeding shelter (37.5 l x 24 b x 24.5 h cm) and a circular feeding tray (11 h x 23 cm diameter). Feeding shelters were specifically made for GUD experiments, to provide both shelter (lower perceived risk of predation) and an additional source of heat/insulation at the site. These shelters, subsequently referred to as feeding stations, had four wooden legs, a tin roof and were each equipped with a feeding tray. The tin roof of the structures were intended to increase the temperature at the feeding stations; further details on the feeding stations can be found in the giving-up density section below. The remaining cameras were placed at additional sites, known to be used only occasionally by *E. rupestris*, to record general activity patterns.

Habituating *E. rupestris* to feeding stations was essential for GUD experiments and started once the four sites had been selected, by providing three bait balls (rolled balls consisting of oats, peanut butter, and wet cat food) daily to the feeding stations for three to four weeks. By providing food continuously at repeated sites, *E. rupestris* learnt to associate these sites with food, and visitation became more frequent.

Weather

The air temperature at the study site was recorded at 30 minute intervals using a portable weather station (Davis Wireless Vantage Pro 2), placed 1.5 m above ground within the study site.

Body temperature

Trapping of *E. rupestris* was carried out between August and December 2021, for four to five consecutive days at a time, using baited (rolled oats, peanut butter and wet cat food) Sherman traps (23.5 x 9 x 7.5 cm). Initially, traps were set up throughout the study site for a month, and thereafter I trapped in targeted areas where *E. rupestris* appeared to be most active (as established through camera trapping). Traps were set in the late afternoon/evening and were checked just after sunrise the following day. Trapped individuals were transported to a veterinary facility (Cole Veterinary Clinic, Makhanda, Eastern Cape) where they were anaesthetised and tagged. Animals were transported in the cabin of a vehicle in cages (33.5 x 22 x 19 cm) lined with pine shavings, and with access to water ad libitum.

Body temperature was measured using passive integrated transponders (PIT), otherwise known as PIT tags, implanted into the peritoneal cavity of the animals. Biotherm PIT tags were chosen to avoid the implanted device exceeding 5% of the animal's body mass (Aldridge and Brigham 1988), as they are lightweight and small in both size and volume, which is essential as *E. rupestris* is a small and lightweight mammal. PIT tags were a better option than iButtons for what I wanted to measure ~ body temperature associated with foraging decisions as an instantaneous measurement rather than continuous body temperature over time. PIT tags were also chosen over iButtons due to the longevity of the study, as PIT tags can record data over an indefinite period (years) while iButtons record high resolution data over a shorted period (months) before the memory is full, and iButtons need to be retrieved from the animal.

At the veterinary facility, animals were initially anaesthetised using a facial mask with 5% isoflurane which was subsequently maintained at 2.5% until the procedure was complete (Boyles et al. 2012 $_{a,b}$). While anaesthetised, a sterile PIT tag (BioTherm13 13mm Thermal FDX-B temperature sensing PIT tag , glass-encased, 13 mm x 2.3 mm ~ 0.1 g) was injected into the peritoneal cavity using a preloaded 12 gauge sterile syringe and needle. The incision from the syringe was sealed using Surgibon Wound Glue (SMI). Tagged individuals were monitored and checked before being released at the site of capture. During the monitoring period the animals remained in transportation cages, where mealworms and water were provided. Cages were covered with a lightweight cloth and placed in a cool area to avoid causing the animals additional stress. The total time the animals remained in captivity after capture, surgical procedure and monitoring was less than 24 hours for each individual.

Animals were captured and tagged under the permit – Addendum permit number HO/RSH/09/2021, issued by the Department of Environmental Affairs of the Eastern Cape. Research ethics was approved by the Rhodes University Animal Research Ethics Committee (protocol 2022-4873-6908).

To measure body temperature associated with foraging, I placed two 9 m cord antenna system ISI1001 PIT tag readers (Biomark, Biose, Idaho, USA), powered by two solar panels (DESERV C12 50 High Performance Multicrystalline Modules, RenewSys) each, at two feeding stations to record individuals identity and body temperature while visiting feeding stations. Since I only had access to two readers, I alternated the reader placement between the four feeding stations, rotating them based on activity levels and ensuring each of the four stations captured body temperature data while animals foraged. Stations with *E. rupestris* visiting every day (classed as high activity) were prioritised with PIT-tag readers over stations with infrequent activity, while also ensuring individual *E. rupestris* occupying different territories were recorded. Alternations occurred roughly every three to four weeks.

Visitation Activity

Seven camera traps were set up to record the presence and activity (visitations to stations) of the target species *E. rupestris* across the study site. Once key sites of high activity had been identified, based on the frequency of visits by *E. rupestris*, four camera traps remained at fixed sites—GUD feeding stations for the remainder of the study period. The cameras at the feeding stations were set to record pictures and 60 second videos, for 24 h a day. The remaining traps were interchanged between sites of suitable habitat and known *E. rupestris* occurrence for the duration of the study.

The photos recorded by cameras containing *E. rupestris* were recorded with the site number, time, date, and temperature. From these images, the general activity patterns as a function of time of day could be recorded. I watched all videos and recorded the behaviours observed, behaviours were categorised into “active” – if the animal was moving through the area, and “foraging” – if the animal entered the feeding station or took food reward items. Initially, I wanted to determine the time (duration) that *E. rupestris* individuals spent at a station, however, due to their sporadic behaviour (frequent coming and going in and out of frame) this proved difficult to quantify accurately. Proportion of visits to feeding station was calculated by the amount of visits at each individual station divided by the amount of visits to all stations collectively.

Giving-up Densities

To determine the giving-up density of *E. rupestris*, I selected four sites for GUD experiments. Site selection was based on *E. rupestris* activity and habituation to the feeding stations. Each site was equipped with a feeding station, comprising of a circular feeding tray (11 cm x 23 cm) placed on the ground, a camera trap (Spypoint – SolarDark), and a metal “afdak” shelter (roofed structure – see Fig. 1).

Figure 1. An afdak – a metal roofed structure to radiate and increase the environmental temperature of the feeding station, whilst providing shelter to foragers from aerial predators.

All stations were located at least 1.5 m away from the nearest refugia (boulders) and were placed in open and exposed areas of sandstone rock. Feeding trays were filled with three handfuls of sawdust, or until the entire bottom of the tray was covered, with seven mealworms as a food reward. Trays with mealworms were placed out during midday (during the hottest hours), between 10:00 and 17:30, and the remaining mealworms were removed and counted at the end of the experimental period. During the experimental period, remote sensing methods such as camera traps and PIT tag readers were set to record individual activity and body temperature data. Camera traps were set to record a single photo and a 60 second video when triggered, allowing for the identification of foragers at each station, without an observer having to be physically present, saving time and allowing for later analysis of behaviour (Abu Baker and Brown 2011; Bedoya-Perez et al. 2013; Morris et al. 2015). PIT tag reader cords were looped around the feeding station, allowing the tagged animal's body temperature and identity to be recorded when coming in and out of the foraging area.

To independently determine the effect of temperature on foraging decision-making, using the giving-up density framework, all additional foraging costs (MOC and P) had to be kept constant. To attempt to account for missed opportunity costs (MOC) and predation risk (P), all feeding stations and trays had to be identical (Orrock and Danielson 2009; Abu Baker and Brown 2014). I therefore placed all four feeding stations in open habitats, placed equidistant to the closest refugia, covered by a metal structure (afdak), and all contained the same food type - mealworms. Metal roofed structures were used to cover feeding trays for two reasons (1) to provide the foraging animal with shelter from aerial predators, thereby reducing perceived predation risk (Morris et al. 2015), and (2) to ensure that the feeding station was nevertheless in a warm micro-habitat environment (given that metal radiates heat when exposed to solar radiation) so that foraging may be associated with heat exposure. By making all patches (feeding stations and trays) identical, I was able to control for missed opportunity costs and predation risk, therefore allowing myself to focus on the sole effect of temperature on GUD and harvest rate.

To determine the effect of air temperature and to test the hypothesis that high air temperatures would lead to trade-offs between thermoregulation and foraging in *E. rupestris,* I manipulated the temperatures at which experiments were carried out, by selecting the experimental days based on weather predictions and forecasts. Using forecasts allowed me to choose which conditions to run experiments under, and ensure that a range of maximum temperatures were included. The weather conditions of each day were used as indicators of foraging risk (Orrock and Danielson 2009) across all four sites. Additional weather data such as cloud cover, precipitation and dew point temperature (to understand the effects of humidity) were also recorded over the experimental period (specifically the days on which

GUD experiments were run) to determine if they played a role in the animals perception of the overall foraging conditions. Dew point temperature was recorded by the same weather station (Davis Wireless Vantage Pro 2) that recorded air temperature, while cloud cover and precipitation were categorical measurements recorded by myself on the day of each experiment. Precipitation was categorised into four categories (no rain, drizzle, rain, and thundershowers), and cloud cover was categorised into three categories (clear, partly cloudy, and overcast).

Data Analysis

Body temperature

To understand the effect of environmental air temperature on *E. rupestris* core body temperature, I first modelled air temperature (average and then maximum) against body temperatures while visiting feeding stations using a general linear mixed effects model (GLM) with site and individual ID as random effects, using the nlme package (v3.1-160 Pinheiro et al. 2022) in the R statistical environment, version 4.2.1 (R Core Team 2022).

Visitation Activity

Out of the seven camera traps, four cameras were placed at feeding stations and recorded approximately nine months of data, while the remaining three cameras recorded three-four months of data, respectively. The three cameras not placed at feeding sites recorded fewer data due to camera and memory card malfunction.

Initially, the overall frequency of visitation rates over the 24h daily period was examined visually, to determine if there were visible patterns to specific hours. I subsequently analysed daily visitation patterns by dividing the 24h period into four time categories, including morning, midday, afternoon and night. I categorised all photos captured between 5:00 and 10:00 as *morning*, between 10:01 and 16:00 as *midday*, between 16:01 and 20:00 as *afternoon* and between 20:01 and 4:59 as *night*. These time categories were based on light intensity of each period.

To determine the visitation patterns of *E. rupestris*, I recorded the number of visits to each feeding station on each day during each time category. Additionally, I created a datasheet that recorded the number of visits or absence of visits for each station and time of day category (morning, midday, afternoon and night), where the absence of visits were recorded as zeros. I performed Poisson, Zero-inflated Poisson and Negative binomial general linear models (GLMs) on the number of visits with maximum temperature and time category as fixed factors, and site as a random factor. These models were selected to account for excessive zeros within the count data and used the packages “ggplot2” (v3.3.6 Wickham 2016), “sandwich” (v3.0-2 Zeilies et al. 2020), “msm” (v1.6.9 Jackson 2011), and “Mass” (v7.3-57 Venables and Ripley 2002. From the full models described above, negative binomial GLMs showed the best fit test for the data based on AIC values. Statistical analyses were performed in the R statistical environment, version 4.2.1 (R Core Team 2022), using the R Studio platform (R Studio Team 2022).

Negative binomial mixed effect models were run using the “lme4” (v1.1-30 Bates et al. 2015) package, to determine which environmental variable (maximum air temperature, time of day and temperature category, or combination of these variables were influencing visitation). I categorised all temperatures between 1 and 15 °C as *cool*, between 15.1 and 25 °C as *mild*, and > 25 °C as *hot*. The “car” (v3.1-0 Fox and Weisberg 2019), “Mass” (v7.3-57 Venables and Ripley 2002), and “pscl” (v1.5.5 Zeileis et al. 2008) were additional supporting packages used for obtaining test statistics and AIC values. Initial models with the lowest AIC values (negative binomial mixed models) were selected to run further statistics, removing temperature category as a variable from further models. Temperature category was removed as exact temperature points yielded more accurate results in AIC values. I tested the effect of time of day (as a categorical factor) and maximum temperature (on each respective day) as fixed effects on the number and proportion of visits of *E. rupestris* to feeding stations, including site as a random effect. The proportion of visits were calculated by dividing the number of visits to a specific sites or at a specific time of day, by the overall visits to all sites or across all times of day. Overdispersal of the data, if found, was accounted for by adding an extra random variable (in this case feeding station) (Harrison 2014). Overdispersal was not a prevalent issue, however, it needed to be corrected for in two of the models. If any significance was found, a Multiple Comparison of Means *Post hoc* test (Tukey's Contrasts for mixed effect models) was run on the models including categorical fixed factors (i.e. time of day where applicable) to determine where significant differences occurred, using the package "multcomp" (Hothorn et al. 2008) and "mvtnorm" (Genz et al. 2020).

Giving-Up Density

To determine the effect of temperature on giving-up density in *E. rupestris*, a linear mixed effect model was used to compare GUD's values under cool, mild and hot air temperatures, with the repeated measure of "sampling day'' within "sites" as random effects. I categorised all temperatures between 13 and 19.9 °C *as cool*, between 20 and 25.9 °C *as mild* and > 26 °C *as hot*. The temperature category as a factor was later excluded based on AIC values. The temperature categories differed between GUD and visitation activity analyses based on the number of individual temperature data points for each. There were fewer GUD temperature data points recorded, thus categories were based on the available data for each section.

Additional mixed effect models were used to test for differences in the dependent variable (GUD) against the main effects of temperature—maximum and mean temperature, which was run separately to determine the best model based on the lowest AIC value.

Maximum temperature was classified as the highest temperature recorded every 24 h over the experimental period, and the average temperature was the mean temperature recorded every 24h over the experimental period. Although highly correlated, I used maximum and mean temperatures as I wanted to account for both the extreme hot conditions as well as the cooler conditions (covered by using mean T_{air}). Additional weather variables such as dew point temperature, cloud cover and precipitation were added to GLM's as potential contributing factors. The GUD values used in the models represented the number of mealworms remaining after each experiment.

Results

Body temperature

A total of 12 *E. rupestris* were captured and tagged during the study period, of which seven were adults (6M:1F ~ 57 ± 3.84 g), two subadults (2M ~ 39.50 ± 4.94 g) and three immatures based on lower body mass (2M:1F ~ 22.33 ± 3.05 g) (See appendix Table 1). Additional individuals of the species were recorded on camera traps, contributing to activity and GUD data, however, they evaded Sherman traps and could not be PIT-tagged (See appendix Table 2). Six of the twelve individuals tagged were captured by PIT-tag receivers, and I obtained body temperature data for these individuals while they foraged and visited the feeding stations.

The mixed effect models showed that maximum temperature had no significant effect ($p > 0.05$) on the body temperature fluctuations of *E. rupestris* when visiting feeding stations. *Elephantulus rupestris* body temperatures remained stable during both the day [mean T_b = 37.49 °C ± 0.64 (34.4 – 40 °C); mean T_{air} = 19.9 °C ± 5.88 (6 – 33.9 °C)], and night [mean T_b = 36.95 °C ± 0.64 (35.7 – 38.4 °C); mean T_{air} = 15.28 °C ± 5.90 (5 – 28.8 °C)]. This showed no significant difference between E. rupestris day and night body temperatures. The

Pearson’s correlation showed a weak positive correlation between body temperature and air temperature (r(429)= 0.45, $p < 0.001$) (Fig. 2).

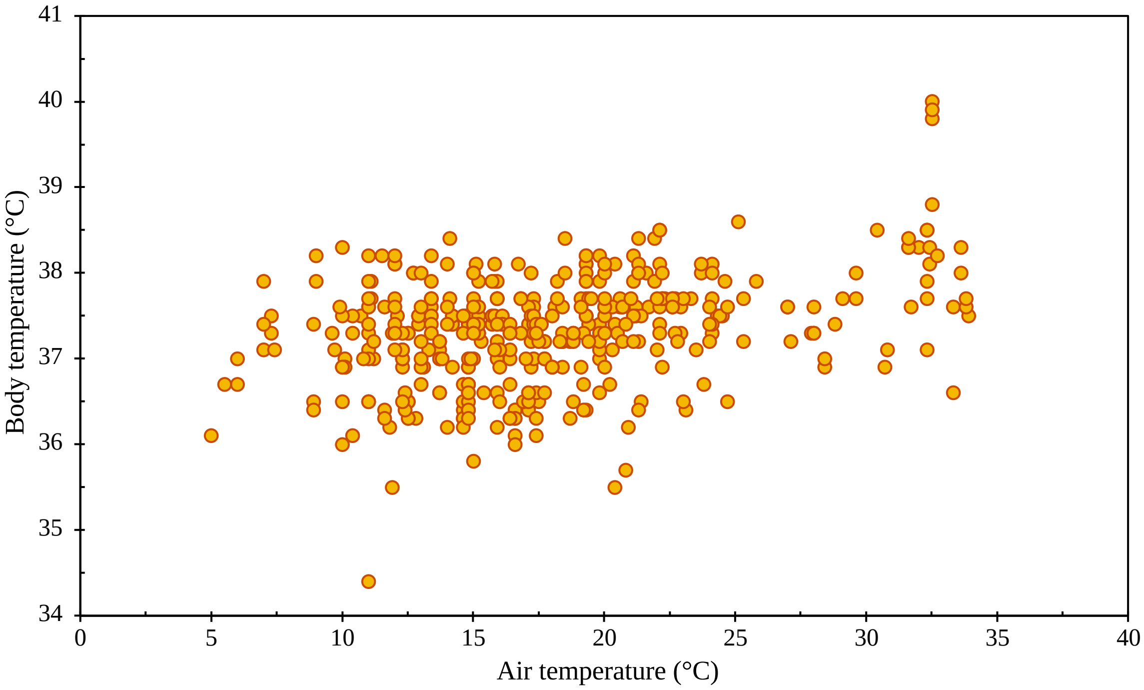


Figure 2. Correlation between *Elephantulus rupestris* core body temperature (°C) and air temperature (°C).

Visitation Activity

Visitation levels were generally higher at night and early morning, showing a marked decline between 10h00 and 17h00, followed by higher levels of activity in the later afternoon and evening (Fig. 3). I looked at the number of visits (activity) as a function of time of day (Fig. 4), and found the highest number of visits to coincide with what was shown in Fig. 5, with morning (178 visits) and night (314 visits) having the highest activity levels.   Negative binomial mixed effect models looking at the effect of maximum temperature and time of day on activity (visitation to camera sites) showed a significant effect of time of day on activity ($\chi^2_{1,6} = 91.20$, $p < 0.01$), but there was no effect of maximum temperature ($p = 0.14$). A Tukey’s post hoc test confirmed the difference in activity levels amongst time of day categories, with afternoon activity being significantly more than midday ($p < 0.01$) and significantly less than at night ($p < 0.01$), and midday activity being significantly less than morning ($p < 0.01$).

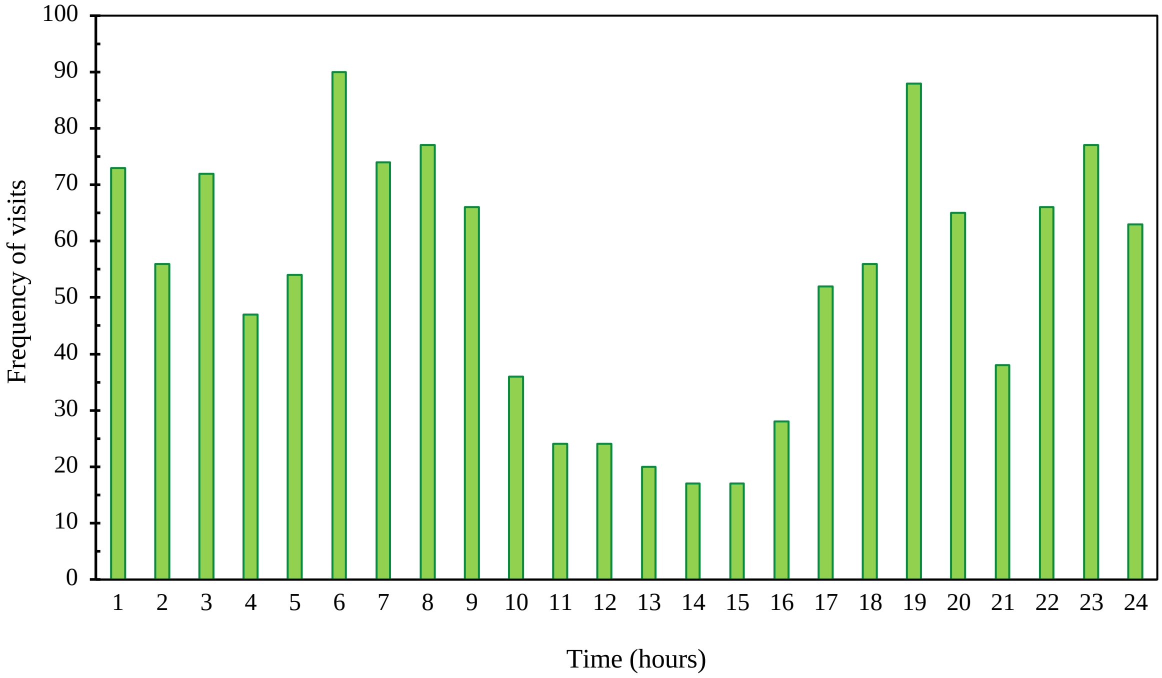


Figure 3. The total number of visits to feeding stations by *E. rupestris* at each hour during a 24h cycle, over the entire research period.

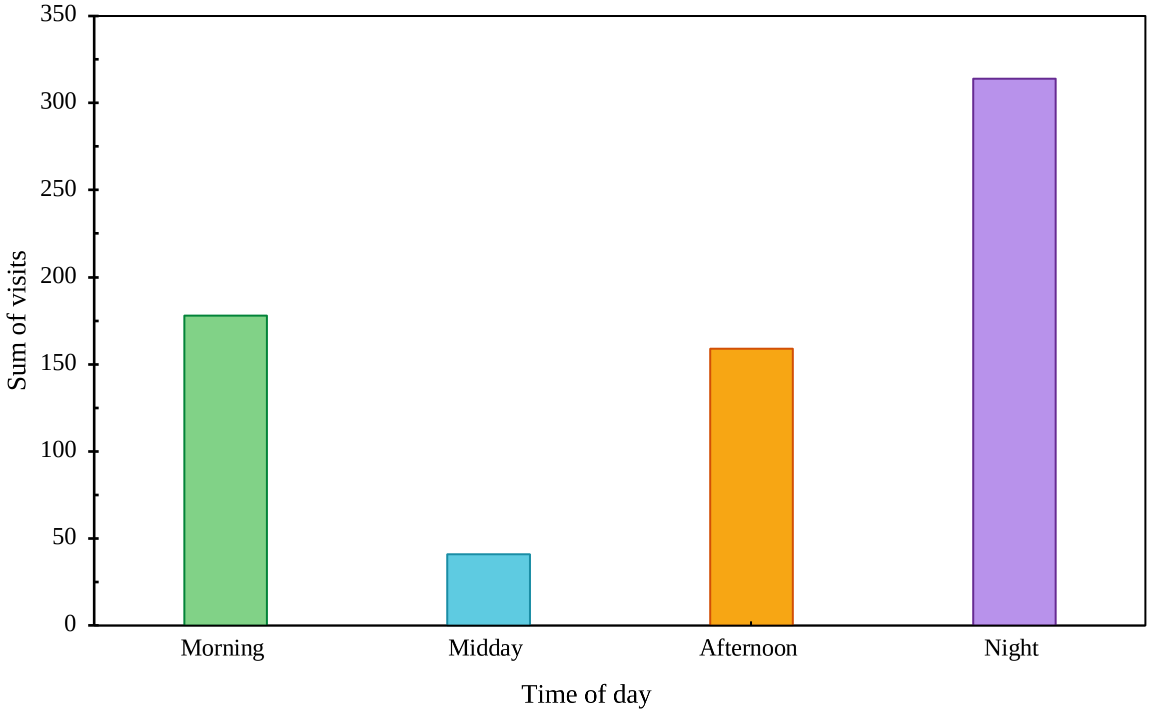
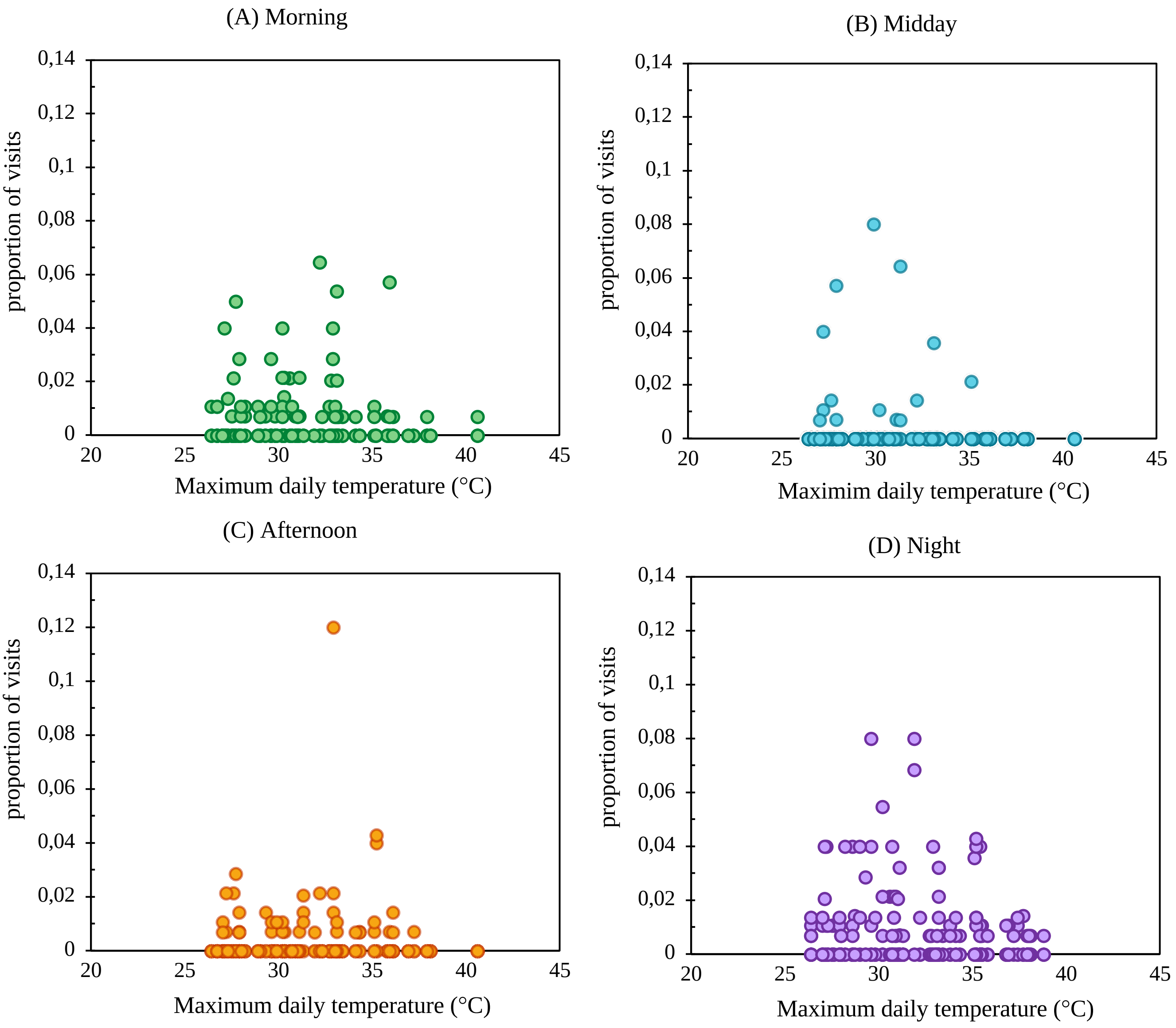


Figure 4. The number of visits of *E. rupestris* to camera sites (activity) at different times of the day.

The proportion of visits to feeding stations as a function of maximum temperature, a subset at each of the four time of day categories, showed high levels of activity during the morning and night, with activity reducing in the afternoon and activity being scarce during midday over a range of air temperatures (T_{air} = 5.6 – 41 °C)(Fig. 5). Maximum temperature had no significant effect on the proportion of visits (both in models with all the time categories pooled, and when time categories were analysed separately) (Fig. 5).



(A) Morning

(B) Midday

(C) Afternoon

(D) Night

Figure 5. Proportions of visits for each time of day category (A – morning, B – midday, C – afternoon and D – night), as a function of maximum daily temperature (°C).

Giving-up Density

Over a period of 24 days, a total of 96 feeding experiments took place at four sites over a range of air temperatures. Because the mean and maximum environmental air temperatures were somewhat collinear, they were run in separate models as the independent variable and not combined within the same model. Maximum and mean temperatures were both initially included as I wanted to account for not only the spikes in hot temperatures (by including maximum temperature) but also the cooler temperatures too. General mixed effect models using maximum and mean temperature as independent variables, against GUD as the dependent variable, showed neither mean nor maximum temperature to have an effect ($p > 0.05$) on the number of mealworms remaining (GUD) (Fig. 6). However, there was considerable variation in the number of mealworms remaining, but this could not be explained by weather variables. Weather variables such as cloud cover, humidity and precipitation were added to the models, however none had an effect on the GUD outcome.

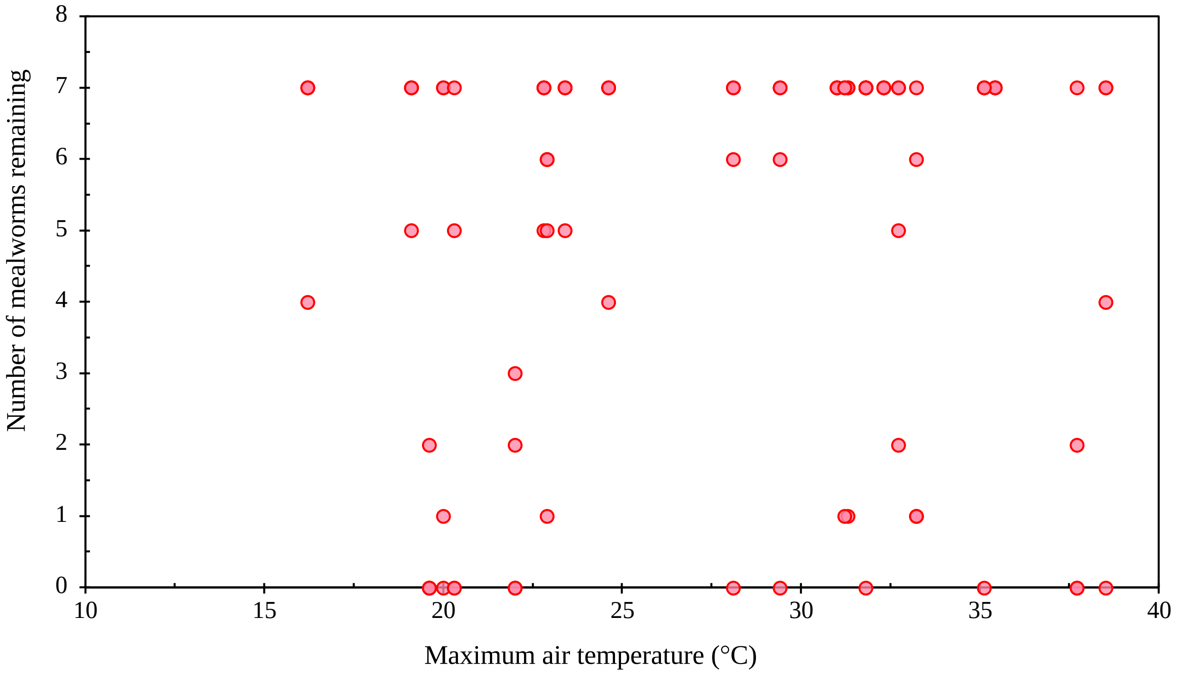


Figure 6. The Giving-up density (the number of mealworms remaining at a patch after a foraging bout) of *Elephantulus rupestris* at maximum environmental air temperatures (°C).

Discussion

In this study, *E. rupestris* showed polyphasic foraging-related activity patterns, with no direct evidence that high temperatures played a significant role in visitation rates to artificial feeding stations. *Elephantulus rupestris* foraged during both light and dark phases, and over a range of environmental air temperatures, showing slight heterothermic patterns under colder conditions and normothermic patterns under hotter conditions. My findings corroborate previous work conducted on elephant shrews under laboratory conditions showing their ability to shift activity and forage time, making them potentially less vulnerable to change and increasing environmental temperatures.

The body temperatures of *E. rupestris* remained within a range of 34.4° - 40 °C across fluctuations in environmental temperatures. This reiterates their ability to regulate T_b within a mostly normothermic range (Lovegrove et al. 2001_b) while active and foraging under extreme conditions with minimal fluctuations in T_b above 38 °C and no clear evidence of facultative hyperthermia (Oelkrug et al. 2012). The mean body temperature of *E. rupestris* was relatively stable (mean T_b = 37.3 °C ± 0.64 STD) over a range of air temperatures from 5° - 33.9 °C, which confirms my predictions.

The frequency and timing of *E. rupestris* visitations to feeding stations did not appear to be influenced by maximum air temperatures. However, I could not account for other factors that may have had the potential to influence visitation to stations, such as resource abundance, guarding of territory and seasonal provisioning (feeding offspring etc.). Although temperature did not influence the visitation of *E. rupestris* to stations, I did find that they favoured visits at certain times of the day. *Elephantulus rupestris* avoided visiting stations during midday under both cool and hot conditions, and preferred to be active (visit) around stations during the morning, late afternoon, and night periods. These visitation patterns make sense under hot conditions as it allows for the avoidance of exposure during the heat of the day (midday period), however, *E. rupestris* still maintained these patterns under cool conditions when heat exposure was not a risk. This suggests that under cooler conditions, *E. rupestris* may be incurring missed opportunity costs as they are choosing to avoid midday activity, regardless of temperature. Thus this does not support my prediction that *E. rupestris* structures their activity/visitation patterns around the thermal environment.

Giving-up densities under cool, mild and hot environmental temperatures were relatively consistent, indicating temperature had no direct effect on foraging effort. There was no significant difference between the number of mealworms left behind (GUD) by *E. rupestris* under cool (82.14%), mild (62.33%), and hot (80.12%) air temperatures. Indicating that foraging continues for *E. rupestris* irrespective of temperature, which does not support the hypothesis/prediction that higher temperatures yield higher GUD's.

Body temperature

Maintaining a core body temperature comes with energetic costs, and failure to do so may be detrimental to an individual's survival, fitness and reproductive ability (Cunningham et al. 2013; Robertson et al. 2020). Elephant shrew species are well known for their heterothermic and normothermic abilities (Lovegrove et al. 1999, 2001_a; Mzilikazi and Lovegrove 2005; Oelkrug et al. 2012), as well as their ability to actively avoid exposure that puts them at risk of heat stress (Roxburgh and Perrin 1994).

The lowest body temperature (T_b = 34.4 °C) recorded for *E. rupestris* was at a relatively low air temperature (T_{air} = 5 °C), and indicates that the individual may have been rewarming from a bout of torpor, as all other body temperature remained above 36 °C. This individual record also occurred in the early hours of the morning, when temperatures were lowest. With the remaining data showing a stable range of body temperatures over varying environmental air temperatures, it is indicative of their normothermic abilities. Heterothermy is the ability of an animal to adjust their body temperature physiologically in accordance with environmental temperature and resource availability (Blight and Johnson 1973; Boyles et al. 2011). The low body temperature record suggests that under cool air temperatures, even in the summer months, that *E. rupestris* uses heterothermy and bouts of torpor to deal with unfavourable conditions. This is suggested as torpor has been documented in both winter and summer for *E. rupestris*, with torpor being used in summer when temperatures reach below 17 °C (Oelkrug et al. 2012). Under mild and hot air temperatures, *E. rupestris* remained mostly normothermic. Nevertheless, there were a few incidences (n= 3) where body temperatures slightly above normothermic levels (T_b = 39-40 °C) where recorded at T_{air} between 31 and 33.6 °C. Higher body temperatures at high air temperatures are expected as animals may be heat stressed. Animals that are active under such conditions will increase their metabolic heat production (and heat gain), and due to the hot environmental conditions, their heat loss will be slower, resulting in higher body temperatures. Higher $T_{b's}$ are also expected as they correspond with fluctuating daily T_{air} across seasons (Oelkrug et al. 2012). *Elephantulus rupestris* body temperatures have been recorded to exceed 38 °C at air temperatures below 31 °C, however these records occurred during midday (10h00 and 16h00), where thermal and solar exposure would have been highest (Boyles et al. 2011). In my study I did not, however, see the body temperatures of *E. rupestris* reach as high as expected, as a recent study recorded their body temperatures reaching around 41.6 °C when exposed to heat under laboratory conditions (Chalwin-Milton et al. 2022, unpublished data). There could be a number of reasons for this. The first reason could be that environmental temperatures did not reach as high as expected for the area during my study, with air temperatures not exceeding 34 °C. With the season being unusually cool, it may be possible that *E. rupestris* were not pushed to their thermal limits as the conditions were simply not hot enough. This is likely to be true based on the unpublished data by Chalwin-Milton et al. 2022 (unpublished data), who found *E. rupestris* body temperature exceed normothermic levels at air temperatures well above 40 °C. Alternatively, it could also be that *E. rupestris* are well adapted to living in hot and arid environments and are simply unaffected by thermal extremes. This can be seen in the literature as *E. rupestris* body temperature remains within a relatively normothermic range (Tb = 36-38 °C) at T_{air} below 30 °C and only reach hyperthermic levels (Tb > 39 °C) at T_{air} over 40 °C (Boyles et al. 2011; Oelkrug et al. 2012; Chalwin-Milton et al. 2022). Lastly, *E. rupestris* use behavioural and physiological mechanisms to avoid environmental extremes. I believe this to be true from my findings on visitation activity, where *E. rupestris* appear to behaviourally choose to be active during periods with lower mean temperatures and the least chance of hyperthermia. Thus, they avoid raising their T_b above normothermic levels. It is also noteworthy that majority of the individuals contributing to the body temperature data were males. It is unclear if there are significant differences between the average body temperatures of male and female *E. rupestris*, however there could be a difference in time and activity allocation between sexes that could lead to differences in both activity patterns and body temperatures.

Visitation Activity

Elephantulus rupestris displayed polyphasic visits to stations with sustained visits throughout the night, with slight peaks in visits during the early morning and the evening period, and a distinctive drop in visits during midday. I predicted that *E. rupestris* avoid visiting feeding stations around the midday period in an attempt to reduce high solar exposure and heat stress, as temperatures during that period are generally the highest (Boyles et al. 2011). This is in accordance with many other species that use altered activity times to avoid heat stress and related trade-offs under high environmental temperatures. Studies done on Degus *Octodon* *degus* (small South American rodent) have shown that thermoregulatory constraints affected the timing of activity, finding that they avoid being active during periods of high solar radiation (Bozinovic et al. 2000; Bacigalupe et al. 2003). This has also been seen in other Macroscelidea species, where animals favour nocturnal activity to avoid heat stress during the hottest parts of the day, an adaption to arid environments which allows for thermally suitable activity to be selected for (Roxburgh and Perrin 1994). This heat exposure avoidance makes sense on hot days, however, on cool days the avoidance of midday activity could result in missed opportunities. The avoidance of thermal extremes to preserve a stable T_b is a thermoregulatory trade-off that leads to missed opportunities, and has been observed to result in reduced foraging efficiency and loss of body condition in some bird species (van de Ven et al. 2019). Missed opportunities may not be an issue for *E. rupestris* as their activity is not confined to the light phase, indicating that they may not be incurring any missed opportunities at all. It is also possible that *E. rupestris* are proficient at acquiring enough energy when they do forage, therefore making it unnecessary to forage during the middle of the day. An alternative hypothesis to what could be driving reduced activity during midday could be increased predation pressure during the light phase, making being active during the middle of the day too high of a risk. I predict predation pressure to be higher during the light phase due to visual exposure and the large number of avian predators in the area (Jackal buzzards *Buteo rufofuscus*, Pale Chanting Goshawks *Melierax canorus* , Rock Kestrels *Falco rupicolus* and Eagles), as well as the presence of domestic cats and large elapids (Cape cobra *Naja nivea* specifically) which were recorded on camera traps. However, the predation pressure during the dark phase should not be discounted as it offers alternative threats from nocturnal avian predators as well as from larger mammals (Caracal *Caracal caracal*, Genet *Genetta sp.*, African wild cat *Felis lybica*). With the larger portion of predators being active during the light phase, it makes sense for *E. rupestris* to avoid being active during periods where predation pressure is at its highest (midday).

Giving-up Densities

Although the GUD part of the study had a number of limitations, the foraging experiments still satisfied two of Brown's (1988) most advocated methods, i.e. (1) controlled field experiments and (2) the use of giving-up densities to measure patch use. By doing an in situ field study, I allowed for foragers to remain in their natural habitats where there was familiarity around predation risk, and other activities and interactions in their landscape. The familiarity of such factors (e.g. predation and landscape interactions), which naturally influence foraging behaviour, therefore allowed for a more accurate interpretation of the findings. Using artificial food patches (referred to as "feeding stations" in this study) allowed for the manipulation of variables (in this case the choice of weather conditions under which experiments were run and patch location) while alternative activities were held constant. Studying the GUD of *E. rupestris* allowed me to gain insight into the effects of temperature on their foraging behaviour and decision making.

When confronted with an opportunity, such as a patch, a forager must decide whether to harvest that patch (Rosenzweig 1974), and what amount of effort and time will be allocated to harvesting such a patch (Charnov 1976). The time allocated to harvesting a patch will determine the foragers net reward (Brown 1988). The end goal of any forager is to allocate sufficient time to both foraging and alternative activities, so as to maximise ones fitness and survival (Brown 1988; Oyugi and Brown 2003).

A previous laboratory study looking at the foraging behaviour of the Round-eared elephant shrew (*Macroscelides proboscideus*) found that under warm environmental conditions (~ 24 °C), animals showed risk-averse foraging strategies, avoiding being active during the light phase and switched their activity to foraging during the dark phase when conditions were more favourable (Lawes and Perrin 1995). This may be relevant for many elephant shrew species due to their dietary shifts and polyphasic activity patterns.

Elephantulus rupestris did not yield higher GUD's under hotter conditions. However, they displayed a continuous, but highly variable foraging pattern across all air temperatures. Foraging under high thermal heat loads usually yields high GUD's, as the increased heat reduces the amount of suitable time for foraging (Mathewson et al. 2017), resulting in foragers trading-off feeding with avoiding hyperthermia (Lima and Dill 1990; Kilpatrick 2003; Hall and Chalfoun 2018). *Elephantulus rupestris* foraging across all air temperatures is an unexpected outcome, but could be explained by the lower than average temperatures of the study period. I also observed, on multiple occasions, that *E. rupestris* individuals would visit the artificial feeding stations but not feed, instead they would sit and guard the patch for short periods of time. This indicates that individuals are not energy stressed for food but want to guard a food source for future need, in a similar sense to male elephant shrews guarding females against extra pair copulations (Ribble and Perrin 2005).

Other studies on the effect of temperature on foraging and giving-up density have shown opposing findings to mine. Studies done on Degus (*Octodon degus*) found foraging time and efficiency to be reduced under high thermal heat loads, and foraging under cooler conditions is favoured (Bozinovic et al. 2000). Another study on American crows (*Corvus brachyrhynchos*) and Eastern grey squirrels (*Sciurus carolinensis*) also found GUDs' to be higher in thermally exposed and sunlit areas, as opposed to lower GUDs' observed under cold conditions (Kilpatrick 2003).

My findings show that *E. rupestris* exhibit strong polyphasic "activity" patterns based on their minimal midday activity and preference for being active during the morning, afternoon and night under both hot and cold conditions. Perhaps due to their wider dietary breadth and their ability to be active during both the light and dark phase, *E. rupestris* can afford to incur missed opportunity costs during midday as they have ample opportunities to make up for them outside of that small timeframe. By doing this, *E. rupestris* avoids the risk of dehydration and hyperthermia during midday, and switches its core foraging time to later in the day/night when high thermal exposure is not an issue.

Limitations

This study had a number of unforeseen limitations that could be resolved for future studies to improve the methodologies and reliability of the outcomes. The study period happened to fall under conditions that experienced higher rainfall and perhaps food abundance compared to many years prior to the study, leading to the landscape not being as harsh and as arid as is usually the case. This was due to the area coming out of a seven year drought (2015-2021), where rainfall and resources had been lower than average and conditions were much harsher. An increase in food abundance and reduction in temperature extremes made it difficult to test the true effect of temperatures on activity and foraging, as temperatures rarely reached above 35 °C and animals were not stressed for food. With elephant shrews not being exposed to $T_{air} > T_b$ (conditions where heat stress is likely to occur) , it is unlikely that the full extent of their foraging behaviour and choices were understood, as the effect of higher temperatures could not be accounted for.

The number of cameras in the field at a given time was also an additional limiting factor, as only 3 or 4 out of 8 cameras were present at feeding stations throughout the duration of the study period. Additionally, cameras only recorded for 90 seconds after being triggered and would therefore not be able to capture the entire foraging bout. Due to this we could not accurately determine the total length of foraging bouts for individual *E. rupestris*.

The number of PIT-tag readers were another limiting factor, as the small number meant that body temperature could only be read at two of the stations at a time, meaning that additional data was missed at the remaining sites. In addition to this, only 12 animals were captured out of what appeared to be a large population, resulting in only a few individuals contributing to body temperature data (See appendix Table 1 and 2). Non-tagged individuals also meant that I was unable to identify all individuals that visited the feeding stations. The number of *E. rupestris* individuals captured was fewer than expected, however, I put many hours into trapping over a five month period, and animals were simply trap-shy. Of the 12 animals tagged, majority (10 out of 12) were male, which in itself could have implications for the results observed. Male and female elephant shrews are not likely to spend similar amounts of time on the same activities, it is more likely that certain behaviours differs based on sex specific tasks – such as mate guarding, reproduction, and gestation (Ribble and Perrin 2005). With different sexes allocating different amounts of time to certain activity, the male bias within the data could have skewed the overall perception of activity for *E. rupestris*.

The number of experimental days on which I conducted the giving-up density experiments, were too few and of non-consecutive days, and were therefore insufficient. It would be beneficial to increase the number of experimental days, specifically over a consecutive time period of varying weather conditions. As foraging behaviour is influenced by multiple factors; including competition, predation pressure, ambient temperature and resource availability (Brown and Kotler 2004; Levy et al. 2016), it is an already complex behaviour to understand and therefore should be done under a controlled setting. Bedoya-Perez et al. (2013), stated that food patches should never be completely depleted as it violates the assumptions of giving-up density. In my study, there were a few cases where food patches were completely depleted, and the number of mealworms provided evidently was insufficient. The feeding trays in this study were left out and empty when experiments were not being run, potentially causing animals to associate these patches as being unreliable and depleted for large portions of time. Additionally, the number of individuals foraging at feeding stations in this study was hard to control, as not all individuals were tagged, and not all feeding stations had readers to pick up tagged individuals' activity. Although I tried to account for missed opportunity costs (MOC) through patch design, it is still possible that individuals incurred these costs while performing daily activities such as sleeping, defending a territory, looking for a mate or simply feeding at a different patch. By choosing to feed at one patch, an individual will incur MOC's at a different and potentially better patch.

Future studies

When carrying out similar giving-up density (GUD) experiments in future studies, it would be ideal to lengthen the study period over a range of environmental conditions, preferably over both summer and winter seasons. Trapping should preferably happen well in advance of the experiments as elephant shrews can be trap-shy, this would ensure that a suitable number of individuals could be captured and tagged. The more tagged individuals, the greater the chance of identifying how many foragers visited each patch and how many times, contributing to a more reliable dataset. Future studies could also include a larger number of independent feeding stations, to reduce the likelihood of multiple animals feeding at a single station. To avoid GUDs' reaching zero, the perception of the patch needs to be lowered, and can be done by increasing the amount of substrate to reward ratio, decreasing reward quality or size or reducing the overall amount of reward offered (Druce et al. 2009; Bedoya-Perez et al. 2013). Removing feeding trays from stations while experiments are not active is advised, as the presence of the tray should be a reliable cue for animals to know that there is a potential food source available.

Alternatively, carrying out these experiments in a controlled lab environment, where temperature can be controlled and manipulated, the effects of temperature on foraging would be easier to determine than in situ studies, where many additional variables contribute to foraging decisions. However, in situ studies would give more accurate insight into the animals natural responses and behaviours.

Conclusion

Temperature appeared to be influential but had no explicit effect on *Elephantulus rupestris* visitation activity and body temperature maintenance. The body temperature of *E. rupestris* remained relatively constant, and they showed no thermal preference for foraging conditions as they chose to forage under all environmental air temperatures (cool, mild and hot). However, time of day had a significant effect on when *E. rupestris* were active and foraging. The giving-up densities and the visits of *E. rupestris* to stations under high temperatures did not follow the expected norm, however, this could be attributed to temperatures not reaching the predicted thermal extremes, animals perhaps not being sufficiently energy stressed, and violation of the reliability of the feeding patch in the experimental design.

Elephant shrews have multiple behavioural and physiological pathways to mitigate risk for better chances of survival. They are heterothermic, allowing for the conservation of energy under unfavourable thermal conditions (Lovegrove et al. 2001_a), as well as polyphasic, which allows them to be active and forage through both the light and dark phases (Woodall et al. 1989; Lawes and Perrin 1995). Their small body size allows for the use of microrefugia, which aids in the avoidance of both predators and thermal exposure (Perrin 1995). The ability to shift activity is again indicative and supportive of polyphasic activity patterns (Lawes and Perrin 1995; Lovegrove et al. 1999; Mzilikazi and Lovegrove 2005), and is what may give elephant shrew species the ability to avoid environmental extremes.

Initially, this study aimed to focus on the round-eared elephant shrew, *Macroscelides proboscideus,* as a model due to its more diurnal activity patterns and occurrence in hotter and more exposed habitats (Skinner and Smithers 1990; Lovegrove 1993; Lawes and Perrin 1995). Unfortunately, I did not find a high population density of *M. proboscideus* in the potential study sites I explored. *Macroscelides proboscideus* faces harsher environmental extremes than *Elephantulus rupestris*, and has fewer options for thermal refugia based on the general lower vegetation density and lack of rocky boulders within their habitats. Without the availability of thermal refugia, it may be easier to test the true effects of thermal exposure on the activity, body temperature and foraging patterns of *M. proboscideus* in future studies. By studying *E. rupestris,* a species with more available refuge options yet one that still avoids thermal exposure on hot days, I found that thermal extremes do play a role in influencing and structuring activity.

The findings of this study suggest that *E. rupestris* are risk adverse animals, keeping their activity to the times of the day when thermal exposure is less and predation risk is perhaps lower. By doing so, they also protect themselves from thermally stressful environments. If *E. rupestris* are showing risk adverse behaviour under mild conditions, such as in my study, it is likely that future warming will cause greater changes in their behaviour in terms of activity and foraging times. I would predict the foraging period for *E. rupestris* to shift predominantly to the dark phase and for the diurnal activity to be limited to cooler conditions. Future increases in temperatures will likely reduce suitable activity and foraging time for the species, which may in turn, result in increased missed opportunities. Future studies should aim to determine the foraging efficiency of elephant shrews to further address the risks they face due to missed opportunities and trade-offs.

The true effect of temperature on *E. rupestris* was not fully quantified, as air temperatures did not reach high enough. My findings represent the effect of mild temperatures on body temperature, food patch visitation rates, and giving-up density. There are still unanswered questions regarding the effect of high air temperatures on the behaviour and physiology of *E. rupestris*, which should be investigated further in future studies under more optimal conditions.

References

Abu Baker MA, Brown JS. 2010. Islands of fear: effects of wooded patches on habitat suitability of striped mouse in a South African grassland. *Functional Ecology* 24: 1313-1322.

Abu Baker MA, Brown JS. 2011. Patch use behaviour of *Elephantulus myurus* and *Micaelamys namaquensis*: the role of diet, foraging substrates and escape substrates. *African Journal of Ecology* 50: 167-175.

Abu Baker MA, Brown JS. 2014. Foraging in space and time structure an African small mammal community. *Oecologia* 175: 521-535.

Aldridge HDJN, Brigham RM. 1988. Load carrying and maneuverability in an insectivorous bat: A test of the 5% "rule" of radio-telemetry. *Journal of Mammalogy* 69: 379-382.

Bacigalupe L, Rezende EL, Bozinovic F. 2003. Activity and space use by degus: a trade-off between thermal conditions and food availability? *Journal of Mammalogy* 84: 311-318.

Bates D, Mächler M, Bolker B, Walker S. 2015. Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software* 67: 1-48.

Bedoya-Perez MA, Carthey AJR, Mella VSA, McArthur C, Banks PB. 2013. A practical guide to avoid giving up on giving-up densities. *Behavioural Ecology and Sociobiology* 67: 1541-1553.

Beever EA, Hall LE, Varner L, Loosen AE, Dunham JB, Gahl MK, Smith FA, Lawler JJ. 2017. Behavioural flexibility as a mechanism for coping with climate change. *Frontiers in Ecology and the Environment* 15: 299-308.

Blight J, Johnson KG. 1973. Glossary of terms for thermal physiology. *Journal of Applied Physiology* 35: 941-961.

Blumstein DT, Bouskila A. 1996. Assessment and decision making in animals: a mechanistic model underlying behavioural flexibility can prevent ambiguity. *Oikos* 77: 569-576.

Bondarenco A, Körtner G, Geiser F. 2014. Hot bats: extreme thermal tolerance in a desert heat wave. *Naturewissenschaften* 101: 679-685.

Booysen J, Rowswell DI. 1983. Die droogteprobleem in die Karoogeiede. *Journal of the Grassland Society of Southern Africa* 18: 40-45.

Boyles JG, Seebacher F, Smit B, McKechnie AE. 2011. Adaptive thermoregulation in endotherms may alter responses to climate change. *Integrative and Comparative Biology* 51: 676-690.

Boyles JG, Smit B, McKechnie AE. 2012$_a$. Variation in body temperature is related to ambient temperature but not experimental manipulation of insulation in two small endotherms with different thermoregulatory patterns. *Journal of Zoology* 287: 224-232.

Boyles JG, Smit B, Sole CL, McKechnie AE. 2012$_b$. Body temperature patterns in two synoptic elephant shrew species during winter. *Comparative Biochemistry and Physiology A* 161: 89-94.

Bozinovic F, Lagos JA, Vasquez RA, Kenagy GJ. 2000. Time and energy use under thermoregulatory constraints in a diurnal rodent. *Journal of Thermal Biology* 25: 251-256.

Briscoe NJ, Handasyde KA, Griffiths SR, Porter WP, Krockenberger A, Kearney MR. 2014. Tree-hugging koalas demonstrate a novel thermoregulatory mechanism for arboreal mammals. *Biology Letters* 10: 20140235.

Brown JS. 1988. Patch use as an indicator of habitat preference, predation risk, and competition. *Behavioural Ecology and Sociobiology* 22: 37-47.

Brown JS. 1992. Patch use under predation risk: I. Models and predictions. *Annales Zoologici Fennici* 29: 301-309.

Brown JS. 2000. Foraging ecology of animals in response to heterogeneous environments. In: *The Ecological Consequences of Environmental Heterogeneity* (eds Hutching MJ, Johns EA, Stewart AJA) pp 181-215. Blackwell Scientific, Oxford.

Brown JS, Kotler BP, Mitchell WA. 1994. Foraging theory, patch use, and structure of a Negev Desert granivore community. *Ecology* 75: 2286-2300.

Brown JS, Morgan RA. 1995. Effects of foraging behaviour and spatial scale on diet selectivity: a test with fox squirrels. *Oikos* 74: 122-136.

Brown JS, Kotler BP, Mitchell WA. 1997. Competition between birds and mammals: A comparison of giving-up densities between crested larks and gerbils. *Evolutionary Ecology* 11: 757-771.

Brown JS, Kotler BP. 2004. Hazardous duty pay and the foraging cost of predation. *Ecology Letters* 7: 999-1014.

Buchholz R, Banusiewicz JD, Burges S, Crocker-Buta S, Eveland L, Fuller L. 2019. Behavioural research priorities for the study of animal response to climate change. *Animal Behaviour* 150: 127-137.

Carroll JM, Davis CA, Fuhlendorf SD, Elmore RD. 2016. Landscape pattern is critical for the moderation of thermal extremes. *Ecosphere* 7: e01403.

Carthey AJR, Banks PB. 2015. Foraging in groups affects giving-up densities: solo foragers quit sooner. *Oecologia* 178: 707-713.

Charnov EL. 1976. Optimal foraging, the marginal value theorem. *Theoretical Population Biology* 9: 129-136.

Clarke CL, Shackleton SE, Powell M. 2012. Climate change perceptions, drought responses and views on carbon farming amongst commercial livestock and game farmers in the semiarid Great Fish River Valley, Eastern Cape province, South Africa. *African Journal of Range and Forage Science* 29: 13-23.

Conradie SR, Woodborne SM, Cunningham SJ, McKechnie AE. 2019. Chronic, sublethal effects of high temperatures will cause severe declines in southern African arid-zone birds during the 21st century. *PNAS* 116: 14065-14070.

Corbet GB, Hanks J. 1968. A revision of the elephant-shrews, family Macroscelididae. *Bulletin of the British Museum of Natural History (Zoology)* 16: 47-111.

Cozzoli F, Ligetta G, Vignes F, Basset A. 2018. Revisiting GUD: An empirical test of the size-dependency of patch departure behaviour. *PLOS ONE* 13: e0204448.

Creel S, Creel NM, Creel AM, Creel BM. 2016. Hunting on a hot day: effects of temperature on interactions between African wild dogs and their prey. *Ecology* 97: 2910-2916.

Cunningham SJ, Martin RO, Hojem CL, Hockey PAR. 2013. Temperatures in excess of critical thresholds threaten nestling growth and survival in a rapidly warming arid savanna: A study of Common Fiscals. *PLOS ONE* 8: e74613.

Cunningham SJ, Gardner JL, Martin RO. 2021. Opportunity costs and the response of birds and mammals to climate warming. *Frontiers in Ecology and the Environment* 19: 300-307.

Druce DJ, Brown JS, Castley G, Kerley GIH, Kotler BP, Slotow R, Knight MH. 2006. Scale-dependent foraging costs: habitat used by rock hyraxes (*Procavia capensis*) determined using giving-up densities. *Oikos* 115: 513-525.

Druce DJ, Brown JS, Kerley GIH, Kotler BP, Mackey RL, Slotow R. 2009. Spatial and temporal scaling in habitat utilization by klipspringer (*Oreotragus oreotragus*) determined using giving-up density. *Austral Ecology* 34: 577-587.

du Plessis KL, Martin RO, Hockey PAR, Cunningham SJ, Ridley AR. 2012. The costs of keeping cool in a warming world: implications of high temperatures for foraging, thermoregulation and body condition of an arid-zone bird. *Global Change Biology* 18: 3063-3070.

Dylda E, Wang KH. 2022. Prior actions influence cost-benefit-related decision-making during mouse foraging behaviours. *European Journal of Neuroscience* 56: 3779-4008.

Fabricius C, Burger M, Hockey PAR. 2003. Comparing biodiversity between protected areas and adjacent rangeland in xeric succulent thicket, South Arica: arthropods and reptiles. *Journal of Applied Ecology* 40: 392-403.

Fox J, Weisberg S. 2019. An R Companion to Applied regression, third edition. Sage, Thousand Oaks, California.

Fuller A, Hetem RS, Maloney SK, Mitchell D. 2014. Adaption to heat and water shortage in large, arid-zone mammals. *Physiology* 29: 159-167.

Fuller A, Mitchell D, Maloney SK, Hetem RS, Fonsêca VFS, Meyer LCR, van de Ven TMFN, Snelling EP. 2021. How dryland mammals will respond to climate change: the effects of body size, heat load and a lack of food and water. *Journal of Experimental Biology* 224: jeb238113.

Genz A, Bretz F, Miwa T, Mi X, Leisch F, Scheiple F, Hothorn T. 2020. mvtnorm: Multivariate normal and t distributions. https://CRAN.R-project.org/package=mvtnorm

Gerson AR, McKechnie AE, Smit B, Whitfield MC, Smith EK, Talbot WA, McWhorter TJ, Wolf BO. 2019. The functional significance of facultative hyperthermia varies with body size and phylogeny in birds. *Functional Ecology* 33: 597-607.

Ha RR. 2010. Cost-Benefit Analysis. *In: Encyclopedia of Animal Behavior, volume 1, pp 402-405*. Academia Press, Oxford.

Hadfield MG, Strathmann MF. 1996. Variability, flexibility and plasticity in life histories of marine invertebrates. *Oceanol Acta* 19: 323-234.

Hall LE, Chalfoun AD. 2018. What to eat in a warming world: do increased temperatures necessitate hazardous duty pay? *Oecologia* 186: 73-84.

Harrison XA. 2014. Using observation-level random effects to model overdispersion in count data in ecology and evolution. *PeerJ* 2:e616.

Heritage S, Rayaleh H, Awaleh DG, Rathbun GB. 2020. New records of a lost species and a geographic range expansion for sengis in the Horn of Africa. *PeerJ* 8: e9652.

Hetem RS, Fuller A, Maloney SK, Mitchell D. 2014. Responses of large mammals to climate change. *Temperature* 1: 115-127.

Houston AI. 1987. Optimal foraging by parent birds feeding dependent young. *Journal of Theoretical Biology* 124: 251-274.

Howe HF, Brown JS. 1999. Effects of birds and rodents on synthetic tallgrass communities. *Ecology* 80: 1776-1781.

Hothorn T, Bretz F, Westfall P. 2008. Simultaneous inference in general parametric models. *Biometrical Journal* 50: 346-363.

Huey RB, Kearney MR, Krockenberger A, Holtum JA, Jess M, Williams SE. 2012. Predicting organismal vulnerability to climate warming: Roles of behaviour, physiology and adaption. *Philosophical Transactions of the Royal Society B* 367: 1665-1679.

Humphries MM, Thomas DW, Speakman JR. 2002. Climate-mediated constraints on the distribution of hibernating mammals. *Nature* 418: 313-316.

IPCC. 2007. Climate change 2007: the physical science basis. *Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge.

Jackson CH. 2011. “Multi-State models for panel data: the msm package for R”. *Journal of Statistical Software* 38: 1-29.

Kerley GIH. 1995. The round-eared elephant shrew *Macroscelides proboscideus* (Macroscelidea) as an omnivore. *Mammalogy Review* 25: 39-44.

Kilpatrick AM. 2003. The impact of thermoregulatory costs on foraging behaviour: a test with American crows (*Corvus brachyrhynchos*) and eastern grey squirrels (*Sciurus carolinensis*). *Evolutionary Ecology Re*search 5: 781-786.

Kingdon J. 1974. East African Mammals: An atlas to evolution in Africa, VIIA (Insectivores and bats). Academic Press, London.

Kingdon J. 2015. The Kingdon field guide to African mammals (2nd ed). Bloomsbury, London,

Kotler BP, Gross JE, Mitchell WA. 1994. Applying patch use to assess aspects of foraging behaviour in Nubian ibex. *The Journal of Wildlife Management* 58: 299-307.

Kotler BP, Brown JS, Oldfield A, Thorston J, Cohen D. 2001. Foraging substrate and escape substrate: patch use by three species of gerbils. *Ecology* 82: 1781-1790.

Kotler BP, Brown JS, Bouskila A, Mukherjee S, Goldberg T. 2004. Foraging games between gerbils and their predators: seasonal changes in schedules of activity and apprehension. *Israel Journal of Zoology* 50: 256-271.

Lawes MJ, Perrin MR. 1995. Risk sensitive foraging behaviour of the round-eared elephant shrew (*Macroscelides proboscideus*). *Behavioural Ecology and Sociobiology* 37: 31-37.

Levy O, Dayan T, Porter WP, Kronfeld-Schor N. 2016. Foraging activity pattern is shaped by water loss rates in a diurnal desert rodent. *The American Naturalist* 188: 205-218.

Lima SL, Dill LM. 1990. Behavioural decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* 68: 619-640.

Lovegrove BG. 1993. The living deserts of Southern Africa. Fernwood, Cape Town.

Lovegrove BG, Lawes MJ, Roxburgh L. 1999. Confirmation of pleisiomorphic daily torpor in mammals: the round-eared elephant shrew *Macroscelides proboscideus* (Macroscelidea). *Journal of Comparative Physiology B* 169: 453-460.

Lovegrove BG, Raman J, Perrin MR. 2001$_{a}$. Heterothermy in elephant shrews, Elephantulus spp. (Macroscelidea): daily torpor or hibernation? *Journal of Comparative Physiology B* 171: 1-10.

Lovegrove BG, Raman J, Perrin MR. 2001$_b$. Daily torpor in elephant shrews (Macroscelidea: *Elephantulus* spp.) in response to food deprivation. *Journal of Comparative Physiology B* 171: 11-21.

Maloney S, Moss G, Cartmell T, Mitchell D. 2005. Alterations in diel activity patterns as a thermoregulatory strategy in black wildebeest *Connochaetes gnou*. *Journal of Comparative Physiology A* 191: 1055-1064.

Mason THE, Brivio F, Stephens PA, Apollonio M, Grignolio S. 2017. The behavioural trade-off between thermoregulation and foraging in a heat-sensitive species. *Behavioural Ecology* 28: 908-918.

Mathewson PD, Moyer-Horner L, Beever EA. 2017. Mechanistic variables can enhance predictable models of endotherm distributions: the American pika under current, past, and future climates. *Global Change Biology* 23: 1048-1064.

McFarland DJ. 1977. Decision making in animals. *Nature* 269: 15-21.

McKechnie AE, Wolf BO. 2010. Climate change increases the likelihood of catastrophic avian mortality events during extreme heat waves. *Biology Letters* 6: 253-256.

McKechnie AE, Wolf BO. 2019. The physiology of heat tolerance in small endotherms. *Physiology* 34: 302-313.

McNab B. 1984. Physiological convergence amongst ant-eating and termite-eating mammals. *Journal of Zoology* 203: 210-485.

Meehl GA, Tebaldi C. 2004. More intense, more frequent, and longer lasting heat waves in the 21st century. *Science* 305: 994-997.

Mitchell D, Snelling EP, Hetem RS, Maloney SK, Straus WM, Fuller A. 2018. Revisiting concepts of thermal physiology: predicting responses of mammals to climate change. *Journal of Animal Ecology* 87: 956-973.

Morris T, Gordon CE, Letnic M. 2015. Divergent foraging behaviour of a desert rodent, *Notomys fuscus*, in covered and open microhabitats revealed using giving up densities and video analysis. *Australian Mammalogy* 37: 46-50.

Moses MR, Frey JK, Roemer GW. 2012. Elevated surface temperature depresses survival of banner-tailed kangaroo rats: will climate change cook a desert icon? *Oecologia* 168: 257-268.

Mucina L, Rutherford MC, Palmer AR, Milton SJ, Scott L, Lloyd JW, van der Merwe B, Hoare DB, Bezuidenhout H, Vlok JHJ, Euston-Brown DIW, Powrie LW, Dold AP. 2006. Nama-Karoo Biome 7: 326-347. In: *The Vegetation of South Africa, Lesotho and Swaziland*. Strelitzia, Cape Town.

Mzilikazi N, Lovegrove BG. 2005. Daily torpor during the active phase in free-ranging rock elephant shrews (*Elephantulus myurus*). *Journal of Zoology* 267: 103-111.

Nguyen M. 2004. Giving up densities of small mammal granivores and their foraging behaviours. *ESSAI* 2: 1-6.

Oelkrug R, Meyer CW, Heldmaier G, Mzilikazi N. 2012. Seasonal changes in thermogenesis of a free-ranging afrotherian small mammal, the Western rock elephant shrew (*Elephantulus rupestris*). *Journal of Comparative Physiology B* 182: 715-727.

Orrock JL, Danielson BJ. 2009. Temperature and cloud cover, but not predator urine, affect winter foraging in mice. *Ethology* 115: 641-648.

Oyugi JO, Brown JS. 2003. Giving-up densities and habitat preferences of European starling and American robins. *The Condor* 105: 130-135.

Parmesan C, Yohe G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421: 37-42.

Perrin MR. 1995. Comparative aspects of the metabolism and thermal biology of elephant shrews (Macroscelidea). *Mammal Review* 25: 61-78.

Piersma T, Dekinga A, van Gils JA, Achterkamp B, Visser GH. 2003. Cost-benefit analysis of mollusc-eating in a shorebird. II. Optimising gizzard size in the face of seasonal demands. *Journal of Experimental Biology* 206: 3369-3380.

Pinheiro J, Bates D, R Core Team. 2022. *nlme: Linear and Nonlinear Mixed Effect Models*. R package version 3.1-161.

Randall D, Burggren W, French K. 2002. *Eckert Animal physiology: mechanisms and adaptions, 5th edition*. Freeman, New York.

Rathbun GB. 1979. The social structure and ecology of elephant-shrews. *Advances in Ethology*. Paul Parey, Berlin.

Rathbun GB. 2005. Macroscelidea. In: Skinner JD and Chimimba CT (eds), *The Mammals of the Southern African subregion, 3rd edition*, pp 22-34. Cambridge University Press, Cambridge, UK.

Rezende EL, Bacigalupe LD. 2015. Thermoregulation in endotherms: physiological principles and ecological consequences. *Journal of Comparative Physiology B* 185: 709-727.

Ritchie ME. 1998. Scale-dependent foraging and patch choice in fractal environments. *Evolutionary Ecology* 12: 309-330.

Ribble DO, Perrin MR. 2005. Social organisation of the Eastern rock elephant-shrew (*Elephantulus myurus*): the evidence for mate guarding. *Belgian Journal of Zoology* 135: 167-173.

Robertson JK, Mastromonaco G, Burness G. 2020. Evidence that stress-induced changes in surface temperature serve a thermoregulatory function. *Journal of Experimental Biology* 223: jeb213421.

Rosenzweig ML. 1974. On the evolution of habitat selection. *Proceedings of the 1st International Congress of Ecology*, 401-404.

Roxburgh L, Perrin MR. 1994. Temperature regulation and activity pattern of the round-eared elephant shrew *Macroscelides proboscideus*. *Journal of Thermal Biology* 19: 13-20.

Sánchez F, Korine C, Kotler B, Pinshow B. 2008. Ethanol concentration in food and body condition affect foraging behaviour in Egyptian fruit bats (*Rousettus aegyptiacus*). *Naturwissenschaften* 95: 561-567.

Sanin YL, Cabrera AMZ, Morales AMT. 2015. Adaptive responses to thermal stress in mammals. *Revista de Medicina Veterinaria* : 121-135.

Scheffers BR, Edwards DP, Diesmos A, Williams SE, Evans TA. 2014. Microhabitats reduce animals exposure to climate extremes. *Global Change Biology* 20: 495-503.

Searle KR, Hobbs NT, Wunder BA, Shipley LA. 2006. Preference in patchy landscapes: the influence of scale-specific intake rates and variance in reward. *Behavioural Ecology* 17: 315-323.

Skinner JD, Smithers RHN. 1990. The mammals of the southern African subregion (2nd ed). University of Pretoria, Pretoria.

Skinner J, Chimimba C. 2005. The mammals of the Southern African Sub-region (3rd ed.). Cambridge University Press, Cambridge.

Smithers RHN. 1971. The mammals of Botswana. *National Museums of Rhodesia, Museum Memoir* 4: 1-340.

Smithers RHN. 1983. The mammals of the southern African subregion. University of Pretoria, Pretoria.

Smit HA, Robinson TJ, Watson J, Janse van Vuuren B. 2008. A new species of elephant-shrew (Afrotheria: Macroscelidea: *Elephantulus*) from South Africa. *Journal of Mammalogy* 89: 1257-1269.

Smit HA, Watson J, Janse van Vuuren B. 2010. Relative importance of habitat connectivity in shaping the genetic profiles of two southern African elephant-shrews. *Journal of Biogeography* 37: 857-864.

Smit B, Harding CT, Hockey PAR, McKechnie AE. 2013. Adaptive thermoregulation during summer in to populations of an arid-zone passerine. *Ecology* 94: 1142-1154.

Smit B, Zietsman G, Martin RO, Cunningham SJ, McKechnie AE, Hockey PAR. 2016. Behavioural responses to heat in desert birds: implications for predicting vulnerability to climate warming. *Climate Change Responses* 3: https://doi.org/10.1186/s40665-016-0023-2

Sotillo A, Baert JM, Müller W, Stienen EWM, Soares AMVM, Lens L. 2019. Time and energy costs of different foraging choices in an avian generalist species. *Movement Ecology* 7: 41.

Speakman JR. 1999. The cost of living: field metabolic rates of small mammals. *Advances in Ecological Research* 30: 177-297.

Speakman JR, Król E. 2010. Maximal heat dissipation capacity and hyperthermia risk: neglected key factors in the ecology of endotherms. *Journal of Animal Ecology* 79: 726-746.

Springer MS, Cleven GC, Madsen O, Jong de WW, Waddell VG, Amrine HM, Stanhope MJ. 1997. Endemic African mammals shake the phylogenetic tree. *Nature* 388: 61-64.

Terrien J, Perret M, Aujard F. 2011. Behavioural thermoregulation in mammals: a review. *Frontiers in BioScience* 16: 1428-1444.

Thompson ML, Cunningham SJ, McKechnie AE. 2018. Interspecific variation in avian thermoregulatory patterns and heat dissipation behaviours in a subtropical desert. *Physiology & Behaviour* 188: 311-323.

Van Buskirk J. 2012. Behavioural plasticity and environmental change. In: Candolin and Wong (Eds). *Behavioural responses to a changing world: mechanisms and consequences*. New York, Oxford University Press.

van de Ven TMFN, McKechnie AE, Cunningham SJ. 2019. The costs of keeping cool: behavioural trade-offs between foraging and thermoregulation are associated with significant mass losses in an arid-zone bird. *Oecologia* 191: 205-215.

van de Ven TMFN, McKechnie AE, Er S, Cunningham SJ. 2020. High temperatures are associated with substantial reductions in breeding success and offspring quality in an arid-zone bird. *Oecologia* 193: 225-235.

Venables WN, Ripley BD. 2002. Modern Applied Statistics with S, Fourth edition. Springer, New York. https://www.stats.ox.ac.uk/pub/MASS4/

Visser ME. 2008. Keeping up with a warming world: assessing the rate of adaptions to climate change. *Proceedings of the Royal Society B* 275: 649-659.

Walton ME, Kennerley SW, Bannerman DM, Phillips PEM, Rushworth MFS. 2006. Weighing up the benefits of work: behavioural and neural analyses of effort-related decision making. *Neural Networks* 19: 1302-1314.

Welbergen JA, Klose SM, Markus N, Eby P. 2008. Climate change and the effects of temperature extremes on Australian flying-foxes. *Proceedings of the Royal Society B* 275: 419-425.

Whitfield MC, Smit B, McKechnie AE, Wolf BO. 2015. Avian thermoregulation in the heat: scaling of heat tolerance and evaporative cooling capacity in three southern African arid-zone passerines. *The Journal of Experimental Biology* 218: 1705-1714.

Wickham H. 2016. *ggplot2: Elegant graphics for data analysis*. Springer-Verlag New York. https://ggplot2.tidyverse.org/

Williams JB, Tieleman B. 2005. Physiological adaptions in desert birds. *BioScience* 55: 416-425.

Williams SE, Shoo LP, Isaac JL, Hoffmann AA, Langham G. 2008. Towards an integrated framework for assessing the vulnerability of species to climate change. *PLoS Biology* 6: e325.

Wolf BO. 2000. Global warming and avian occupancy of hot deserts; a physiological and behavioural perspective. *Revista Chilena de Histroria Natural* 73: 395-400.

Woodall PF, Woodall Lb, Bodero DAV. 1989. Daily activity patterns in captive elephant shrews (Macroscelididae). *African Journal of Ecology* 27: 63-76.

Yahnke CJ, Dizney L, Varner J, Duggan JM, Erb LP, Lanier HC, Flaherty EA, Connors PK, Hanson JD. 2020. Sorry to eat and run: a lesson plan for testing trade-off in squirrel behaviour using Giving up densities (GUDs). *CourseSource* https://doi.org/10.24918/cs.2020.30.

Ydenberg RC, Welham CVJ, Schmid-hempel R, Schmid-hempel P, Beauchamp G. 1994. Time and energy constraints and the relationships between currencies in foraging theory. *Behavioural Ecology* 5: 28-34.

Zeilies A, Kleiber C, Jackman S. 2008. Regression models for count data in R. Journal of Statistical Software 27: 1-25.

Zeilies A, Köll S, Graham N. 2020. Various versatile variances: An object-oriented implementation of clustered covariance in R. *Journal of Statistical Software* 95: 1-36.

Appendix

Table 1. Individual PIT-tagged *Elephantulus rupestris* data, including sex, age and weight.

Individual	Tag number	Sex	Age	Weight	Capture date
Atticus	3D9.20D4506767	Male	Adult	/	September 11 2021
Attenborough	3D9.20D4518C2E	Male	Adult	55	September 8 2021
Badger	3D9.20D4518C2E	Female	Adult	55	September 8 2021
Gizmo	3D9.20D4506E98	Male	Adult	53	September 10 2021
Beesly	3D9.20D4518B93	Male	Adult	57	September 16 2021
Dwight	3D9.20D4507FD6	Male	Adult	64	October 6 2021
Finn	3D9.20D45189FA	Male	Adult	58	November 5 2021
Scout	3D9.20D4507BCE	Male	Juvenile	19	November 10 2021
Franklin	3D9.20D4518C01	Male	Juvenile	23	November 10 2021
Delilah	3D9.20D4506540	Female	Juvenile	25	November 10 2021
Don Pablo	3D9.20D44F2800	Male	Sub-adult	43	December 10 2021
Jem	3D9.20D4518BDA	Male	Sub-adult	36	December 13 2021

Table 2. All individual *Elephantulus rupestris* that were captured, recaptured or contributed to body temperature data over the study period (2021-2022).

Individual	**Tag number**	**Capture date**	**Recaptured**	**Recapture times**	**PIT-tag reader**
Atticus	3D9.20D4506767	31st August	✓	4	x
Attenborough	3D9.20D4518C2E	8th September	x	0	✓
Badger	3D9.20D4522B30	8th September	x	0	✓
Gizmo	3D9.20D4506E98	10th September	✓	3	✓
Beesly	3D9.20D4518B93	16th September	✓	1	x
Dwight	3D9.20D4507FD6	6th October	✓	2	x
Finn	3D9.20D45189FA	5th November	✓	1	✓
Scout	3D9.20D4507BCE	10th November	x	0	x
Franklin	3D9.20D4518C01	10th November	✓	1	x
Delilah	3D9.20D4506540	10th November	x	0	✓
Don Pablo	3D9.20D44F2800	10th December	x	0	✓
Jem	3D9.20D4518BDA	13th December	x	0	x