Social, ecological and personality factors influencing bat-eared fox foraging behaviour

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GENERAL ABSTRACT

The foraging behaviour of carnivores has been extensively studied and while we know quite a bit about the foraging behaviour of generalist carnivores, there are still many unanswered questions about the foraging behaviour of dietary specialists. There’s renewed interest in dietary specialists as their specialization not only constrains dietary options, but in some cases their social behaviour as well. The bat-eared fox (*Otocyon megalotis*) is a group-living, group-foraging mesopredator that forages almost exclusively on termites (*Hodotermes* sp.). Diet plays a pivotal role in the social dynamics of these canids, contributing to the cohesiveness of this group-living species and impacting on their parenting behaviour, as males cannot provision females or offspring with large food items, like many canid males do. However, most information on its diet comes mainly from scats and stomach content analyses and we know little about its foraging behaviour in the wild, diet choices across seasonal variations and how social, environmental and phenotypic factors impact on these foxes’ foraging behaviour. To address these gaps in literature, I documented the foraging behaviour of 20 free-living adult foxes, on a daily basis, over a 2-year observational period, making it the first study to date to have such a fine scale data on the diet and foraging behaviour of this canid. I found that while they foraged on no fewer than 18 different food categories in varied quantities across seasons, termites (*Hodotermes mossambicus*) constituted the majority of fox diet, ranging from 57 % in warmer seasons to 82 % in the colder seasons. Importantly, I simultaneously documented the invertebrate prey communities within their home ranges using varied assessment techniques, linking prey choice with prey availability. I found that their utilisation of supplementary food may not have been purely opportunistic as they would selectively feed on larger prey such as beetles, when available. Furthermore, I demonstrated through a literature review that local conditions had considerable effects on their diet types, and that despite being termite specialists, they showed dietary flexibility based on both temporal and spatial variations in food abundance. To understand how individual phenotype influenced their foraging behaviour, I evaluated individual differences (repeatability) and behavioural syndromes (correlations) in a suite of virtually unexplored behavioural traits (foraging and movement traits) in this species. I demonstrated that there were low individual differences in these traits thus showcasing a foraging specialist that has evolved to behave similarly in these behavioural traits. Furthermore, I demonstrated a lack of correlations between these traits, suggesting that these traits are unlikely to constrain each other and likely to evolve independently. Finally, previous research has suggested that females require extensive foraging periods to meet with the energetic demands of lactation, while males "baby-sit" offspring. However, there has been no investigation of changes in physiological stress or foraging behaviour in bat-eared fox parents. I demonstrate for the first time how parents utilised varied foraging strategies to maintain fairly low levels of physiological stress (as measured by faecal glucocorticoid metabolites). Presumably due to the shorter foraging periods available to them, male parents consumed more large food items than the female parent and non-parents when they were not at the den with offspring. The mother in this study population, by contrast, exhibited some unusual hunting behaviour, including caching rodents. This research is the first recording of surplus killing and caching behaviour ever documented in these myrmecophagous canids. My research therefore provides evidence of limited flexibility in the foraging behaviour of a dietary specialist, as it changes with seasonal and reproductive demands. Importantly, limited flexibility in dietary specialists as shown here in the bat-eared fox may have extensive implications for their survival in the face of rapid environmental changes and social stressors.

Keywords: caching, diet, foraging behaviour, limited flexibility, mesopredator, *Otocyon megalotis*, seasonal variation.

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Prelude:

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Postlude:

A lesson in perseverance and humility

I moved to Qwaqwa campus from a prestigious South African University with an MSc. degree (*cum laude*) —completed on time and with all chapters published! I had *no idea* what awaited me on this PhD journey —that I would be humiliated and humbled by life, endure many hurdles (both internally and externally), muster up resilience, accrue grey hairs and all of *eight awards* totalling R42,500 (*Forty-two thousand five hundred rand*) in monetary prizes from several PhD competitions. As I continue to *strive for excellence*, I will stay grounded in humility and kindness (God knows, the world *needs* kindness right now). Above all, I chose to remain anchored in Jesus Christ my Rock and Saviour!

DECLARATION

"I, Keafon Ranissi Jumbam, declare that the PhD research dissertation or interrelated, publishable manuscripts/published articles that I herewith submit for the PhD qualification in Zoology at the University of the Free State is my independent work, and that I have not previously submitted it for a qualification at another institution of higher education."

"I, Keafon Ranissi Jumbam, hereby declare that I am aware that the copyright is vested in the University of the Free State."

"I, Keafon Ranissi Jumbam, hereby declare that all royalties as regards to intellectual property that was developed during the course of and/or in connection with the study at the University of the Free State, will accrue to the University."

Signature: ____

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CHAPTER 1

GENERAL INTRODUCTION

1.1. Factors affecting foraging behaviour in carnivores

Foraging behaviour of animals comprises the search for, and acquisition of food, which has direct fitness consequences for individuals (Dingemanse et al. 2002). Unlike herbivorous mammals that do not require hunting strategies to obtain food, carnivores often employ complex and multiple hunting techniques to effectively capture their prey (Stander 1991; Creel and Creel 1995; Muro et al. 2011). Their social system, environmental stochasticity, and phenotypic variation are central in individual hunting success and therefore, fitness. For instance, in certain carnivore social systems, cooperative efforts in hunting enhances prey capture, protecting the kill from scavengers and improving the quality, quantity and range of food types consumed (Lamprecht 1981; Scheel and Packer1991; Stander 1991; Fanshawe and Fitzgibbon 1993; Creel and Creel 1995). However, hunting as a group can also bring about several disadvantages including inter-specific competition, with larger hunting packs reducing each individual's food intake (Creel and Creel 1995), and the increased need of such a large pack to defend its limited food resources from outside competitors (Eide et al. 2004). Environmental factors such as seasonal changes may lead to predictable variation in food availability (Eide et al. 2004), while events such as droughts may considerably alter this availability (Loveridge et al. 2006), thus affecting the foraging success of predators. Phenotypic variation such as individual differences in behaviour (i.e. personality type) may equally influence how animals obtain food through variations in exploratory/movement traits (e.g. speed and percentage of home range explored; Spiegel et al. 2017). Other personality factors include individual differences in behavioural traits along the boldness-shyness spectrum (Wesley et al. 2012; Patrick et al. 2017), risk perception (Urban and Richardson 2015; Welch et al. 2017), and innate energetic differences (Dingemanse and Wolf 2013), all of which could impact on individual exploratory tendencies and ultimately, on foraging success. Apart from personality related factors, physiological factors such as individual's age (Carss 1995), sex (Beck et al. 2007) health (Veasey et al. 1996), and hormonal variations (Guenther et al. 2018) can also affect foraging behaviour. Furthermore, early and past life experiences are likely to influence individual's learning abilities and consequently shape their foraging behaviours (see Dingemanse and Wolf 2013; Biro and Stamps 2015). Given the complexities surrounding the foraging behaviours of carnivores, I will be exploring in detail below, how their social systems, environmental changes and phenotypic variations affect their foraging behaviour.

1.1.1. Individual variation: repeatability and behavioural syndromes

Traditional animal behavioural studies have been mainly at the level of the population, with broad-scale patterns derived from average behaviours and no distinction made between individuals (Wilson 1998). However, because natural selection occurs at the level of the individual, and individual differences could have a genetic basis for evolution (Lewontin 1970; Boake 1989; Dingemanse et al. 2002; Nussey et al. 2007), the importance of individual variability assessments cannot be overemphasized. Individual level assessments have unmasked striking behavioural patterns often concealed at higher levels (Nussey et al. 2007; Dingemanse and Wolf 2010; Welch et al. 2018) such as individual variations in vigilance patterns which could impact on how individuals perceive and manage predator pressures (Welch et al. 2018). Additionally, individual level assessments can unravel biologically important behavioural patterns useful in making predictions about environmental effects on species (Roche et al. 2016). Moreover, individual level responses to environmental variables may provide insight into the origin and maintenance of foraging strategies such as specialisations at large spatial scales (Patrick et al. 2014).

In many species, individuals exhibit distinct differences in behaviour or “personalities” that are consistent over time and across contexts (Sih et al. 2004). Personality types affect the depth of resource exploration, movement pathways and foraging behaviour of individuals. For instance, bolder individuals tend to have less tortuous movement trajectories (Wesley et al. 2012), shallow resource exploratory tendencies and high dispersive potential (Wesley et al. 2012; Spiegel et al. 2017). Bolder individuals are therefore more likely to explore new territories, encounter new food resources and extend their diet breadth compared to their shy counterparts (Wesley et al. 2012). Assessing correlations (i.e. behavioural syndromes; Sih et al. 2004) between exploratory and foraging behaviours is therefore an important determinant factor of the dispersive potential of a species. To date, no study has examined behavioural syndromes beyond aggression-boldness syndromes to include diet breadth and exploratory behaviours of individuals. Additionally, there has been limited behavioural research focusing on individuals and particularly in free-living carnivores.

Direct behavioural studies are crucial to evaluate individual differences in behaviour and particularly in free-living animals, as such studies provide more reliable estimates of individual differences and natural selection than laboratory-based studies (Dingemanse et al. 2002; Dingemanse and Wolf 2013; Biro and Stamps 2015). However, studies on carnivore foraging behaviour are limited to a few diurnal taxa such as banded mongooses (*Mungos mungo*) and meerkats (*Suricata suricatta*), and even in these species, there has been no exploration of behavioural repeatability and plasticity. Further, carnivore biologists have not moved significantly past population-level studies of spatial exploration (Young and Shivik 2006). The challenge, of course, is that many carnivores are nocturnal, with long daily travelling distances, making repeated observations of individuals (necessary for repeatability studies) quite difficult. In this study therefore, I assessed individual differences in a suite of exploratory and foraging traits in free-living, nocturnal bat-eared foxes (*Otocyon megalotis*), to understand how these traits vary and co-vary individually. These foxes have a monogamous social system and forage socially, all of which may affect foraging behaviour at an individual and population level.

1.1.2. Social systems

Social carnivores do not necessarily just forage as a group but may employ cooperative hunting behaviour that enhance their prey-capture success. For instance, the grey wolf (*Canis lupus*) uses multiple tactics such as prey encircling, ambushing and relay running to outpace its prey (Muro et al. 2011). Such cooperative hunting strategies can be combined flexibly. The lion (*Panthera leo*), for example, typically stalks its prey by encircling, followed by ambush (Stander 1991). African wild dogs (*Lycaon pictus*) often depend on speed to capture their prey (Hubel et al. 2016) and chase distance has been shown to significantly decrease with pack size (Creel and Creel 1995). Nonetheless, hunting success in wild dogs is often related to other factors such as distance at which prey flee, age and group size of prey, and pack size of the wild dogs (Fanshawe and Fitzgibbon 1993). In some rare cases, pack size does not impact on hunting success (Lamprecht 1981) but most often, pack sizes provide several other benefits such as the ability to effectively defend and rapidly consume carcasses, leaving little room for interspecific competition from scavengers (Lamprecht 1981). Wild dog packs have been shown to significantly reduce interspecific competition from spotted hyaenas (*Crocuta crocuta*) through improved defence of their kill (Fanshawe and Fitzgibbon 1993). Another advantage to cooperative hunting groups is the improved quality and range of food types consumed. For instance, while individual wild dogs can hunt Thomsons gazelles (*Gazella thompsoni*), they are able broaden their scope to include all ages of blue wildebeest (*Connochaetes taurinus*) when hunting as a pack (Fanshawe and Fitzgibbon 1993). Similarly, lions can successfully hunt larger prey such as elephant calves when in a pack (Loveridge et al. 2006).

Hunting as a group, however, has several disadvantages especially during food scarcity. For instance, energy intake per individual reduces with increased pack sizes (Creel and Creel 1995), which ultimately curbs pack sizes through natural selection to maximise per capita gain (Lamprecht 1981; Eide et al. 2004). Additionally, energy expenditure and division of labour between sexes during hunts is typical uneven within lion packs where male participation is often limited (Scheel and Packer1991; Stander 1991; Lehmann et al. 2008), particularly with easy to capture preys such as warthogs (*Phacochoerus africanus*; Lehmann et al. 2008). These discrepancies in division of labour and sometimes food partitioning (but see Lehmann et al. 2008), could become highly divisive through intraspecific food competition in the face of food scarcity, potentially even leading to the exclusion of individuals from hunting packs (Eide et al. 2004).

Not all social carnivores are cooperative hunters. For instance, the yellow mongoose (*Cynictis penicillata*) forages alone despite being a group-living herpestid (Veron et al. 2004; le Roux et al. 2009). This likely reduces their conspicuousness and therefore vulnerability to predation that comes with large foraging groups (le Roux et al. 2009). Indeed, the presence of conspecifics during foraging has been shown to negatively affect foraging success in this species due to increased individual vigilance (le Roux et al. 2009). Solitary predators have developed several strategies to increase their hunting efficiency. For instance, the yellow mongoose adopts inconspicuous vigilance posture and makes extensive usage of habitat features such as vegetation cover and proximity to burrows to increase safety (le Roux et al. 2009). Meerkats on the other hand, are group living and group-foraging mesopredators that forage for themselves within the group (Doolan and Macdonald 1996) but also cooperate in pup-provisioning (Thornton 2007; Clutton-Brock et al. 2008). They benefit from communal vigilance (le Roux et al. 2009) as often one or more members of the group play a sentinel role (Ewer 1963; Moran 1984). By producing several discrete calls that vary depending on predation risk, group members are better able to escape predation (Rauber and Manser 2017). The viability of the social foraging strategy in meerkats is partly due to their generalist, largely insectivorous foraging habits, with the relative predictability and dispersed distribution of their vertebrate prey facilitating group-living in this species (Doolan and Macdonald 1996). Other group-living social foragers include the banded mongoose which also communally provisions its pups using helpers (Hodge 2005) and, similar to meerkats, feeds predominantly on invertebrates and particularly millipedes and beetles (Rood 1975). Its foraging strategy involves utilising spaces often ignored by or inaccessible to other mesopredators such as underneath stones and arboreal niches including holes and crevices in trees (Rood 1975). Other large group-living social foragers such as the bat-eared fox reduce interspecific food competition by exploring exclusive foraging niches, through an extremely specialised diet comprised mainly of termites (Berry 1981).

Many carnivores are solitary and employ specific foraging strategies. Larger solitary predators include the cheetah (*Acinonyx jubatus*; Scantlebury et al. 2014; Elbroch et al. 2017), which uses short bursts of astonishing high speeds (Scantlebury et al. 2014) facilitated by the flexible, independent sets of leg and back muscles, enabling longer strides during hunts (Hildebrand 1959). Its slender build, use of open habitats, balance between energy expendable in hunting and energy intake from prey, all contribute to the success of cheetah's hunting tactics (Scantlebury et al. 2014). The puma (*Puma concolor*) is equally a solitary predator (Williams et al. 2014; Elbroch et al. 2017) that uses sit-and-wait as well as stalk and pounce hunting tactics (Williams et al. 2014) Its prey acquisition success is based on reducing hunting costs by being cryptic and selecting rugged habitat types to enable its varied hunting methods (Williams et al. 2014). It's an efficient hunter, precisely matching energy exerted on pouncing on its prey with prey size, thus limiting hunting costs (Williams et al. 2014). The aardvark (*Orycteropus afer*) is of particular interest as a large solitary forager (Melton 1976) because it predates predominantly on ant and termite nests (Taylor and Skinner 2000; Taylor et al. 2002) and such insect-based diet is said to allow social foraging because the prey items are renewable (Waser 1981). Nonetheless, the aardvark prefers to forage alone partly because of its acute sense of smell and hearing which propels it to quickly seek shelter if disturbed (Melton 1976). In other words, it maximises its foraging efficiency without compromising its safety by foraging solitarily. Therefore, despite assumptions about insect-eaters being social foragers, exceptions do exist.

1.1.3. Reproduction

The breeding season presents unique challenges to carnivores' foraging behaviour, as lactating females need to maintain a positive energetic balance while gestating and/or lactating. This is the only time when even solitary carnivores are temporarily social and are responsible for feeding not only themselves, but also offspring. Lactation presents high nutritional demands (Oftedal and Gittleman 1989), which can be facilitated either through provisioning by the male (Rasmussen and Tilson 1984; Bell 2010), or —potentially —foraging adaptations in the mother. Given that in many monogamous species, parental investment is at its peak in the first month following parturition due to pup vulnerability to predation (Kauhala et al. 1998), and that stress levels of fathers could increase before parturition (da Silva Mota et al. 2006), it would be reasonable to expect variation in stress levels with parenting, especially for parents that invest time in pup rearing at the cost to foraging time. Parents are constrained by time budgets and constantly need to navigate between spending time away foraging for themselves or for pup-provisioning, and spending time at the den to protect pups (Royle et al. 2014; Figure 1.1). How these parenting pressures affect parents physiologically in terms of their stress levels is not well understood.

Figure 1.1. A male bat-eared fox parent watching over its pup at the den

Evaluating stress levels in species is crucial to identify causes to stress which could have direct implications for animal reproduction and survival (Van der Weyde et al. 2016). Faecal glucocorticoid metabolite (fGCM) assessments can be used as a proxy for physiological stress in animals (Ganswindt et al 2010; van Kesteren et al. 2012; Van der Weyde et al. 2016). For instance, in African wild dogs, captive females have been shown to have higher fGCM concentrations than free-ranging females, but fGCM levels were not affected by breeding season, age or sex (Van der Weyde et al. 2016). Rather, social hierarchy (i.e. dominance) was a key driver of stress levels within this species, as dominant males had significantly higher fGCM concentrations than unrelated subordinates (Van der Weyde et al. 2016). Similarly, in Ethiopian wolves (*Canis simensis*) where male helpers provision pups regardless of paternity, pup rearing was shown to have no significant effect on their stress levels (van Kesteren et al. 2012). Nonetheless dominant males were seen to have significantly higher fGCM levels than subordinates due to higher rates of aggression and mate protection by these dominant males (van Kesteren et al. 2012). Thus, we are left with many unanswered questions about how carnivores adapt behaviourally and physiologically to the demands of parenting.

1.1.4. Interspecific competition

Intense resource competition with food scarcity may not only force species to forage outside of their preferred food range, but could lead to the evolution of specialists, provided such resources are maximised to the exclusion of generalists (Futuyma and Moreno 1988). Specialist foraging strategies become increasingly beneficial when species maximise their energy intake (Berumen and Pratchet 2008) through, for instance, specialised mandibular adaptations to effectively assimilate energy, as with the bat-eared fox (Maas and Macdonald 2004). Having a specialised diet allows for exploitation of different niches and therefore facilitates co-existence with other predators. For instance, Kamler et al. (2012a) found little overlap between the diets of three sympatric canid species —the Cape fox (*Vulpes chama*), the bat-eared fox and black-backed jackal (*Canis mesomelas*), with the bat-eared fox having the most specialised diet among them. Successful coexistence among these canids was also aided by differing levels of diurnal and nocturnal activities between them.

Other carnivores tend to avoid competition through an opportunistic, generalist foraging strategies (Hanski et al. 1991; Symondson et al. 2002). Such predators are said to have catholic tastes, feeding on any prey items they come across and are hence referred to as "Jack of all trades" (Ali and Agrawal 2012; Barkae et al. 2012). Generalist feeders include black-backed jackals with their diet ranging from mammals to insects and fruits (Kamler et al. 2012b), the red fox (*Vulpes vulpes*) known to consume hares, birds and murids among others (Dell'Arte et al. 2007) and coyotes (*Canis latrans*) whose diet is equally broad and includes lagomorphs, fruits and seeds (McKinney and Smith 2007). A generalist foraging strategy allows species to minimise energy costs associated with prey search (Hughes 1979), exploit a wider range of nutritionally balanced diet (Bernays and Minkenberg 1997), and withstand temporary reductions in the availability of their preferred prey base (Berumen and Pratchet 2008). Generalist species have an added advantage of exploiting anthropogenic resources. For instance, Fedriani et al. (2001) showed that exploiting anthropogenic resources increased coyote numbers.

Regardless of the foraging strategy employed, carnivores seek to optimise energy intake through low handling cost and time. Moreover, carnivores can vary their foraging strategies based on environmental factors such as seasonal variations. The arctic fox for instance, despite being a lemming (*Lemmus lemmus*) specialist, opportunistically feeds on birds, voles and shrews, reindeers and hares based on seasonal availability (Elmhagen et al. 2000). Similarly, the red fox —a generalist species, is largely dependent on *Microtus* voles*,* particularly in winter when alternative prey is scarce. (Dell'Arte et al. 2007). Clearly, foraging strategies in carnivores can be dynamic and vary along the specialist-generalist continuum.

1.1.5. Prey abundance and behaviour

Seasonal changes, which alter the behaviour of prey, impact on carnivore prey choice. Rainfall during the months of March and November in northern Tanzania promotes vegetation growth, which is then used by ungulates such as Thomson's gazelle for protecting their young (Robinette and Archer 1971). The term "hiders" is used to describe such animals that hide their young in tall vegetation (Nowak et al. 2000; Klare et al. 2010). Birthing peak of ungulate lambs therefore correlates with wet seasons (Robinette and Archer 1971) and this impacts on the quantities of hiders consumed by predators. For instance, Klare et al. (2010) noted that during ungulate birthing peak, black-backed jackal fed almost exclusively on hiders regardless of availability of other species of ungulates. Cheetah have also been shown to select ungulate prey depending on prey birth peak (Cooper et al. 2007). Interestingly, birthing peak of prey can also instigate reproductive success in carnivores such as spotted hyaenas (Holekamp et al. 1999).

Variation in prey abundance with environmental conditions can also impact on the spatial distribution of carnivores. For instance, the arctic fox expands and contracts its home range in relation to its prey source distribution (Eide et al. 2004). This fox also shows varying degrees of territoriality depending on food availability, with food scarcity driving territoriality (Eide et al. 2004). Food scarcity as a result of unfavourable environmental conditions such as drought tend to force animals such as lions, hyaenas and elephants (*Loxodonta africana*) to travel long distances in search of food and watering holes (Loveridge et al. 2006). Such travels provide opportunities for predators to target vulnerable species. Lions, for instance, switch diet from their preferred ungulates to predominantly elephant calves during dry spells (Loveridge et al. 2006). Environmental factors therefore play a significant role in carnivore prey choice and spatial ecology. However, the study of predator foraging behaviour is largely constrained to indirect methods, inhibiting our fine-scale understanding of predator behaviour in a changing environment.

1.2. Methods for describing foraging behaviour in carnivores

The study of foraging behaviour in carnivores is often centred on a description of diet breadth (food types consumed), using a suite of non-behavioural data. Importantly, diet breadth could be a useful indicator of a species' potential geographical range size and a crucial parameter for predicting the likelihood of its extinction (Slayter et al. 2013). Studies on diet breadth use varied methods including stable isotope analyses of whiskers (Voigt et al. 2018), scats, and the manual processing of stomach or scat content (Nel 1978, Berry 1981, Angerbjörn et al. 1994, Stuart et al. 2003). Of these methods, scat analyses are most prevalent in the literature because they are easy to collect and non-invasive (Mukherjee et al. 1994). However, methodological limitations include determining accurately when the scat was deposited, locating and collecting enough samples, correct sample identification and processing time. Stable isotope analyses of hair samples are also becoming increasingly common, which advances the research field in understanding the overall diet of animals throughout its lifetime, and not just for a specific season (Angerbjörn et al. 1994). However, isotope techniques are costly and unable to differentiate between individual prey items —they are useful for broad generalisations of food categories, such as marine vs terrestrial prey (Klare et al. 2011). Stomach-content analyses make use of carcasses, but they are invasive, time consuming and often impacted by the degree of decomposition of the carcass (see Berry 1981). Moreover, controversy surrounds the use of scats and stomach content, such as identification bias from similar body parts amongst different prey items resulting in erroneous diet descriptions (Dickman and Huang 1988).

Modern technology has significantly advanced our understanding of animal foraging behaviour beyond the limits of traditional methods such as scats and stomach content assessments. Camera traps are deemed useful for snapshot capturing of cryptic and elusive species but can be limiting in their content as they often provide only basic information regarding presence or absence of animals (Swann et al. 2011). Nonetheless, better, high resolution equipment is currently being used to understand a wide range of animal behaviour without the interference of human presence. For instance, temperature and motion-sensitive bio-loggers have been used to monitor the deleterious effect of drought in aardvarks, and results show progressive temperature decline leading to animal death (Rey at al. 2017). Using miniature data-loggers, Hetem et al. (2012) were able to show that size differences did not matter when comparing body temperature and activity between large and small mammals. Both Arabian oryx (*Oryx leucoryx*) and Arabian sand gazelle (*Gazella subgutturosa marica*) were seen to respond to variations in environmental conditions by employing similar behavioural and body regulatory techniques (Hetem et al. 2012). Similarly, by using miniature temperature-sensitive bio-loggers and fitted GPS satellite radio-telemetry collars, Trethowan et al. (2017) were able to not only track animal movements to watering holes but to decipher vital information about core body temperature fluctuations in these animals. They found that animal mane size or the lack thereof had no effect on core body temperatures in lions (Trethowan et al. 2017). Even more fascinating is the ability of modern technology to capture complex foraging behaviours in animals. For instance, Hubel et al. (2016) utilised high-resolution GPS and inertial technology which is sensitive to animal's relative body position and provides detailed insight into its foraging behaviour and speed levels. Equally, by using GPS satellite radio-telemetry collars and acoustic accelerometer bio-loggers, Trethowan et al. (2017) could match movement patterns in lions with audio data to determine whether or not the lions were feeding.

Modern technology is thus a crucial tool that advances our knowledge of animal behaviour, especially for species that are either not accessible on foot or could be a threat to human safety. Despite these advantages, technology is not without drawbacks, with the cost of equipment a primary limiting factor to its implementation —especially in developing nations. Additionally, the use of expertise from trained and licenced personnel such as veterinary surgeons is needed for ethical purposes and for effective implementation of equipment such as collars and bio-loggers. This could be a costly endeavour because such expertise is often scarce and financially demanding. There is also the issue of managing large volumes of data and/or retrieving data from equipment in the event of animal death, signal interference, equipment malfunction or theft (see Cagnacci et al. 2010; Swann et al. 2011). Therefore, in situations where advanced technology is impractical, direct behavioural observations are a useful and sometimes better tool for providing detailed information on animal behaviour, particularly with regards to foraging behaviour.

Direct behavioural observations, when feasible, can offer detailed data on animal age, sex, prey choice variation on a daily basis and also therefore subtle changes in behaviour over time. Direct observations are also useful when the application of technology is not possible. For example, where young animals are not ethically allowed to be collared, direct observations can describe the foraging behaviour of juvenile individuals, and document learning over time (Thornton and McAuliffe 2006; Thornton 2008). Moreover, through direct observations, prey choice can be recorded *in-situ*, thus saving time in processing dietary data from scats and mitigating taxonomical errors in identification of prey items consumed (Dickman and Huang 1988). Furthermore, direct behavioural observations are necessary to determine if prey were captured in an active hunt, provisioned, or scavenged. Additionally, only behavioural observations can document hunting techniques such as ambushing and encircling (Creel and Creel 1995).

The foraging behaviour of an animal is best understood within the context of food availability (Hayward et al. 2017), yet combined studies of food availability with diet consumed are still rare for carnivores (Kuntzsch and Nel 1992). Food availability assessments allow for unravelling of subtle foraging behaviours such as prey preference (Hayward et al. 2017), efficient foraging strategies (Graeb et al. 2004) and reasons thereof. For instance, the grey wolf limits prey handling costs associated with prey search and capture by preferentially selecting larger prey (Meriggi et al. 1996). Importantly, assessing food availability enables our understanding of key factors driving certain foraging strategies in species. For instance, the Arctic fox is a small canid species that adopts a generalist foraging strategy in coastal areas due to the availability of a wide range of prey (Dalerum et al. 2012), but becomes specialised in tundra areas with a more limited resources (Elmhagen et al. 2000). Despite the clear advantages of conducting prey availability assessments, few diet studies have incorporated such assessments which hinders our holistic understanding of animal foraging behaviour (Hayward et al. 2017).

In this study, I combined a suite of techniques to describe population-level and individual variation in foraging behaviour in a dietary specialist, the bat-eared fox. My data sources included faecal samples (yielding data on circulating hormone levels), direct observations, GIS data, and prey availability assessments. This suite of techniques was eminently useful in describing the foraging behaviour of a termite-eating canid whose social system and reproductive behaviour may be strongly determined by its restrictive diet.

1.3. Bat-eared foxes: specialist foragers under pressure

The bat-eared fox is named for its peculiar large ears that offer it a heightened sense of hearing while hunting (Renda and le Roux 2017). It is a small canid (< 5 kg), classified as least threatened (Hoffmann 2014) with life expectancy of ≤ 14 years in captivity. Longevity records in the wild are rare, but a study has reported a life span of nine years for free-living bat-eared foxes (Kamler and Macdonald 2006). This low life expectancy in the wild is partly due to predation and diseases, as bat-eared foxes are important carriers of diseases such as rabies, which spread rapidly by contact through the highly social structure of these canids (Maas 1993; Kamler et al. 2017). They are preyed upon by larger carnivores such as black-backed jackals and are mistaken for jackals by farmers and targeted as vermin (Kurberg 2005; Kamler and Macdonald 2006). The bat-eared fox is ashy grey in colour, although variants in fur hue and thickness exist with location and climatic variations. Breeding pairs are formed in winter, and pups (≤ 6) are born in summer following a gestation period of ~ 75days (Maas and Macdonald 2004). They reach dispersal age at 9 months (Maas and Macdonald 2004), although we observed dispersal in our study population at 7 months. The bat-eared fox is an annual breeder with two distinct populations —one distributed across eastern Africa (*Otocyon megalotis virgatus*) and the other, across southern Africa (*O. m. megalotis*; Malcolm 1986). The eastern African populations are known to breed earlier, from August – October (Malcolm 1986) compared with the southern populations which breed from September to December (Nel 1984; Clark 2005). Reasons for these discrepancies in breeding seasons could lie with food availability, at least for the southern populations (see Jumbam et al. 2019). The southern populations —and particularly in South Africa, are known to be diurnal in winter and nocturnal in summer (Lourens and Nel 1990). The bat-eared fox is known to feed on invertebrates and small mammals (Lamprecht 1979; Nel and Mackie 1990; Pauw 2000; Jacobs and le Roux 2015) and its main prey base is the harvester termite *Hodotermes mossambicus* (Berry 1981; Nel 1984, 1990; Stuart et al. 2003). It is also known to occasionally feed on a different species of harvester termites called *Microhodotermes viator* (Lourens and Nel 1990) depending on the geographic distribution of the termite species. The activity patterns and distribution of the bat-eared fox is linked to termite activity (Mackie and Nel 1989; Lourens and Nel 1990; Clark 2005). *Hodotermes* workers become inactive at temperatures < 11°C (Mitchell et al. 1993), which may be why the normally nocturnal fox becomes diurnally active in winter (Lourens and Nel 1990). Their dentition is well adjusted to their insectivorous diet, comprising several extra pairs of molars and teeth that are much smaller than those of other canids (Maas and Macdonald 2004). The unique mandibular arrangement which lacks carnassial shear, allows for rapid food ingestion (Maas and Macdonald 2004).

The bat-eared foxes' specialist diet may be at the heart of its skewed parental care, behaviour, and monogamous mating system. Fathers spend significant time at the den, unable to provision mothers or pups like most canids do, since it is not economically viable to carry insects back to the den (Malcolm 1986). Male parents can only provision with larger prey such as rodents and lizards when available (Pauw 2000) and they seldom regurgitate food (Lamprecht 1979). Fathers' parenting roles are vital to the survival and fitness of offspring, with den attendance positively correlated with pup survival and growth (Wright 2006). These limitations on their provisioning abilities mean that pups will depend solely on milk for survival, prompting mothers to spend more time away foraging to meet this nutritional demand (Malcolm 1986). Maternal care is nutritionally taxing in terms of nursing (Pauw 2000) and brain size investments (Gittleman 1994). In carnivore parenting systems where maternal care is predominant, mothers have bigger brains (Gittleman 1994). It is thus plausible that mothers would be physiologically stressed, but how uneven parenting in bat-eared foxes affect their foraging behaviour has not been thoroughly investigated. Given the time invested by fathers in parenting, paternal cost is likely to be considerable too, but still largely unexplored.

1.4. Study area and population

The study location is Kuruman River Reserve (KRR, 28°58'S, 21°49'E) which covers an area of 32km^2 and is situated in the Northern Cape province of South Africa. The vegetation structure is classified as Kalahari Thornveld (Low and Rebelo 1996; Clutton-Brock et al. 1999), consisting of camel and black thorns (*Acacia spp.*), thickets (*Prosopis* sp.), perennial grasses (*Stipagrostis, Aristida, Schmidtia* and *Eragrostis* spp.), perdebos (*Galenia africana*) and driedoring bushes (*Rhizogum trichotomum*). During this study, the reserve was home to a myriad of wildlife including: reptiles such as horned adder (*Bitis* sp.), birds of prey such as the martial eagle (*Polemaetus bellicosus*) which is a predator of the bat-eared fox (see Welch et al. 2017), Cape fox (*Vulpes chama*) which we saw regularly chased away from food resources by the bat-eared fox, eland (*Tragelaphus oryx*), wildebeest (*Connochaetes sp.*) and steenbok (*Raphicerus campestris*). This reserve also had varying degrees of ongoing research on the following animals: meerkat, mongooses —yellow and slender (*Galerella sanguinea*), fork-tailed drongo (*Dircrurus adsimilis*), hornbills (*Tockus* sp.), pied babbler (*Turdoides bicolor*) and Cape ground squirrels (*Xerus inauris*). The only domesticated animals on site were cattle which were few.

This study population was under observation for two years at the KRR before research was abruptly cut short by a rabies outbreak. We know that that these foxes' patterns of habitat selection do not overlap completely with termite distribution, suggesting that other prey may be influencing how they utilise space (Périquet and le Roux 2018). Environmental factors such as lunar phase considerably affect foraging behaviour of these canids, with moonlit conditions representing increased activity and safety (Welch et al. 2017). Low predation pressure at this study site may have contributed to considerably more low-cost vigilance behaviour (i.e. engaging in activities like foraging or movement while still being vigilant), than high-cost vigilance (i.e. when vigilance interrupts all other activities; Welch et al. 2018). Environmental factors such as vegetation height and seasonal changes —particularly winter, correlated with increased high-cost vigilance (Welch et al. 2018). Perhaps one of the most intriguing behaviours of these canids has been the first-ever record of a new mother successfully hunting a lagomorph during the physiologically stressful period where pups were dependent on her (Jacobs and le Roux 2015). Overall, however, the population had low concentrations (≤ 0.31 µg/g organic content) of faecal glucocorticoid metabolites, fGCM —a measure of stress levels, which did not differ significantly between the sexes (de Bruin et al. 2018). In this population, the concentration of faecal androgen metabolite —synonymous to the male hormone testosterone, was significantly higher in males than females, and was also associated with territorial behaviour (scent-marking) in males, but with social tolerance in females (de Bruin et al. 2018). What we still don't know about this species is how their foraging behaviour is affected by seasonal changes, social factors and individual phenotype.

1.4.1. Study aims and objectives

My overall aim of this thesis is to evaluate the foraging behaviour of bat-eared foxes, and how it is affected by environmental factors, social factors, and individual phenotype, using an approach that combines detailed behavioural, prey availability and physiological data. Each chapter of this thesis, except for the general introduction and conclusion, has been written as a stand-alone publication, with the first chapter published and the second under review. Given this style, repetitions are unavoidable but I have limited these to the bare minimum.

In chapter 2 (Jumbam et al. 2019), my explicit aims are to address how seasonal variation impacted on this canid's diet and on the invertebrate community in its home range. I then investigated how my findings corresponded to the diet of other bat-eared fox populations in southern Africa. I approached these objectives as follows: Firstly, I carried out a detailed assessment of dietary proportions of the different categories of food consumed by these canids across seasons, and then evaluated the diversity of food categories (i.e. diet breadth) consumed seasonally using Levin's standardised index as a measure of diversity index. Furthermore, I assessed prey availability within the foxes' home ranges using pitfall traps and sweep net data, providing a better understanding of their foraging behaviour in relation to food availability. I characterised how seasonal variation influenced food availability and finally, reviewed the (limited) available literature on bat-eared fox diet to investigate how our study findings correspond with other fox populations across southern Africa. I equally provided patterns of similarities and differences between our study and literature findings as well as plausible reasons for these.

My second objective (Chapter 3; Jumbam et al. submitted) was to evaluate personality factors affecting both foraging and movement behaviours through individual level assessments of a suite of foraging and movement traits. I explicitly aimed to investigate individual differences (i.e. repeatability) in two foraging traits —diet breadth and foraging rates; and in four movement traits —speed, tortuosity (i.e. movement pathway), distance covered, and percentage of home range explored. I then investigated if these traits were correlated (i.e. behavioural syndromes; Sih et al. 2004), a phenomenon known to maintain individual variation within populations. I hypothesized that mobility in individuals would correlate with distance covered and acquisition of new food items, thus impacting on diet breadth and foraging rates. I expected seasonal variation to affect both foraging and movement behaviours in these canids owing to previous findings of food availability fluctuating with seasonal changes (see Jumbam et al. 2019).

My final objective (Chapter 4) was to assess how parenting might affect foraging behaviour with relation to seasonal activity (e.g. breeding), food size selection and foraging rate differences between parents and non-parents. Owing to low predation pressures and limited competition in our study population (de Bruin et al. 2018; Welch et al. 2018) I expect the main drivers of variation in foraging rate to include foraging time constraints imposed by parental responsibilities and the effect of seasonal changes on prey availability. Little is known about variations in foraging rates of parents with changing parental activities (e.g. newborn/breeding phase vs pup-chaperoning phase), what they eat (food size variations), and how it relates to their physiology (hormone levels). I hypothesize that given the nutritional demands of mothers, they would tend to select for larger prey than fathers and would also have higher foraging rates than males. I expect male parents to feed more on smaller and less energetically costly prey items such as termite patches, due the constraint on their foraging time. Finally, I predict that parents would show higher stress levels that would diminish as pups mature and parents become less burdened by parental responsibilities.

I, Keafon Ranissi Jumbam, conducted all the data collection, analyses and led the manuscript writing. Prof. Aliza le Roux conceptualised and supervised the study and edited manuscripts. Co-authors provided critical feedback on theory, analytical methods, editorials, and occasionally, snippets of content.

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CHAPTER 2

SPATIAL AND TEMPORAL VARIATION IN THE USE OF SUPPLEMENTARY FOOD IN AN OBLIGATE TERMITE SPECIALIST, THE BAT-EARED FOX

Jumbam KR, Périquet S, Dalerum F, le Roux A. 2019. *African Zoology* 54: 63–71.

2.1. Abstract

The bat-eared fox (*Otocyon megalotis*) is considered a termite specialist. However, studies of its diet have been limited to indirect methods, such as scat and stomach content analyses, resulting in intraspecific dietary variations due in part to methodological differences. Because diet plays a central role in the social dynamics of these canids, we hereby contribute further to our knowledge about their dietary habits. We present 2-year data of direct observations of foraging bouts of 19 habituated bat-eared foxes in the Kalahari Desert of South Africa, as well as data on seasonal variation in invertebrate prey communities obtained through pitfall and sweep net trapping. Despite showing a diet breadth reflective of a specialised forager across all seasons, foxes exhibited substantial seasonal variation in diet breadth with a broader range of food categories utilised in summer compared to the other seasons. Supplementary food categories appear to not have been utilised opportunistically, but it is unclear what drove the preference for some food categories over others. A literature review indicated strong effects of local conditions on the utilisation of supplementary food across southern Africa. Our data support bat-eared foxes as obligate termite specialists but highlight that they appear to have the ability to show dietary flexibility based on both temporal and spatial variations in food abundance.

Keywords: diet breadth, food availability, *Otocyon megalotis*, seasonal variation, termite specialist

2.2. Introduction

Specialist foragers are characterised by consistently consuming their main prey to a greater extent than expected regardless of its abundance (Fox and Morrow 1981). This contrasts with generalist predators which typically only start to consume a particular prey type once it has reached a specific threshold in abundance (Hassell and Comins 1978). Factors contributing to specialist foraging strategies include intense resource competition (Futuyma and Moreno 1988) and resource depletion (Berumen and Pratchett 2008). Factors promoting generalist foraging strategies include avoidance of resource competition (Hanski et al. 1991; Symondson et al. 2002); minimising energy costs associated with prey search (Hughes 1979); and selecting prey to achieve a nutritionally balanced diet (Bernays and Minkenberg 1997). These contrasting dietary strategies can have profound impacts on the population dynamics of both predators and prey (Andersson and Erlinge 1977). Because specialised predators feed only on a limited set of prey and continue to feed on these prey types even at very low abundances, specialist strategies are associated with high risk of species decline, due to resource depletion (Dalerum and Swanepoel 2017). Generalist predators, by comparison, can still thrive if a particular prey class declines, since they switch to supplementary food instead. Because they stop feeding on a particular prey at low densities, they are generally regarded as having stabilizing effects on prey populations (Reid et al. 1997).

Both specialist and generalist strategies can either be obligate or facultative. In obligate specialists, predators maintain a narrow diet breadth even in the presence of supplementary food, whereas facultative specialists have the capacity to utilise supplementary food under certain conditions (Taylor 1984). Similarly, although generalist species typically have a broad diet breadth, some species may adapt specialist strategies either at specific points in time or in specific areas. For instance, the Arctic fox (*Vulpes lagopus*) is a small canid that exploits a vast range of food resources in coastal areas (Dalerum et al. 2012); but, is highly specialised in tundra areas where there are limited resources (Elmhagen et al. 2000). The European otter (*Lutra lutra*), on the other hand, is highly specialised on fishes which constitute ≥ 80 % of its prey base regardless of seasonal variations (Chanin 1981). Similarly, the stoat (*Mustela erminea*) is an obligate rodent specialist (Erlinge 1983), whose sole reliance on rodents have been suggested as one of the driving causes for temporal fluctuations in rodent abundance (Andersson and Erlinge 1977).

One challenge in categorising predators along the specialist–generalist continuum lies in generating information on variation in diet breadth across time and space, both within and between populations. For instance, the diet of the arctic wolf (*Canis lupus arctos*) has been shown to vary considerably between environments with different prey availability (Dalerum et al. 2018). Across temporal scales, the raccoon dog (*Nyctereutes procyonoides*) has been shown to have a wider diet range in summer than in winter (Sutor et al. 2010), and the diet composition of the red fox (*Vulpes vulpes*) fluctuates with availability of its predominant prey, *Microtus* spp. (Dell'Arte et al. 2007). Similarly, the diet composition of black-backed jackals (*Canis mesomelas*) is markedly influenced by both geographic and seasonal variation in food abundance, as well as in seasonal variation in the physiological needs of nursing mothers (Klare et al. 2010; Kamler et al. 2012; Van de Ven et al. 2013).

The bat-eared fox (*Otocyon megalotis*) is a small canid that feeds predominantly on termites (Berry 1981; Nel 1984, 1990; Stuart et al. 2003), with jaw musculature well adapted to its insect prey (Clark 2005; Grant and Samways 2015). Termites play a central role in the social dynamics of the bat-eared fox by promoting communal foraging and socialisation among group members (Nel 1984), which enhances group participation in antipredatory strategies (Clark 2005). However, emerging studies suggest that the bat-eared fox may exhibit substantial intraspecific variation in its foraging habits, including a high consumption of wild fruits and non-invertebrate food resources in some populations (Kuntzsch and Nel 1992; Klare et al. 2011; Kamler et al. 2012). We acknowledge that some of the discrepancies have likely been caused by methodological differences, where most previous diet studies have used scat or stomach content examination (Nel 1978; Berry 1981; Kok and Nel 1992; Kuntzsch and Nel 1992; Stuart et al. 2003), and others have included random or *ad hoc* direct observations (Kleiman 1967; Lamprecht 1979; Koop and Velimirov 1982; Nel 1984, 1990; Malcolm 1986; Nel and Mackie 1990; Lourens and Nel 1990). However, these findings suggest that this obligate termite specialist appears to be able to utilise locally abundant supplementary food resources in different parts of its range.

To explore if such dietary variation also exists within a single population, we implemented an alternative approach to diet assessment which involved daily animal observations on foot in the wild, for two years. To our knowledge, this is the first time that wild bat-eared foxes have been closely observed on a daily basis over a long-term period to expressly describe their foraging behaviour. We also conducted a crude assessment of prey availability for a better understanding of their diet choices. Prey abundance assessments are essential for understanding the underlying reasons for a predator's dietary strategy (Holling 1959a, 1959b). Our explicit aim was to address the following questions: (1) What is the seasonal variation in diet breadth of this population of bat-eared foxes at the study site in the Kalahari Desert? (2) What is the seasonal variation of its alternative (non-termite) prey at the study site? (3) How do our findings correspond to the diet of other bat-eared fox populations in southern Africa?

2.3. Methods

2.3.1. Study area

The study was conducted at Kuruman River Reserve (KRR, 28°59' S, 21°49' E) in the Northern Cape province of South Africa, where a wild population of bat-eared foxes had been habituated to close range observations on foot. KRR covers an area of 33 km^2 with Kalahari thornveld vegetation and sandy dunes dominated by perennial grasses (Clutton-Brock et al. 1999). This study location experiences four distinct seasons with the coldest temperatures dropping below 0 °C in winter (June–August) and the hottest in summer (December–February) averaging to 40 °C (Périquet and le Roux 2017). Seasons were defined as summer (December– February), autumn (March–May), winter (June–August) and spring (September–November).

2.3.2. Study population and foraging behaviour recordings

Pregnant or lactating females were excluded from analyses to standardise reproductive status that could influence physiological needs. Our study population consisted of eight non-lactating adult females and eleven adult males located in three sections of the reserve (Figure 2.1). As foraging areas overlapped between most individuals, and because social interactions did not suggest any clear boundaries between individuals, we do not associate these sections with unique social groups. Individuals were identified by a combination of unique natural markings —such as earlobe indentations, artificial markings using dyes, or by fitted GPS collars. Animals were trapped using two protocols: pre-baited live walk-in traps (1.5x0.5x0.6 m; Global Supplies, South Africa) and medicated raisin baits stuffed with midazolam or diazepam tablets and hand delivered to habituated individuals. Both protocols were effective for our long-term study as they neither inhibited habituation nor deterred animals from the study area. Once sedated, veterinary surgeons administered anaesthesia by intramuscular injection of 0.4 mg medetomidine with 2 mg atipamezole injected intralingually as anaesthetic reversal after 30 minutes. Animals were fitted with GPS tracking collars (13 – 17 cm in circumference; Africa Wildlife Tracking) and general health conditions noted. Observers and veterinarians stayed with animals until full recovery before releasing them into the wild. Animal habituation process involved targeting artificial animal watering holes frequented by foxes and baiting them with raisins. An observer would sit still a few meters from the baited area, occasionally humming and rattling a raisin packet until the animals got accustomed to their presence. This process gradually advanced to the observer slowly walking around and then following the animals, which had come to associate the hum and bag rattle to a raisin treat. To minimise foraging interference, raisin treats were limited (~10 raisins) and each fox was followed once a week, with data recording only starting after the animal resumed its normal activities. Animals were followed daily for two hours between dusk and dawn, and foraging behaviour recorded on an Android Samsung tablet programmed with Cyber tracker software (www.cybertracker.org).

Diet data were collected from July 2014 to April 2016, resulting in a mean observation time of 57 h per individual (SD = 29 h). Based on the close proximity of observers to study animals (2–5 m), most prey items (averaging 60 %) consumed over the duration of the study were easily identifiable. Large prey items, such as beetles or grasshoppers, could easily be identified by the observer when the fox chased after such prey. Additionally, the fox would often spend time chewing at the head of its prey, which gave observers ample time to confirm the prey type from the rest of its body parts sticking out of the fox's mouth or lying on the ground. Smaller prey, such as termites and ants that occur in clusters, were also easily identifiable as animals would spend considerable time in the same location when foraging. The challenge was with small and solitary prey items hidden underneath foliage or vegetation (possibly insect larvae), which could not be identified and were thus excluded from data analyses. In such instances, the observer would confirm that the fox had successfully obtained prey from its jaw movements or chewing sounds. These unseen prey items were recorded as "unknowns" but were omitted from data analyses.

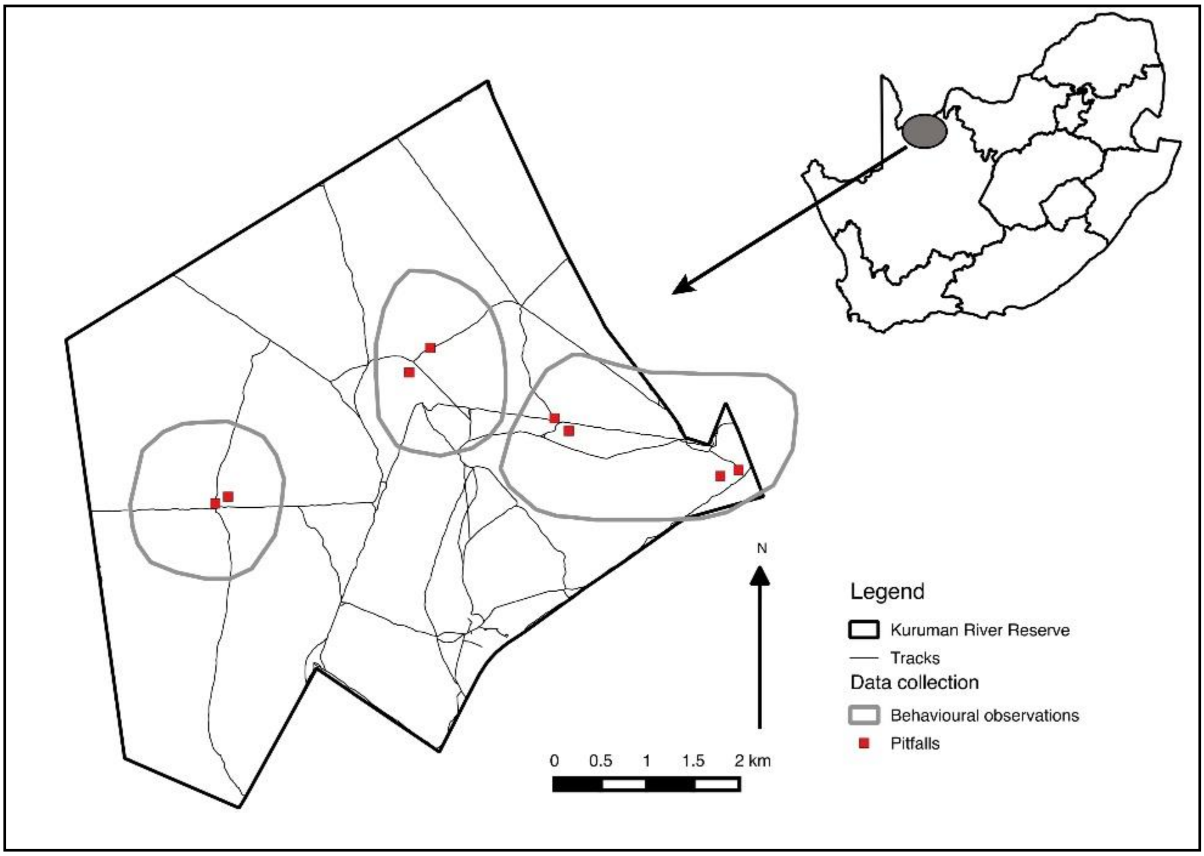

Figure 2.1. Map depicts South Africa and study site shows pitfall trap locations (squares), unpaved roads (tracks), and home ranges (grey enclosures) where behavioural studies were conducted.

2.3.3. Pitfall and sweep net data

Prey availability was estimated from a total of 360 pitfall traps deployed across winter, summer and autumn, with spring season forfeited, due to logistical challenges in the field. These pitfalls were deployed at eight randomly chosen sites within the demarcated areas where behavioural observations were conducted (Figure 1). Pitfalls at each site were deployed in three parallel transects, which were spaced 10 m apart, with each measuring 20 m in length and consisting of five pitfall traps placed 5 m apart. Therefore, each site consisted of a total of 15 traps with an overall sum of 120 traps collected across all eight sites per season. The trap dimensions were 6 × 6.5 cm (diameter by height) and volume ~184 ml. Traps were half-filled with 75:25 water and propylene glycol mixture, a low toxicity mixture harmless to wildlife and suitable for trapping invertebrates (Braschler et al. 2010). Pitfalls were deployed in the morning and left undisturbed for three consecutive days (~72 h) before collection on the third day.

After collection, pitfall trap samples were immediately washed using a fine mesh sieve to remove debris before storing content in 70 % ethanol. Invertebrates were identified using Leica MZ6 and MZ12 stereomicroscopes and the taxonomic reference book *Insects of Southern Africa* (Scholtz and Holm 1985). Although pitfall traps are a widely utilised method for quantifying invertebrate communities (Botes et al. 2006; Braschler et al. 2010), they can bias estimates against some invertebrates, such as termites (Kuntzsch and Nel 1992) and flying insects (Doxon et al. 2011). To alleviate some of these methodological biases, we added sweep net data for a broader representation of invertebrates in the study area. Data were collected along the same transects used for pitfall trapping as described above, by sweeping (42 cm diameter sweep net ring) across and above vegetation patches, using synchronised effort of sixty pendulum sweeps for five minutes per site. Insects caught were immediately emptied into labelled containers with 70 % ethanol for later identification. We collected sweep net data on the same day as pitfall data collection but only in summer and autumn seasons, due to logistical challenges in the field.

2.3.4. Data analysis

We expressed dietary proportions as relative percentage of occurrence (RPO), quantified as the number of identified items of a food category divided by all observed ingested diet items, multiplied by 100. Unknown prey items were excluded from analyses and we used the levels of Class and Order to define categories of known prey items. Prey availability proportions were derived from pooling together seasonal data per site (Figure 1) and dividing the sum of each food category (defined as above into Class or Order) by its corresponding seasonal data. Levins' standardised index (Smith 1982) was used as a measure of diversity index, defined here as:

$$\boldsymbol{Bi} = (\mathbf{B}-\mathbf{1})/(\mathbf{n}-\mathbf{1})$$

Where *Bi* = standardised index of niche breadth; ranging from zero to one (highest prey diversity index), B = Levins' index in unstandardised form and *n* = number of food categories. We calculated the unstandardised B following Levins' (1968) formula as:

$$\boldsymbol{B} = \mathbf{1}/\,(\boldsymbol{\Sigma}\,\boldsymbol{Pi}^2)$$

Where P_i = proportion of food category *i* per pitfall site or in an individual diet. Due to lack of dimorphism in these canids and the exclusion of pregnant or lactating females from our analyses, there was no *a priori* expectation for sex to influence diet breadth (Nel 1990). Diet data analyses were conducted on all food categories including Isoptera (Table 1).

Statistical analyses were performed in R (R Core Team 2018) with significance level set at 0.05. We used linear mixed-effects models to investigate the effect of season on Levins' standardised index (B_i) calculated on diet and prey availability data. Our observation unit for diet data comprised of nineteen bat-eared foxes from which we calculated B_i values per individual fox per season. For prey communities, we based our calculations on invertebrate abundance for each season per site. We added animal identity (in the model on diet data) and pitfall location (in prey availability data) as random factors. A variance function provided the best fit for prey availability data and log transformation for diet data. We evaluated the significance of season using likelihood ratio tests (LRT) and used the lsmeans package (Lenth

2016) to conduct pairwise contrasts between each pair of seasons, with alpha set at 0.05, and Tukey’s *post hoc* test to determine significant differences between the seasons.

2.3.5. Literature compilation on bat-eared fox diet

To further quantify geographic variation in the dietary habits of this species, we conducted a literature survey of bat-eared fox diet studies across South Africa. We narrowed our survey to seven articles based on their comprehensive prey lists, to better understand diet breadth in these canids. Because all studies were either conducted on scats or stomach content, we provided RPO of stomachs containing food items (Kok and Nel 1992) or RPO of food items in scats (Stuart et al. 2003). In studies with varied diet quantification methods, such as percentage volume of food items in faeces and percentage occurrence of food items in faeces (e.g. Nel and Mackie 1990), we chose the latter, to keep comparisons across studies standardised.

All dietary proportions per study represented here were expressed as RPO. We also excluded non-prey items, such as grit and sand (Kok and Nel 1992), as well as unidentified matter (Nel 1978). We used our study list of 18 food categories as the template for comparison with other studies, due to the shared commonality of food items between most studies. Finally, in the few instances where seasonal data were available, we averaged the data across seasons. We also added a final category where we grouped all other identified food categories to reach 100 % of the diet content.

2.4 Results

2.4.1. Seasonal effect on diet breadth

A total of 18 different food categories were recorded from dietary observations (Table 1). Isoptera was the most consumed food category with an average RPO of ~70 % in fox diet across all seasons. Its consumption peaked in autumn (82 %) and winter (76 %) but declined in the warmer months of summer and spring (≤ 65 %). Other invertebrate food categories consumed in relatively large amounts across all seasons included Coleoptera (11 %), Hymenoptera (8 %) and Orthoptera – specifically grasshoppers (5 %). Least prominent food categories in fox diet (< 0.05 %) were Diplopoda and Amphibia.

There was a significant effect of season on bat-eared fox diet breadth ($\chi^2 = 29.6$, df = 2, $p < 0.01$), with foxes having had a significantly wider diet breadth in summer (Figure 2) than in every other season (winter: $t_{91} = 3.00$, $p < 0.01$; spring: $t_{81} = 2.50$, $p < 0.01$; autumn: $t_{91} = 3.75$, $p < 0.01$). The narrowest diet breadth was in autumn, which differed significantly from all seasons except winter ($t_{95} = 1.8$, $p = 0.07$), while spring and winter did not differ significantly from each other ($t_{81} = 1.00$, $p = 0.33$). Levins' standardised index was on average very low across all seasons ($B_i < 0.5$) denoting a narrow diet breadth in these animals.

Table 4.1: Seasonal diet data from 19 bat-eared foxes and prey availability data from 360 individual pitfall traps distributed in groups of 15 traps in each home range of respective fox groups. Pitfall trapping was done in 2015 (autumn and winter) and 2016 (summer), and prey availability data from sweep net surveys, at the same sites as the pitfall trapping (sweep net data were obtained for summer and autumn only). Values are expressed as relative percentage of occurrence (RPO), i.e. number of identified items of a food category divided by all consumed or trapped diet items, multiplied by 100.

	Summer			Autumn			Winter		Spring	All seasons		
Order and Class††	Diet	Pitfall	Sweep net	Diet	Pitfall	Sweep net	Diet	Pitfall	Diet	Diet	Pitfall	Sweep net
Hymenoptera (Ants)	5.73	84.56	89.00	1.85	74.89	15.00	9.62	85.89	15.45	8.16	81.78	52.00
Neuroptera (Antlions)	6.99	0.07	-	0.74	0.03	9.00	0.00	-	0.48	2.05	0.03	5.00
Coleoptera (Beetles)	4.26	12.08	-	12.97	18.84	24.00	11.76	11.37	13.57	10.64	14.10	12.00
Lepidoptera (Caterpillars)	0.00	-	-	0.00	-	6.00	2.27	-	0.07	0.59	-	3.00
Diplopoda (Millipedes)	0.01	-	-	0.00	-	-	-	-	0.10	0.03	-	-
Hemiptera (Cicadas)	3.94	-	-	0.00	-	-	-	-	0.06	1.00	-	-
Orthoptera (Crickets)	0.18	-	-	0.01	-	-	-	-	0.10	0.07	-	-
Orthoptera (Grasshoppers)	14.30	0.13	-	1.57	2.88	-	0.11	-	2.90	4.72	1.00	3.00
Mantodea (Mantises)	0.11	-	-	0.00	-	-	0.00	-	0.11	0.06	-	-
Lepidoptera (Moths)	0.74	-	-	0.30	-	-	0.32	-	1.20	0.64	-	-
Scorpiones (Scorpions)	0.54	0.05	-	0.04	0.13	-	0.05	-	0.33	0.24	0.06	-
Arachnida†† (Spiders)	2.16	3.11	11.00	0.08	3.24	6.00	0.00	2.74	0.69	0.73	3.03	9.00
Isoptera (Termites)	57.33	-	-	81.51	-	-	75.73	-	64.58	69.79	-	-
Hemiptera (Shield bugs)	-	-	-	-	-	3.00	-	-	-	-	-	2.00
Diptera (Houseflies)	-	-	-	-	-	21.00	-	-	-	-	-	11.00
Phasmatodea (Stick insects)	-	-	-	-	-	9.00	-	-	-	-	-	5.00
Reptilia†† (Reptiles)	0.31	-	-	0.02	-	-	-	-	0.27	0.15	-	-
Amphibia†† (Frogs)	0.01	-	-	0.01	-	-	-	-	-	0.01	-	-
Rodentia (Rodents)	0.34	-	-	0.49	-	-	0.05	-	0.12	0.25	-	-
Other (Plant seeds)	3.05	-	-	0.00	-	-	0.05	-	-	0.78	-	-
Other (Fungi)	0.00	-	-	0.41	-	-	0.03	-	-	0.11	-	-
Levins standardised index	0.12	Na		0.038	na	na	0.054	na	0.069	0.083	na	

† = Order Orthoptera (common names not specified in cited articles) †† = Class name

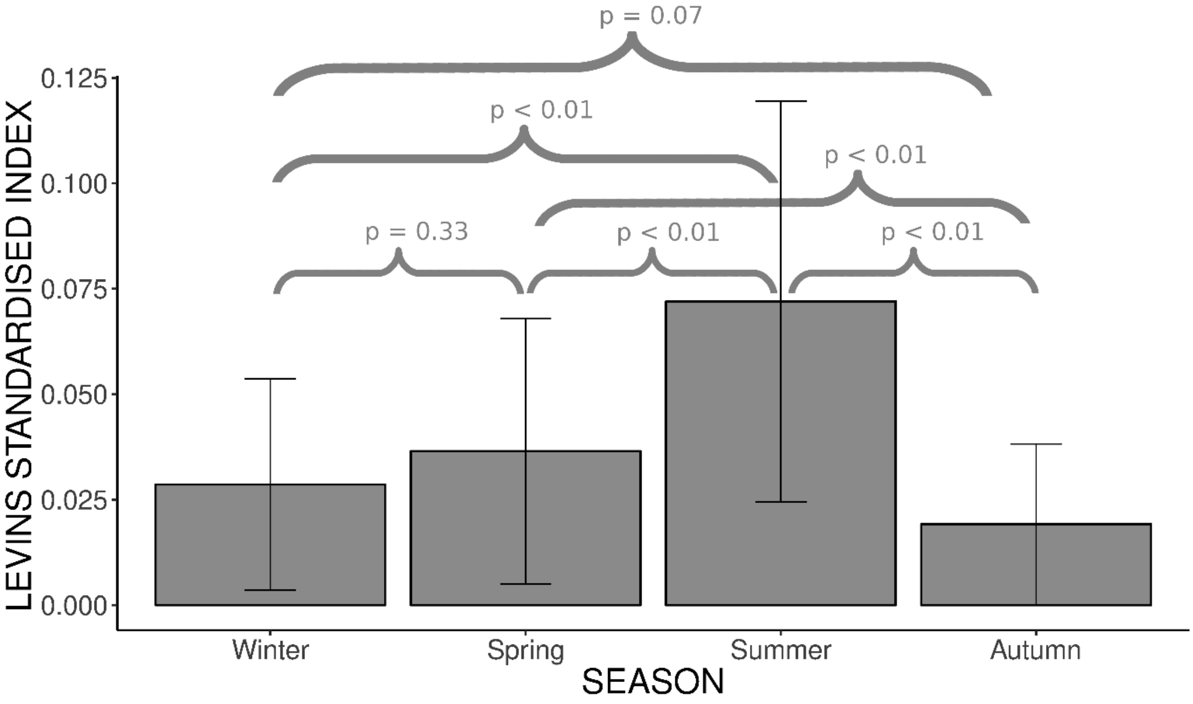

Figure 2.2. Bat-eared fox diet breadth, quantified as Levins' standardised index (B_i) in the Kuruman River Reserve during four seasons: summer (December–February), autumn (March–May), winter (June–August) and spring (September–November). Error bars represent ± 1 standard error from the mean. Tukey's post hoc test: $\alpha \leq 0.05$.

2.4.2. Seasonal influence on invertebrate composition

The non-termite invertebrate community from both pitfall and sweep net data comprised of a total of 10 insect categories of which Hymenoptera and Coleoptera dominated in both sampling datasets (Table 1). Season did not significantly influence invertebrate composition (pitfall: $\chi 2 = 3.70$, df = 2, $p = 0.15$; sweep net: $\chi 2 = 0.30$, df = 2, $p = 0.63$, Figure 3).

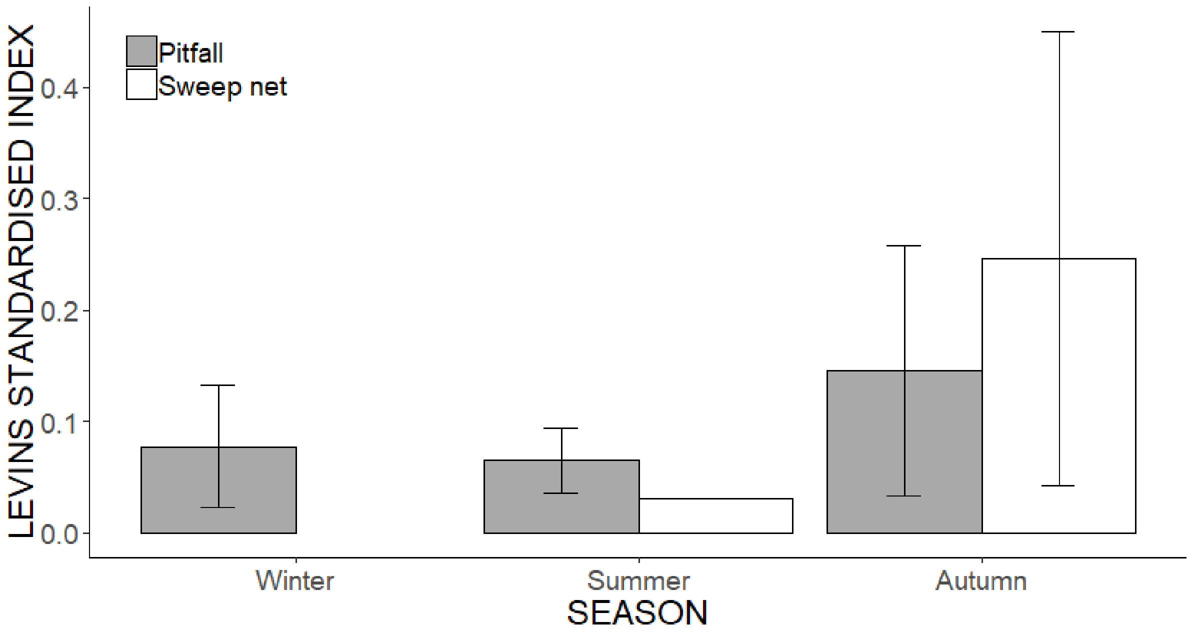

Figure 2.3. Invertebrate diversity quantified from pitfall and sweep net data across three seasons: summer (December–February), autumn (March–May) and winter (June–August). Sweep net data available for summer and autumn only. Error bars represent ± 1 standard error from the mean. Tukey's post hoc test: $\alpha \leq 0.05$.

2.4.3. Invertebrate variation across South African provinces

Invertebrates dominated bat-eared fox diets across all provinces (Table 2). Isoptera was the most frequently consumed food category with an average RPO of 33 % in diet across all studies. Also featuring prominently across various diet studies was Coleoptera, which was the most consumed invertebrate food category in the Western Cape (24.2 %), as well as the Free State and Northern Cape studies (21.4 %). Coleoptera was the third and fourth most consumed food category in the three remaining studies from the Northern Cape and Limpopo provinces, respectively. Completing this list of the most consumed invertebrates across the provinces is Hymenoptera, with an average of 13.1 % occurrence in diet across all diet studies, consistently ranking third in all four of the Northern Cape diet studies including this study, as well as in one study from the Free State. Orthoptera and Arachnida ranked fourth and fifth in several diet studies, while the least consumed food categories included Neuroptera, Lepidoptera, Hemiptera, Mantodea and Diplopoda.

2.4.4. Non-invertebrate diet variation across South African provinces

Plant material (seeds and wild fruits) had the highest dietary contribution (≥ 29.3 %) in two Northern Cape studies, and second highest in Limpopo, Free State and Northern Cape studies (≥ 17.5 %). Mammals were the second most abundant non-invertebrate prey in half of the fox studies (4.0 % occurrence on average) but were rarely consumed in this study (0.25 % occurrence), and absent in three other studies (Table 2). Ranking third in fox diet were reptiles with occurrences between 0.1–1.9 % across most studies, except for the Free State, Western Cape and in one Northern Cape study with no record of reptiles in fox diet. Lastly, while Limpopo province had the highest record of amphibians in fox diet (0.4 %), this prey was the least consumed in our study (0.01 %) and absent in five other studies. We therefore considered it a food category of least importance to these foxes, together with fungus (0.11 %) which was only present in this study.

Table 2.2. Literature compilation of detailed diet lists from this study conducted in the Northern Cape province and three other provinces (Western Cape, Free State and Limpopo province) in South Africa. Diet values are expressed as relative percentage of occurrence (RPO), with individual values adjusted so that the total equals ~100 % per study.

Geographic location	Northern Cape	Northern Cape	Northern Cape	Northern Cape	Western Cape	Limpopo Province	Free State	Free State and Northern Cape
Source	**This study**	**Klare et al. 2011**	**Stuart et al. 2003**	**Nel 1978**	**Kuntzsch and Nel 1992**	**Berry 1981**	**Nel and Mackie 1990**	**Kok and Nel 1992**
Study method	Forage (n = 19)	Scats (n = 177)	Scats (n = 450)	Scats (n = 382)	Scats (n = 157)	Stomach content (n = 18)	Scats (n = 180)	Stomach content (n = 103)
Hymenoptera (Ants)	8.16	20.0	15.5	13.6	13.5	-	8.04	11.7
Neuroptera (Antlions)	2.05	-	-	-	-	-	-	-
Coleoptera (Beetles)	10.6	8.41	31.7	12.6	24.2	10.8	20.9	21.4
Lepidoptera (Caterpillars)	0.59	-	-	-	-	-	-	-
Hemiptera (Cicadas)	1.00	-	-	-	-	-	-	-
Orthoptera (Crickets)	0.07	-	1.04[†]	-	-	-	10.5[†]	10.0[†]
Orthoptera (Grasshoppers)	4.72	5.08		4.50	20.7	-		
Mantodea (Mantises)	0.06	-	-	-	-	-	-	-
Lepidoptera (Moths)	0.64	-	-	2.50	-	-	-	9.95
Isoptera (Termites)	69.8	27.9	32.1	18.8	24.2	44.3	26.8	16.3
Diplopoda (Millipedes)	0.03	-	-	1.50	-	-	-	1.37
Scorpiones (Scorpions)	0.24	4.22	5.52	1.10	-	-	-	4.89
Arachnida[††] (Spiders)	0.73	-	1.03	4.90	-	2.50	1.07	-
Reptilia[††] (Reptiles)	0.15	0.52	1.03	-	-	0.10	-	1.90
Amphibia[††] (Frogs)	0.01	-	-	-	-	0.40	-	0.28
Mammalia[††]	0.25	4.52	4.14	-	-	-	2.68	4.61
Other (Plants)	0.78	29.3	8.62	36.4	17.4	33.0	5.63	17.5
Other (Fungi)	0.11	-	-	-	-	-	-	-
Levins standardised index	0.12	0.94	0.42	0.43	0.95	0.32	0.53	0.61

[†] = Order Orthoptera (common names not specified in cited articles) [††] = Class name

2.5. Discussion

Isoptera was the most consumed invertebrate food category by bat-eared foxes, which confirms the results of previous studies suggesting that these canids to a large extent depend on this prey (Berry 1981; Nel 1984, 1990; Stuart et al. 2003). However, despite this reliance on a single prey type, we found seasonal variation in bat-eared foxes' diet breadth, with the broadest variety of prey items consumed in summer. This mirrors previous studies that have examined seasonal effects on the diet of this, and other, canids, such as the raccoon dog (Sutor et al. 2010; Klare et al. 2011). The narrow diet breadth seen in this study during the colder months of autumn and winter appears to have been caused by an absence of supplementary food categories during these months, such as Diplopoda, Hemiptera, Reptilia and Amphibia. Such an interpretation is supported by our observations of a significant reduction in the dietary contribution of termites during the warm and wet months of spring and summer, which coincided with an increased consumption of supplementary food. Hence, despite their heavy reliance on Isoptera, bat-eared foxes exhibited some dietary flexibility and appear to have used supplementary non-termite food resources if available. Such utilisation of supplementary food has previously been observed both in this and other facultative specialists (Waser 1980; Sutor et al. 2010; de Vries et al. 2011; Klare et al. 2011; Grant and Samways 2015). Utilisation of supplementary food may improve the energy budgets of a predator by reducing the costs associated with food search (Hughes 1979) and could thus be an adaptive feeding strategy even for obligate specialists, such as the bat-eared fox.

Our dietary observations further suggest that the utilisation of supplementary food may not have been opportunistic, but that some food categories were preferred, while others selected against. This selectivity among supplementary food categories appears to have been most pronounced during summer. They appear to have fed on large prey if available, such as Coleoptera and Neuroptera, although they did not necessarily seem to have selected for food based on nutritional value. For instance, Coleoptera has higher energy (266 kcal 100 g–1) and protein content (20.2 % weight for weight; w/w) than some less utilised prey, such as Hymenoptera (128 kcal 100 g–1 vs 17.4 % protein content) (Bukkens 1997), but the utilisation of Coleoptera appear to have been lower than what could have been expected based on their relative abundance in the traps. Similarly, Orthoptera (≤ 200 kcal 100 g–1) (Bukkens 1997; Ramos-Elorduy 2008) and Scorpiones (331 kcal 100 g–1) (Abulude et al. 2006) both have high energy content but appear to only have been used more than expected based on their relative occurrences in the traps during summer. However, Neuroptera, with a very high energy content (550 kcal 100 g–1) (Robel et al. 1995), was consistently utilised more than what could be expected based on their relative occurrence in the traps, and Arachnida, with a low energetic value (≤ 5.74 kcal 100 g–1) (Norberg 1978), was consistently utilised less. Hence, we suggest that the observed utilization of supplementary food may not have been opportunistic, but it is unclear what factors were driving the preference for certain supplementary food categories over others.

2.5.1. Seasonal impact on bat-eared foxes' diet breadth

Insect development is temperature dependent with warmer temperatures promoting larval growth (Ratte 1984). Seasonal variation in invertebrate communities have also been strongly linked to variation in rainfall, and invertebrate seasonality appears to be a consequence of interactions between temperature, water availability and the life history tactics among and within individual species (Wolda 1988, Nylin and Gotthard 1998). In most environments, these processes result in a higher abundance and diversity of invertebrates during warm and wet seasons. These results are confirmed by our study where a higher invertebrate diversity was recorded in summer. Subsequently, since foraging behaviour of the bat-eared fox is closely linked to invertebrate activity patterns (Lourens and Nel 1990), variations in rainfall and temperature appear to directly influence utilisation of alternative invertebrate prey by the bat-eared fox. We note, however, that in our study the seasonal variation in invertebrate communities was only partly reflected in bat-eared fox diet breadth. Although this finding may have been influenced by our sampling effort which was limited to two seasons, it nonetheless re-iterates our previous suggestion that supplementary food utilisation by this species may not be entirely opportunistic.

2.5.2. Bat-eared fox diet pattern across different geographic locations in South Africa

Isoptera was one of the most utilised prey across most studies. These results generally confirm bat-eared foxes as being largely an obligate dietary specialist on termite prey. However, we note a disparity between the dietary proportions of Isoptera found in this and other studies, with more than a two-fold difference in the dietary contributions. Although some of these differences could have been caused by real dietary differences, we suggest that a large part of this difference can be attributed to sampling differences. We quantified dietary contributions directly as proportion of individual diet items consumed, whereas the other studies have relied on indirect methods, such as content in faeces or stomachs. Hence, our method would bias dietary contributions towards small prey that are fed on in higher frequencies.

We note a consistent occurrence of Isoptera, Coleoptera and Hymenoptera as the top three most utilised invertebrate food categories in two of the Northern Cape studies (including this study), and in the Free State province. These study locations share common microclimatic abiotic factors suitable for survival of these top three prey types, such as fynbos vegetation cover (Stuart et al. 2003) and Karoo veld vegetation cover (Clutton-Brock et al. 1999; Stuart et al. 2003; Welch et al. 2017). These types of vegetation cover have been shown to increase Hymenoptera abundance, particularly species that use fynbos vegetation cover for nesting and as energy source in the Cape Floristic region (Botes et al. 2006). In addition to vegetation cover, these study sites also experience moderate annual rains of ≤500 mm (Stuart et al. 2003; Welch et al. 2017) which is a significant contributing factor to Hymenoptera species richness (see Botes et al. 2006).

By contrast, study sites in which these invertebrate prey categories were not utilised heavily have different vegetation structure and microclimatic conditions that appear to influence bat-eared fox diet. For instance, in two studies with approximately 30 % of the diet consisting of plants, the dominating vegetation was Nama Karoo (Klare et al. 2011) and scrub savanna vegetation with heavy rainfall (Berry 1981). These microclimatic conditions differ from those of our study site with predominantly Karoo veld vegetation accompanied by dominant supplementary prey, such as Coleoptera and Hymenoptera, all of which highlight the influence of environment on the diet and foraging ecology of these canids.

2.6. Study limitations and way forward

While direct observations are useful in understanding the foraging behaviour of predators, we acknowledge a few shortcomings with our methodological approach. Firstly, direct observations quantified as RPO biased dietary contributions towards small and commonly used prey, such as termites. We suggest that future studies include weight measurements of prey and volumetric analyses of each prey category to avoid such biases. Secondly, our sampling efforts and techniques in assessing the invertebrate community in our study site were limited. This reduced our analytical power, an in-depth understanding of the invertebrate community, and the relationship between fox diet and their prey base. We advise long-term monitoring of invertebrate communities and the use of multiple invertebrate sampling techniques that will capture the wide spectrum of invertebrates in the environment. Such a comprehensive invertebrate dataset will highlight any patterns in invertebrate abundance or decline, as well as how foxes relate to these changes. Finally, we acknowledge that differences in diet content across our literature survey may have been influenced by the diverse methodological approaches (e.g. scats, stomach contents) utilised in the different studies. Nonetheless, the literature survey provides an overall view of the variety of prey items foraged on by foxes in different locations across South Africa and it highlights the important role of their microhabitats on their prey choices. With the improved data techniques suggested above, direct observations can provide great in-depth information on the foraging behaviour of these canids that would otherwise not be captured by other techniques.

2.7. Conclusions

Our data support results from previous studies that have defined the bat-eared fox as an obligate termite specialist. Despite this specialisation, we noted substantial differences in diet breadth across seasons. Our data suggest that the utilisation of supplementary food was not entirely opportunistic, but it is unclear what was driving the preference of certain alternative prey over others. Comparisons of dietary content found in studies across South Africa revealed a strong effect of local environmental conditions on the relative dietary contributions of supplementary food types, which lends further support for the ability of this species to adapt its dietary strategies to spatial and temporal variation in food availability. However, we suggest that further studies provide direct quantification of dietary strategies using combined and, if possible, unbiased assessments of dietary contributions and abundance of the main and supplementary food categories used by this species.

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CHAPTER 3

INDIVIDUAL DIFFERENCES IN FORAGING RATE AND MOVEMENT METRICS, BUT NOT IN DIET BREADTH OF A WILD CANID

Jumbam KR, le Roux A, Périquet S, Petelle MB. (Under Review) *Journal of Ethology.*

3.1. Abstract

Individual differences in movement and foraging behaviours offer insight into complex behavioural patterns at the population level. These two behavioural traits have traditionally been studied in isolation. A combined study of both traits is important to assess correlations (behavioural syndromes) between them, thus furthering our understanding of trait covariation, likelihood of traits constraining each other, co-evolution and maintenance of individual variation in animals. Such combined long-term studies are still lacking for wild mesopredators. We studied 20 free-living bat-eared foxes over two years, to evaluate individual differences (repeatability, *R*) and behavioural syndromes in two foraging metrics — daily diet breadth (food categories consumed) and daily foraging rates; as well as in four movement metrics —speed, tortuosity, total distance travelled, and percentage of home range explored. We found little evidence for repeatability in daily diet breadth (*R* = 0.02) and in daily tortuosity (*R* = 0.04), indicating that individuals ate similar food categories and had equivalent movement tortuosity across the population. Repeatability was low but significant for daily foraging rates (*R* = 0.13) and in the three remaining movement metrics (*R* range: 0.07–0.12). Season significantly affected both foraging and movement metrics, with daily diet breadth notably broader in summer than in every other season. Most metrics were exceedingly higher in autumn, suggesting that this season could be a pivotal transitional period into winter that necessitates rapid food acquisition by individuals. We found no behavioural syndrome between any of the traits, suggesting that these traits are unlikely to constrain each other in this population.

3.1.1. Significance statement

It is widely accepted that behavioural syndromes maintain individual variation within a population. However, long term studies assessing this phenomenon in the wild and on large sample sizes are still lacking. We assessed the movement and foraging behaviours of 20 free-living bat-eared over a 2-year period to evaluate individual differences (repeatability) and behavioural syndromes in both behaviours. We found low repeatability in three of the four movement metrics examined and in one of two foraging metrics. Season significantly affected all metrics except for the movement metric tortuosity (movement pathway). Our results highlight the absence of behavioural syndromes between traits examined in this study and taken together, showcase a foraging specialist that has evolved to behave uniformly in the behavioural measures examined here.

Keywords: bat-eared fox, behavioural syndrome, exploratory behaviour, personality, repeatability

3.2. Introduction

Foraging and movement behaviours have direct consequences for species' survival and distribution patterns (Nathan et al. 2008; Forister et al. 2015; Abrahms et al. 2017) and these behaviours are inherently linked to personality differences at the individual level (Spiegel et al. 2017; Schirmer et al. 2019). For instance, highly active individuals are often risk-takers that explore wider territories than less active individuals (Boon et al. 2008; Wesley et al. 2012; Spiegel et al. 2017; Hertel et al. 2019). Moreover, individuals that explore larger territories also tend to consume greater amounts of food (Serrano-Davies et al. 2017) and to forage at a faster rate than their shy counterparts (Wesley et al. 2012). These findings highlight the importance of individual-level assessments, as they reveal behaviours often concealed at the population level (Nussey et al. 2007; Dingemanse et al. 2010; Welch et al. 2018). Moreover, evolution acts on an individual level (Lewontin 1970; Boake 1989; Dingemanse et al. 2002; Nussey et al. 2007), thus, the importance of individual-based variability assessments cannot be overemphasized. Another important aspect of individual level assessment is that they evaluate factors that maintain individual variation such as trait covariation or correlations (behavioural syndromes). Previous studies suggest that foraging and exploratory traits could be correlated, necessitating an integrated study of these behavioural traits, which have traditionally been studied in isolation (Toscano et al. 2016, see also Réale et al. 2010).

Behavioural syndromes describe the correlation between behavioural traits across contexts and underpin the co-evolution of traits which may be adaptive or constrain optimal behavioural expression of those traits, thus maintaining behavioural variation within populations (Sih et al. 2004). Behavioural syndromes have been established for activity level, boldness and aggression (Dingemanse and Wolf 2010; Spiegel et al. 2017). Little is known about behavioural syndromes in other ecologically important traits such as foraging and movement behaviours. Equally, long-term studies of such traits are lacking for wild populations.

The bat-eared fox (*Otocyon megalotis;* "fox" here-after) is a socially monogamous canid that forages alone or in groups with minimal antagonistic behaviour among members (Maas and Macdonald 2004; de Bruin et al. 2018). It is termed a termite specialist based on population level studies (Berry 1981; Nel 1984; Stuart et al. 2003) but it also consumes seasonally available prey items (Chapter 2; Jumbam et al. 2019). However, individual differences in their foraging and movement behaviours remain unexplored. Using an extensive two–year dataset on daily foraging and movement behaviours collected from free-living foxes, we examined individual differences (repeatability) in the foraging metrics: diet breadth and foraging rates, and also in four movement metrics—speed, total distance travelled, tortuosity and percentage of home range explored. Diet breadth provides crucial insight on animal and diet co-evolution, ecosystem processes such as food webs, community assemblages and coexistence of competitors (Forister et al. 2015). Foraging rate on the other hand provides information on animal personality such as boldness (Wesley et al. 2012), predator presence and perceived risks (Urban and Richardson 2015; Welch et al. 2017) as well as intraspecific competition (Urban and Richardson 2015). Animal movement is central to understanding broad scale distribution patterns, underlying mechanisms contributing to movement patterns and overall survival of animals (Nathan et al. 2008). Additionally, movement patterns can be shaped by spatial clusters of similar personalities resulting in environmental heterogeneity and thus providing insight into both animal personalities, habitat use as well as foraging behavior (Spiegel et al. 2017)

In this study, therefore, we investigated repeatability in foraging and movement traits, together with behavioural syndromes between them. We hypothesized that bolder individuals would cover longer distances, have larger home ranges and possibly encounter new food resources more frequently, which will influence both their diet breadth and foraging rates. We also expect seasonal change to affect foraging and movement behaviours in foxes owing to seasonal changes in food availability (see Jumbam et al. 2019).

3.3. Material and Methods

3.3.1 Study location and population

We conducted this study on 20 habituated adult foxes (nine females and eleven males) in the Kuruman River Reserve (KRR, 28°59’S, 21°49’ E) which covers an area of 32 km^2 and is in the Northern Cape province of South Africa. The reserve consists of Kalahari Thornveld and perennial grasses on sandy dunes (Clutton-Brock et al. 1999; Périquet and le Roux 2017) and experiences a mean rainfall of 282 mm with temperatures during our study period ranging from –4.60 °C to 41.0 °C (Welch et al. 2017). Four seasons were defined as follows: summer (December–February) when most of the rainfall occurs, autumn (March–May), winter (June–August) and spring (September–November).

3.3.2. Behavioural data collection

Trained observers (n = 8) monitored habituated foxes on foot from ≤ 5 m for two hours per “follow” (observation session) at least once per week, from 2014 to 2016. To ensure inter-observer reliability, trainees would job-shadow experienced observers for days and pose questions when in doubt. Ongoing discussions within observers ensured data collection accuracy. Given the nocturnal nature of these canids, flashlights were used for direct observations beginning at dusk with each follow session lasting 2 hours. The proximity of observers to foxes (≤ 5 m) made it possible to identify most food categories consumed by foxes (60 %) with the only exceptions of prey hidden underneath foliage and underground, recorded as “unknown”. We excluded these unknown items from diet breadth assessments (food categories consumed) but included in foraging rate evaluations (food items consumed per min). For a detailed list of food categories consumed, see Jumbam et al. 2019. We identified foxes by unique body markings such as ear indentations (n = 12) and by VHF —very high frequency collars (n = 8). During animal follows, we recorded foraging and social behaviours on an Android tablet programmed with Cyber tracker software (www.cybertracker.org). We recorded the GPS location of the focal fox at 15 min intervals as well as of each foraging event.

3.3.3. Diet breadth estimates

We derived diet breadth from a total of 566 follows, averaging 28 follows per individual (range: 7–55; see details in Appendix). We used Levins' standardised index (Smith 1982) as a measure of food diversity index, calculated as:

$$Bi = (B-1)/(n-1)$$

Where B_i = standardised index of niche breadth, ranging between zero and 1 (highest prey diversity index), B = Levin's unstandardised form and n = number of food categories. We calculated B following Levins' (1968) formula as:

$$B = 1/\,(\Sigma\, Pi^2)$$

Where P_i = proportion of food category i consumed per follow. We quantified dietary proportions per follow as the sum of identified items per food category divided by all ingested food items during the follow.

3.3.4. Foraging rate assessment

We derived foraging rates from a total of 575 follows (data includes unknown items), averaging 29 follows per individual (range: 7–58; see details in Appendix). We calculated foraging rate per follow by dividing the sum of all ingested food items during the follow by the duration of the follow.

3.3.5. Movement metrics assessment

All movement metrics — speed, total distance travelled, tortuosity and percentage of home range explored, were derived from 250 follows averaging 13 follows per individual (range: 3–28; see details in Appendix). Using all GPS locations collected during each follow (i.e. starting and ending points of the follow, foraging and social interactions events, scans every 15 min), we computed four movement metrics at the individual-follow level. We estimated the total distance travelled during the follow by summing the distances between each successive GPS location over the follow and the average speed by dividing the total distance travelled (m) by the follow duration (min). We then estimated path tortuosity as the distance between the end and starting location of the follow (i.e. net displacement) divided by total distance travelled. Tortuosity therefore ranges from 1, if the animal moved along straight line, to theoretically 0 if the movement was infinitely tortuous. Lastly, we estimated the percentage of the seasonal home range area that was travelled during a given follow. We defined seasonal home ranges using 95 % isopleth movement-based kernel estimation (Benhamou 2011) pooling all GPS locations belonging to a given season. We used the same home range estimation method to compute follow-specific home range using GPS locations of the given follow. We obtained the percentage of seasonal home range travelled during each follow by dividing the follow specific home range size by the seasonal home range size.

3.3.6. Seasonal effects and repeatability estimates

We fit six univariate models, one for each trait. Each model included season as a fixed effect and fox ID as a random effect. We included season because available prey composition changes across season. All models were fitted with a Gaussian distribution with the R software (R Core Team 2019, version 3.5.3), and we checked model normality visually with QQ-plots. We log-transformed foraging rate to meet normality assumptions and determined significant differences between seasons using Tukey's *post hoc* test with alpha set to 0.05, using the lsmeans package (Lenth 2016). We estimated repeatability of diet breadth and movement parameters using the rptR package (Nakagawa and Schielzeth 2010; Stoffel et al. 2017).

3.3.7. Behavioural syndrome (or correlation estimate) assessment

To understand behavioural syndromes between the studied traits, we used 250 follows with both movement and foraging data. We investigated the correlation between diet breadth and exploratory behaviours using four bivariate models in the package MCMCglmm (Hadfield 2010). We scaled and centred both dependent variables (mean = 0 and SD = 1) to help with model convergence and ease interpretation. We used an uninformative prior and the posterior distribution was sampled every 100 iterations with a burn-in of 30 000 for an effective sample of 250. For both R (residuals) and G (random effects) priors, we specified V = 2 and nu = 2 and for both G and R priors we used V = 0.5*I2 (2*2 diagonal matrix with 0.5 on the diagonal) and nu = 2.002. We estimated variance components as the posterior mode with 95 % credible intervals (CI), rescaled covariance estimates into correlations and extracted 95 % CI. We investigated MCMC diagnostics using trace plot autocorrelation which was under 0.05 for all metrics.

3.4. Results

3.4.1. Individual differences in traits

We observed significant individual differences in foraging rates but not in the diet breadth of these canids (Table 3.1). We found low ($R \leq 0.12$) but significant individual differences in three of the four movement metrics, with tortuosity being the only metric that did not differ significantly between individuals.

Table 3.1. Repeatability estimates (*R*; measured using rptR package) of daily variation in diet breadth (n=566), foraging rate (n=575) and movement metrics (n=250) of the bat-eared fox.

Trait	*R*	C.I.	LRT	*P*
Foraging metrics				
Diet Breadth	0.02	0–0.07	2.21	0.07
Foraging rate	**0.13**	**0.042–0.22**	**48.00**	**<0.01**
Movement metrics				
Speed	**0.068**	**0.0–0.15**	**5.17**	**<0.05**
Tortuosity	0.040	0.0–0.11	0.50	0.24
Total distance	**0.077**	**0.01–0.17**	**8.46**	**<0.01**
Percentage home range explored	**0.12**	**0.021–0.24**	**9.96**	**<0.01**

C.I = Confidence interval, LRT = Likelihood ratio test, P = significance level set at 0.05

3.4.2. Effect of season

Season had a significant effect on both foraging metrics (daily diet breadth: $F_{3,534}$ = 53, *p* <0.001; daily foraging rates $F_{3,34}$=566, *p* <0.001), as well as on all movement metrics (speed: $F_{3,314}$=3.22, *P*<0.05; total distance travelled: $F_{3,318}$=6.20, *p* <0.001; percentage of home range explored: $F_{3,262}$=6.12, *p* <0.001), with the exception of tortuosity ($F_{3,284}$ = 0.40, *p* = 0.76). Foraging rate was significantly higher in Autumn than in other seasons (Figure 3.1) and the percentage of home range explored by foxes, which was also higher in autumn than in most seasons (Figure 3.2). Individuals had a significantly higher diet breadth in summer than other months (Figure 3.3). We also noted lowest foraging rates and diet breadth in winter (Figures 3.1 and 3.3). Other traits varied only slightly with seasonal change (Figure 3.4).

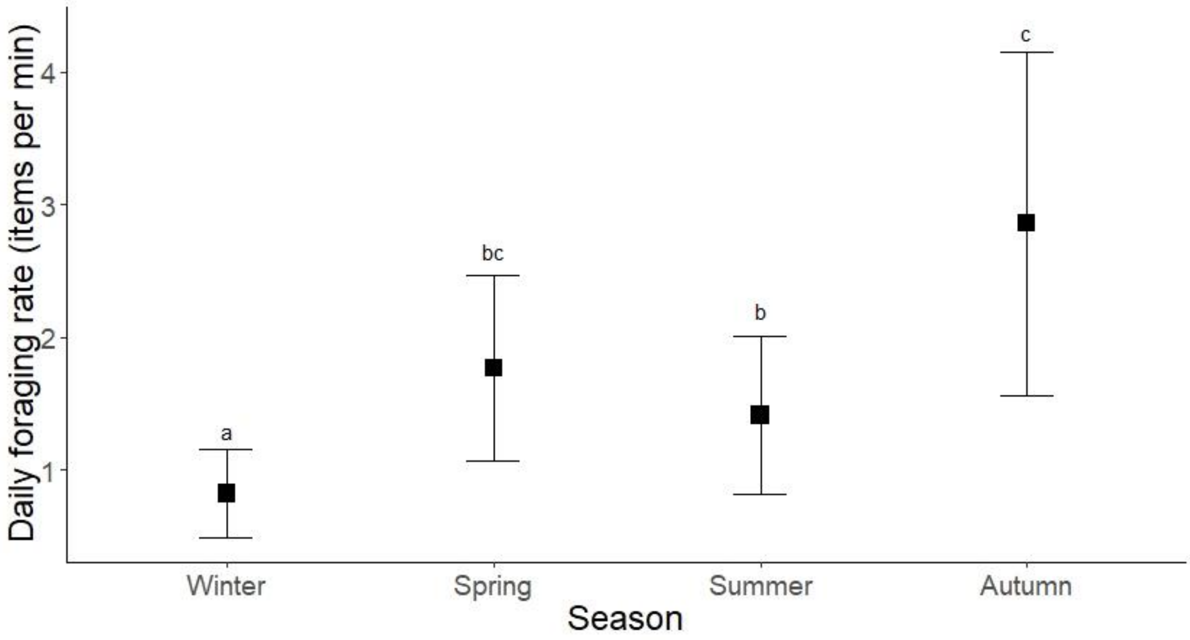

Figure 3.1. The relationship between season and daily foraging rate of bat-eared foxes. Boxes indicate means, and bars are 95 % confidence intervals. Seasons sharing a letter are not significantly different (Tukey-adjusted comparisons).

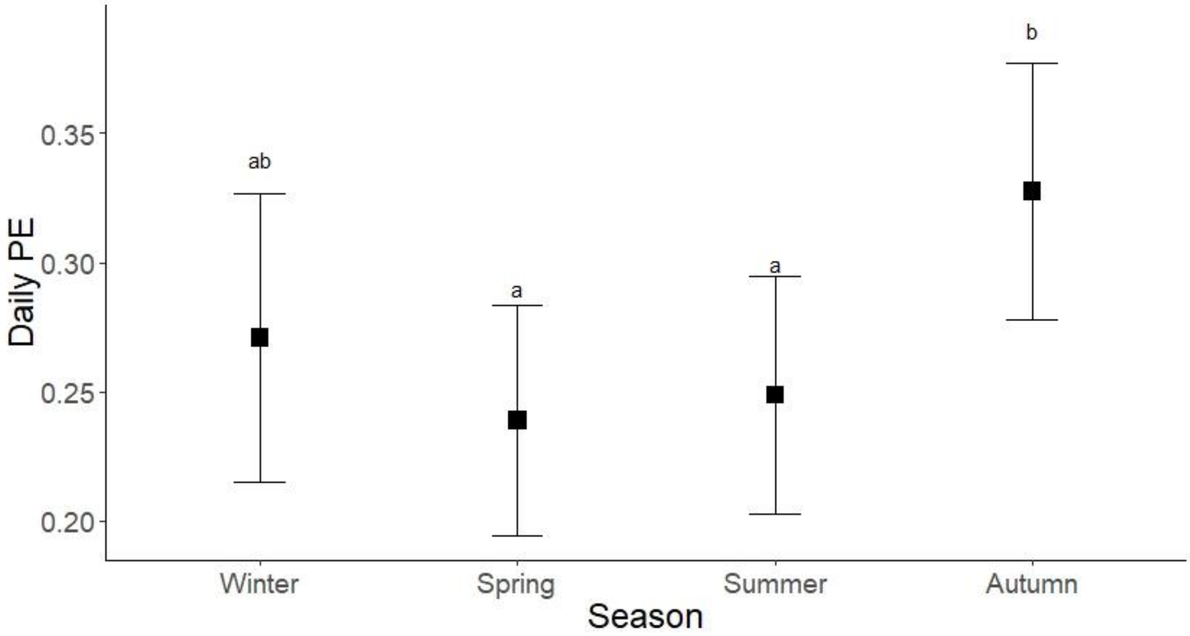

Figure. 3.2. The relationship between season and daily percentage of home range explored (PE) by bat-eared foxes. Boxes indicate means, and bars are 95 % confidence intervals. Seasons sharing a letter are not significantly different (Tukey-adjusted comparisons).

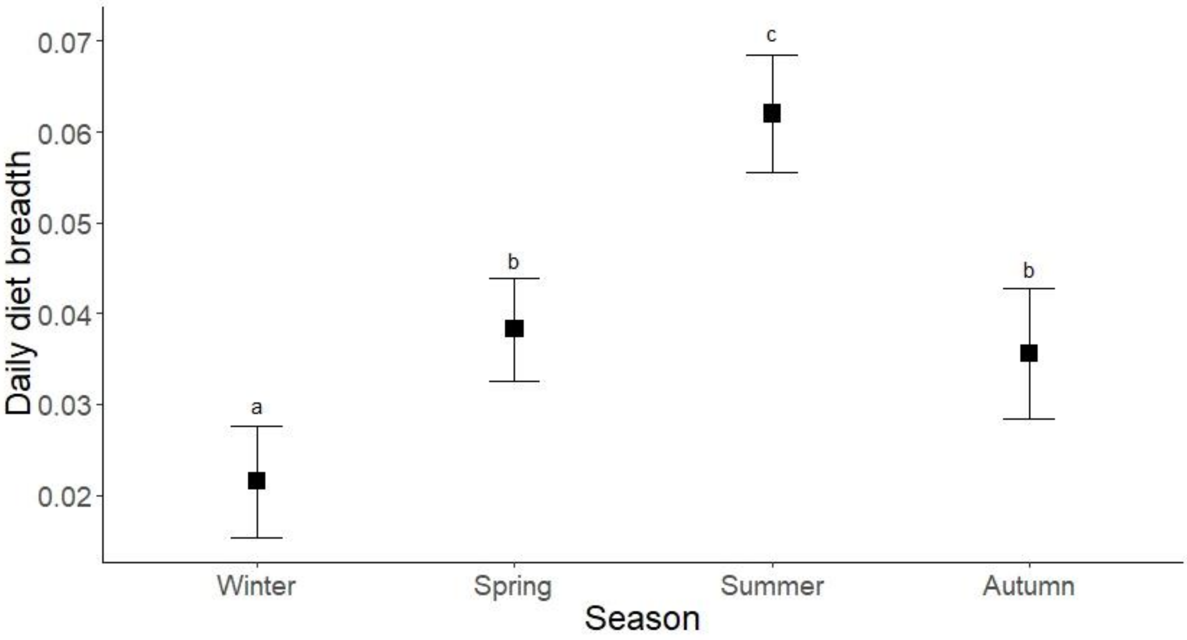

Figure 3.3. The relationship between season and daily diet breadth of bat-eared foxes. Boxes indicate means, and bars are 95 % confidence intervals. Seasons sharing a letter are not significantly different (Tukey-adjusted comparisons).

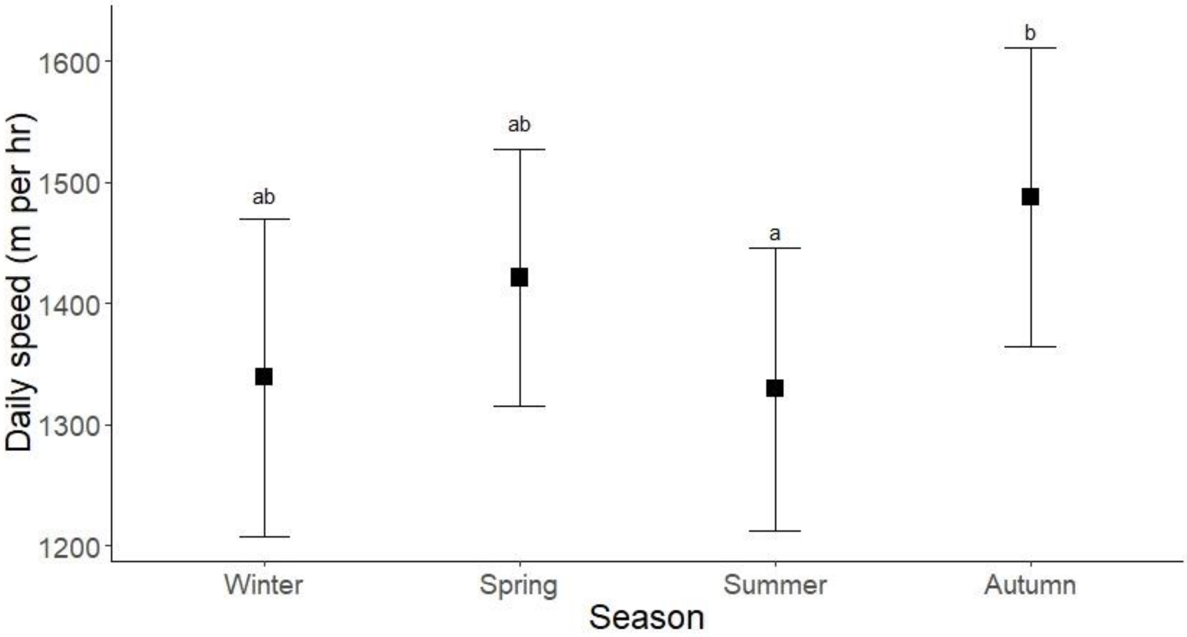

Figure 3.4. The relationship between season and daily speed of bat-eared foxes. Boxes indicate means, and bars are 95 % confidence intervals. Seasons sharing a letter are not significantly different (Tukey-adjusted comparisons).

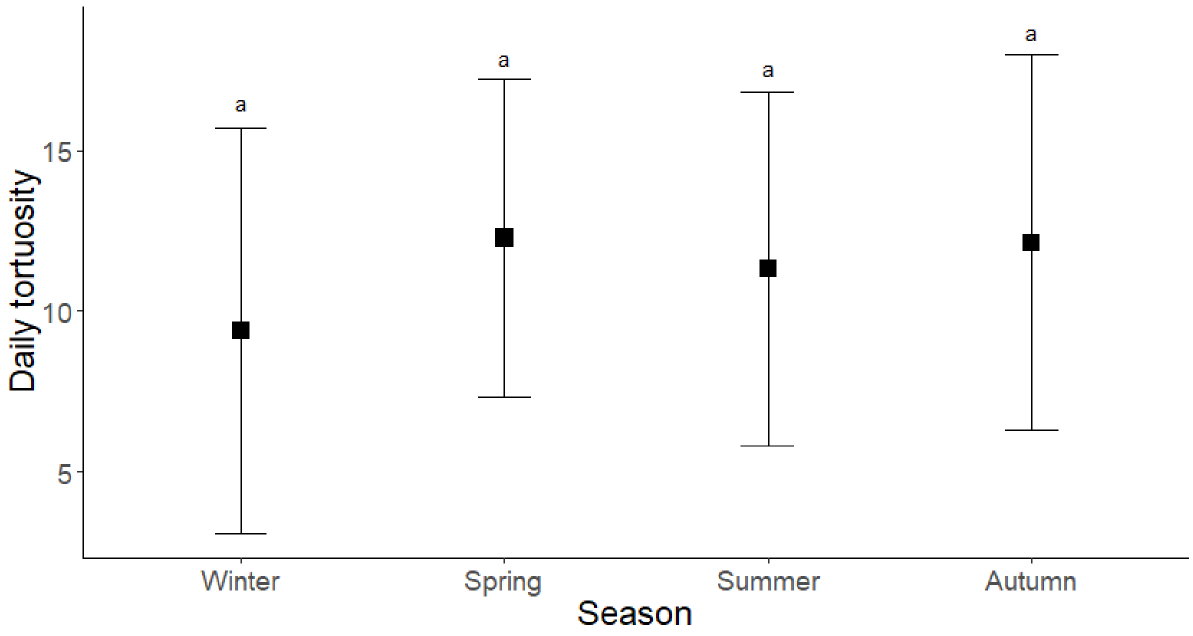

Figure 3.5. The relationship between season and daily tortuosity of bat-eared foxes. Boxes indicate means, and bars are 95 % confidence intervals. No seasons were significantly different (Tukey-adjusted comparisons).

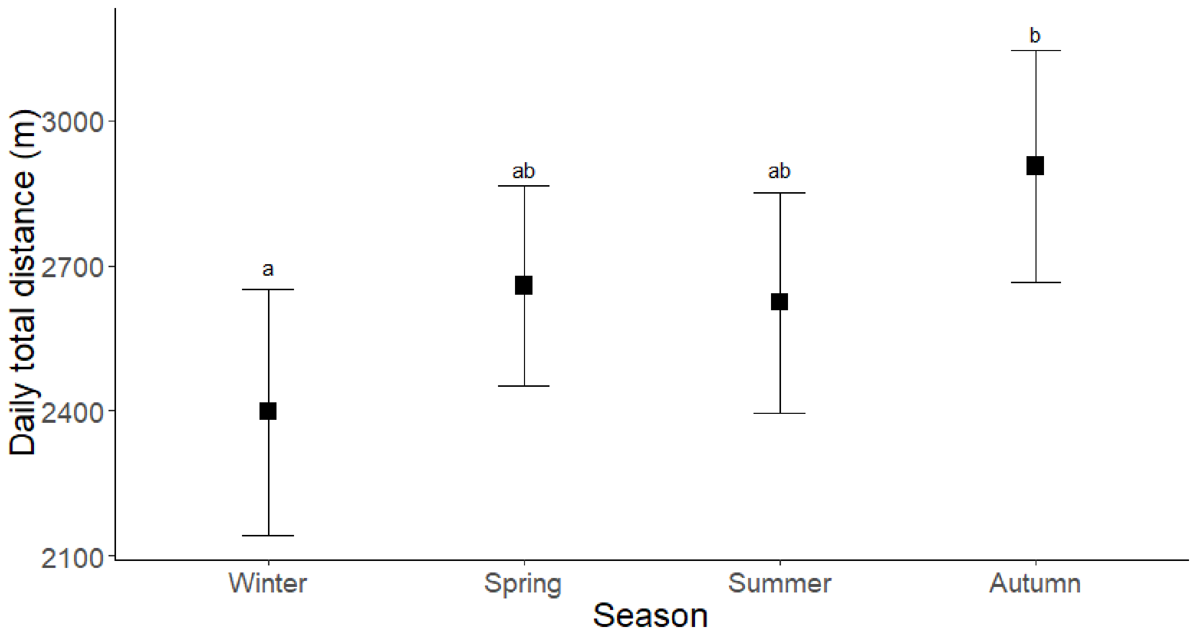

Figure 3.6. The relationship between season and daily total distance travelled by bat-eared foxes. Boxes indicate means, and bars are 95 % confidence intervals. Seasons sharing a letter are not significantly different (Tukey-adjusted comparisons).

3.4.3. *Behavioural syndromes*

In order to determine whether bat-eared foxes displayed behavioural syndromes (i.e. correlations) that were consistent across behavioural traits and thus establish if traits would evolve independently, or would otherwise be constrained (i.e. when significantly correlated), we used bivariate models to estimate any such significant correlations. We did not find any significant correlations between diet breadth and movement metrics (Figure 3.7 a), between foraging rate and any other metric (Figure 3.7 b), nor between the four movement metrics (Figure 3.7 c).

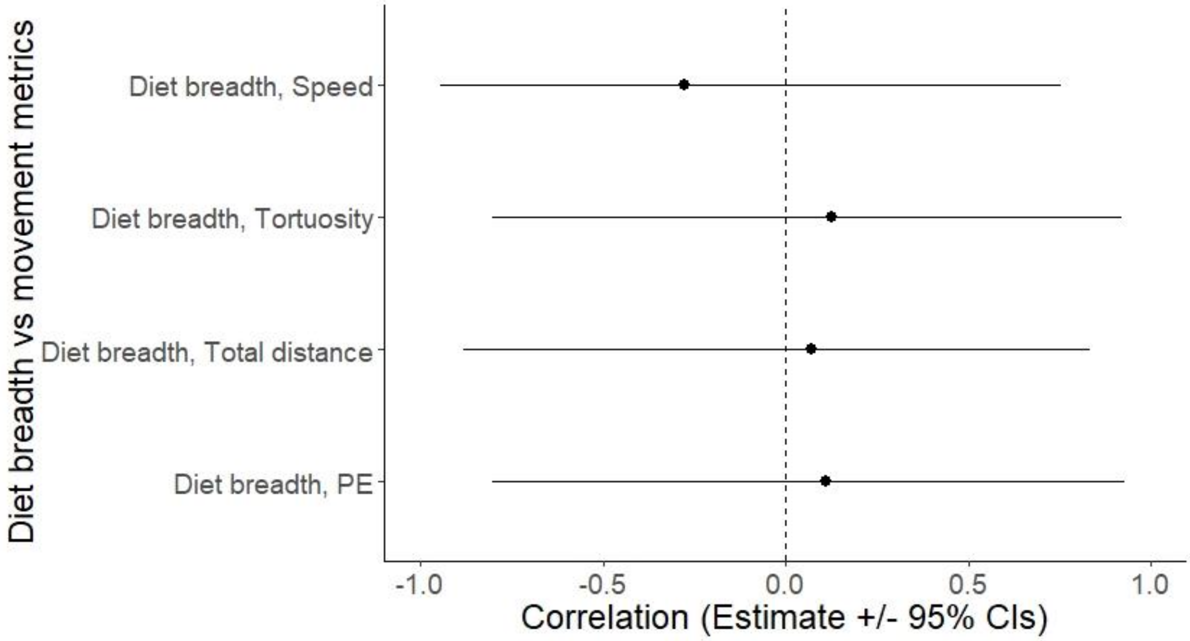

Figure 3.7 (a). Correlations between daily diet breadth and movement metrics estimated from posterior distributions of MCMCglmm bivariate model with statistical significance assessed using their 95 % credible intervals. PE = percentage of home range explored

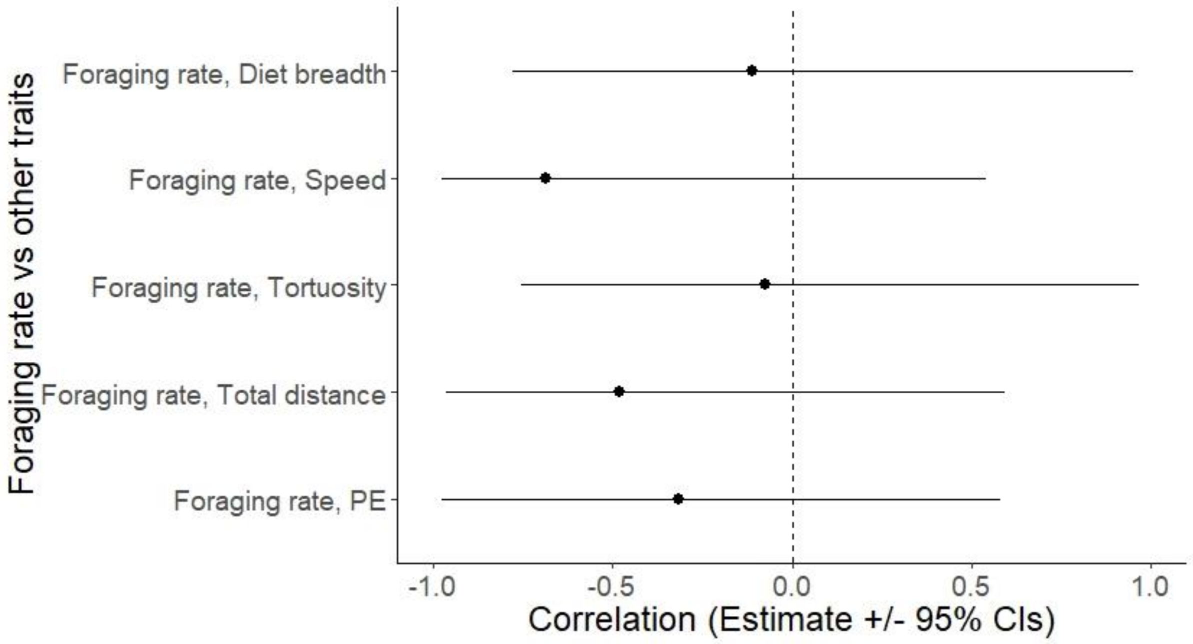

Figure 3.7 (b). Correlations between foraging rate, diet breadth and movement metrics estimated from posterior distributions of MCMCglmm bivariate model with statistical significance assessed using their 95 % credible intervals. PE = percentage of home range explored

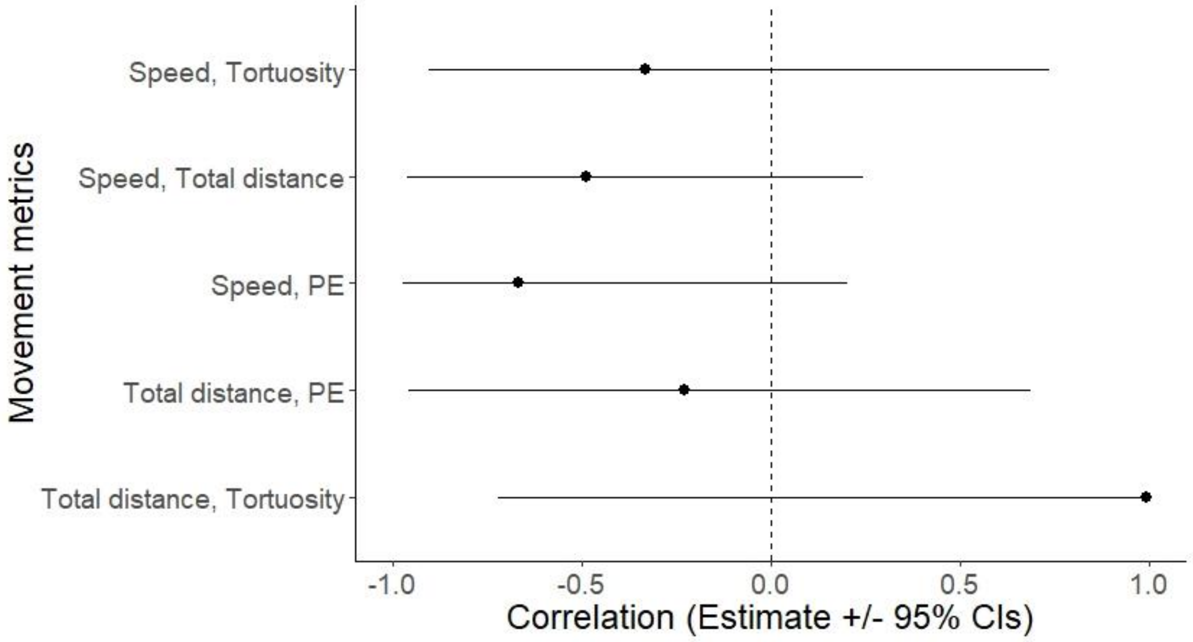

Figure 3.7 (c). Correlations between movement metrics estimated from posterior distributions of MCMCglmm bivariate model with statistical significance assessed using their 95 % credible intervals. PE = percentage of home range explored

3.5. Discussion

This study provides the first assessment of both multiple foraging metrics and movement metrics in a free-living canid. Our results reveal individual differences in four of the six metrics examined and a significant effect of season for all metrics except for tortuosity. They also highlight the absence of any behavioural syndromes within and between foraging and movement metrics.

3.5.1. Foraging metrics—diet breadth and foraging rate

The absence of individual differences in diet breadth for foxes is not unusual as these canids are considered termite-specialists (Berry 1981; Nel 1990; Stuart et al. 2003; Maas and Macdonald 2004). Indeed, a recent study revealed an average of 70 % termite occurrence in fox diet across all seasons (Chapter 2; Jumbam et al. 2019). However, as earlier hypothesized, season significantly influenced the population’s daily diet breadth, with the broadest daily diet breadth in summer and the narrowest in winter. Our study location experiences the highest rainfall and temperatures in summer (Clutton-Brock et al. 1999) and these factors together promote the proliferation of invertebrate communities (Nylin and Gotthard 1998). It is therefore not surprising that a reduction in rain after summer resulted in the lowest diet breadth, as alternative food categories would decline concomitantly.

Foraging rate, on the other hand, differed significantly between individuals. To our knowledge, this is the first study to uncover individual differences in the foraging rate of a canid. Rapid foraging rates have been shown to be selected under combined conditions of high predation risk and intraspecific competition in a population of spotted salamanders (Urban and Richardson 2015). Owing to the low predation risk at our study site (Welch et al. 2018), we suspect an increase in intraspecific competition for food resources with the onset of autumn and a decline in alternative food categories may have contributed to higher foraging rates in this season.

Environmental variables can influence foraging rate. For instance, day–time wind speeds in winter have been shown to significantly increase foraging rates of bat-eared foxes at night because of reduced foraging time (S. Renda and A. le Roux unpubl. data). However, lunar phase variations have no significant effect on bat-eared fox foraging rate (Welch et al. 2017). In our population, foxes had the highest foraging rate in autumn and the lowest in winter, suggesting a deliberate strategy to maximise available supplementary food categories in autumn, in preparation for winter when such food categories are notably absent (see Chapter 2; Jumbam et al. 2019), or when increasing wind speeds inhibit foraging activity.

3.5.2. Movement metrics—speed, tortuosity, total distance travelled, and percentage of home range explored

Tortuosity was the only non-repeatable movement metric. Previous studies show an increase in tortuosity with patchy food distribution, with an animal's movement pathway increasingly convoluted when a food source is encountered (Spiegel et al. 2017). In our study site, food resources are homogenously distributed across different habitats (Périquet and le Roux 2017) and since individuals did not differ in diet breadth, these findings together offer a reasonable explanation for the absence of repeatability in tortuosity. We did find significant individual differences in the three remaining movement metrics—speed, total distance and percentage of home range explored. A possible factor contributing to these individual differences include the energetic state of individuals, which has been shown to affect animal exploratory abilities (Dingemanse and Wolf 2013). Other factors may include fluctuations in environmental cues (Patrick et al. 2017), predator risk, intraspecific competition, foraging time constraints and temperature changes (Urban and Richardson 2015). These notwithstanding, repeatability estimates observed in this study were generally low (≤ 0.12) compared to repeatability of behaviour in general (see Bell et al. 2009), and could be suggestive of external factors such as animal home range/territoriality or habitat type differences that may inflate repeatability estimates, thereby causing pseudo-repeatability (Niemelä and Dingemanse 2017). Although the bat-eared fox is said to be non-territorial, a decline in its dominant prey base could instigate territoriality (Maas 1993). Nonetheless, we did not find reason to suspect territoriality in our study population owing to their overall non-aggressive social structure (de Bruin et al. 2018), the homogenous distribution of their food resources (Périquet and le Roux

2017) and the proximity of individuals' home ranges. It is possible that seasonal activity such as den attendance during parenting season and dispersal of individuals in search of mates in the breeding season (Malcolm 1986; Maas and Macdonald 2004; Wright 2006) may have contributed to these individual differences. Indeed, *post hoc* investigations confirmed our suspicion that seasonal activity significantly affected these metrics, with the exception of tortuosity.

At the population level, season had a significant impact on all movement metrics except for tortuosity. This suggests that patchiness of food resources did not change seasonally, and remained homogenous throughout the year. Interestingly, all three movement metrics peaked in autumn, with speed exceeding 1 600 m/hr, total distance exceeding 3 000 m/hr and the highest PE values (> 0.35) recorded in this season. These findings, together with the highest foraging rates recorded in autumn, highlight this season as a pivotal transitional period into winter that necessitates rapid food acquisition by foxes. This urgency to accrue food reserves is supported by the absence of alternative food categories in winter and a diurnal shift in foraging pattern in winter that has been linked to termite activity (Mackie and Nel 1989; Clark 2005).

3.5.3. Behavioural syndromes

Contrary to our hypotheses, we did not find any correlations between foraging and movement metrics. The absence of correlations possibly stems from the absence of repeatability in metrics such as diet breadth and tortuosity, as well as the generally low repeatability values observed in this study (≤ 12.5 %). The lack of correlations suggest that these metrics are unlikely to constrain each other or co-evolve.

3.6. Conclusion

This is the first long-term study in wild carnivores to have documented a combined assessment of foraging and movement metrics, and evaluated the relationships between them. We have highlighted the emergence of individual differences in foraging rate and in three of the four movement metrics examined, as well as uncovering a significant effect of season on all metrics except for tortuosity. Nonetheless, the absence of individual differences in diet breadth and tortuosity, the overall low repeatability in most metrics, and the lack of behavioural syndromes between all metrics lend support to the likelihood that these foxes have evolved to exhibit similar behavioural characteristics in most traits.

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3.7.1. Compliance with ethical standards

Ethical approval: All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All protocols were evaluated by The University of the Free State's ethical committee and were in accordance with The University of the Free State's ethical standards protocol under the ethical clearance number 11/2013. The Department of Nature Conservation approved all fieldwork under permit number 476/2/2013.

Conflict of interest: The authors declare that they have no conflict of interest.

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CHAPTER 4

EFFECT OF REPRODUCTIVE STATUS ON FORAGING BEHAVIOUR AND GLUCOCORTICOID LEVELS IN A WILD CANID

Jumbam KR, Ganswindt A, Renda S, le Roux A. (In Prep.)

4.1. Abstract

Diet has been described as fundamental to extensive paternal care and limited maternal care seen in bat-eared foxes (*Otocyon megalotis*). This termite specialist can only increase its energetic intake by spending more time foraging, not by hunting larger prey, or provisioning such prey items to a mate or pups. Therefore, physiologically-stressed lactating mothers are forced to invest more time foraging, while fathers take on additional parenting responsibilities. Few studies have documented how parenting demands impact on both foraging behaviour and stress levels in bat-eared fox, particularly for free-living animals. We studied foraging behaviour in 20 wild bat-eared foxes for two years with the aims of evaluating how parental status may affect 1) daily foraging rates 2) food sizes consumed, and 3) faecal glucocorticoid metabolite (fGCM) levels, as a proxy for physiological stress. Given that this canid is a seasonal breeder, we further considered how behaviour and physiology may vary in relation to seasonal activities, namely —breeding season (pregnant or new parent phase), denning season (pup-rearing phase including den-intensive guarding phase) and non-breeding season (independent adult phase). Daily foraging rates in the population were highest (> four food items per min) during denning season, with no variation between males and females in the population. However, when parental status was factored in, male parents had higher foraging rates than female parent and non-parents. Large food items were consumed the most within the study population during breeding season, with females eating significantly more large items than males. Interestingly, parental status interacted with sex to influence these foraging dynamics, such that male parents consumed more large food items than the female parent and non-parents. During denning season, male parents also consumed significantly more small items than other foxes in the population, once again indicating the impact of parental status on foraging behaviour. We noted the first caching behaviour ever recorded in this species from a female parent raising three pups; she also consumed the highest number of rodents (n=35) in the study population. Hormone levels in the population were generally low (fGCM < 0.4 $\mu g\ g^{-1}$ organic content) and not related to sex or parental status, but rather to seasonal activity: we measured significantly higher fGCM levels during denning season, suggesting that this season —which precedes dispersal and food-scarce winter —may be a source of stress within this population. This is the first study to determine the intricate relationship between foraging rates, parenting behaviour, and hormone levels in the bat-eared fox. Despite the small sample of parents (n=3), it seems that parental care has a significant impact on foraging behaviour —but not physiological stress —in adult bat-eared foxes.

Keywords: foraging rate, glucocorticoid levels, parental care, reproductive status, seasonal activity

4.2. Introduction

Like most canids, bat-eared foxes (*Otocyon megalotis*) are mainly monogamous and live in small family groups but rare incidences of polygamy have been reported (Pauw 2000; Wright et al. 2010). Unlike most other canids, this species is a dietary specialist, feeding predominantly on termites and small items (Berry 1981; Nel 1984; Stuart et al. 2003), which appears to have had significant consequences for parental care in bat-eared foxes (McNab 1984; Oftedal and Gittleman 1989; Pauw 2000). Because of this dietary restriction, male bat-eared foxes cannot provision lactating females with large food items, and such provisioning (typical of paternal care in other canids) has rarely been documented. Furthermore, female bat-eared foxes are expected to be under physiological stress due to the demands of pregnancy and lactation (Oftedal and Gittleman 1989). Females cannot, however, increase their energetic intake by hunting or caching larger food items and are therefore forced to spend considerably longer foraging periods on their small-bodied primary prey base, i.e., termites. This leads to the prevalence of heavy male investment in paternal care (Maas and Macdonald 2004), while the mothers' primary contribution to parental care is nursing. Indeed, it is presumed that the extensive maternal nursing periods coupled with her nutritional needs could be driving allonursing and polygamous breeding groups within this species (Pauw 2000).

Despite the likely centrality of diet in the formation of bat-eared foxes' monogamous social system and unusual paternal care patterns, most studies of parental care in this species have focused on time spent with pups (Wright 2006) or a description of limited instances of provisioning (le Roux et al. 2014). We do know that in this species, male food provisioning occurs occasionally, and is typically restricted to large items such as lizards provided to pups (Pauw 2000). It is also clear that males spend significantly more time at den caring for offspring than do females (Wright 2006), which restricts the time available for males to forage. The presumed nutritional demands on parents and particularly the mothers may be expected to drive behavioural coping mechanisms such as food caching of larger prey items, as has been observed in other fox species (Macdonald 1976; Nel 1984; Careau et al. 2007). However, caching has never been documented in this species. Changes in bat-eared foxes' foraging behaviour or physiological stress have not yet been examined in relation to parenting. Indeed, the endocrinology of parental care in canids remains a largely unexplored topic (de Bruin et al 2016).

Our aim in this study was to assess how parenting might affect foraging behaviour and stress physiology in wild bat-eared foxes, controlling for changes that may simply be ascribed to austral seasonal changes that are known to impact foraging behaviour (Chapter 2 and 3; Jumbam et al. 2019). We predicted that (A) both male and female parents should increase food intake during parenting season, by elevating foraging rates and increasing the size of prey items consumed. Further, we expected that (B) both sexes would exhibit heightened glucocorticoid levels while pups were dependent on their care, with faecal glucocorticoid levels serving as an indicator of physiological stress in the animals. These phenotypic changes in parents would exceed any similar changes occurring throughout the population due to seasonal changes in, for example, food availability.

4.3. Material and Methods

4.3.1 Study location and population

We conducted this study on 20 habituated adult foxes (nine females, including one parent, and eleven males, including two parents) at Kuruman River Reserve (KRR, 28°59’S, 21°49’ E), which covers an area of 32 km^2 in the Northern Cape province of South Africa. The reserve consists of Kalahari Thornveld and perennial grasses on sandy dunes (Clutton-Brock et al. 1999) and experiences a mean annual rainfall of 282 mm, with temperatures during our study period ranging from –4.60 °C to 41.0 °C (Welch et al. 2017). We defined austral seasons as summer (December – February), autumn (March – May), winter (June – August) and spring (September – November). Three categories of seasonal “activity” (which aligned with austral seasonal changes to some extent) were further defined as breeding season (November to February), denning season (March to June) and non-breeding season (July to October). These activities symbolised periods when individuals were likely to have become new parents or were expectant/pregnant (breeding season), pup-rearing phase —which includes parents chaperoning pups on foraging trips and also protecting the den (denning season) and lastly, when pups became independent or parents/adults were pup-free (non-breeding season).

4.3.2. Foraging behaviour recordings

We habituated animals and recorded their foraging behaviour on Android Samsung tablets programmed with Cybertracker software as described in Jumbam et al. (2019). A "follow" session is defined as an observation period in which trained observers would locate a habituated fox and follow it around for a maximum of two hours, starting at dusk when these nocturnal animals were most active. Observers used flashlights to enable direct observations of animal behaviour at night but limited its interference with normal activity by not focusing the light into the animal's gaze. Animals could be recalled only once if lost during follows and recalling involved using habituation calls to locate the individual, and then feeding it limited number of raisins (≤ 10). Recalled individuals were often located within a few minutes and data collection would proceed as normal, with the recall incident noted for clarity. Focal animals were in close proximity to observers during follows (≤ 5 m), making it possible to record their social interactions and foraging behaviours on a Samsung tablet during these follows.

4.3.3. Faecal sample collection

We collected 332 fresh faecal samples from focal animals (n_{males} = 203, $n_{females}$ = 129), labelled them according to individual identity and date of collection, and immediately placed the samples on ice blocks in cooler bags for the duration of the follow. Upon arrival at the research base, we immediately transferred samples to temperatures of -20°C until further hormonal processing at Endocrine Research Laboratory (ERL) in Onderstepoort, University of Pretoria, South Africa.

4.3.4. Hormone extraction from faecal samples and analyses

We started hormone extractions by lyophilising the frozen faecal samples at -58°C, followed by pulverisation and sieving the faecal powder using a fine mesh to remove fibrous material. Due to ongoing field data collection, we extracted hormones in two separate batches —the first batch (n = 297) in September 2015, and the second batch (n = 40) in April 2016, resulting in a total of 337 samples. We excluded five samples from our analyses as they belonged to an unhabituated individual for which we did not have further information. This resulted in a total of 332 samples from which the results described in this study are based on. In the first batch of samples, we extracted the supernatant containing hormone content by weighing 0.05–0.06g of faecal powder which was vortexed for 15 min with 1.5 ml vol of 80 % ethanol followed by 10 min centrifugation at 1500 relative centrifugal force. In the second batch we doubled faecal powder and ethanol measurements to improve metabolite content extraction but retained the centrifugation time and speed of the first batch. We transferred the resulting supernatant into microcentrifuge tubes and stored them at -20°C for metabolite extraction. Subsequently, we used enzyme immunoassays (EIA) to measure faecal glucocorticoid hormone (fGCM) levels following the same procedure as outlined in de Bruin et al. (2018).

4.3.5. Determination of organic content and analyses

We accounted for organic content in faeces due to high mineral content from accidental soil ingestion, which could impact on hormone concentration measurements (see de Bruin et al. 2018). We determined organic content by oven-drying (at 70°C) previously weighed faecal powder sediments for which all the supernatant had evaporated. To confirm complete evaporation of supernatant, we weighed sediments repeatedly until the weights were constant. Thereafter, we transferred the sediments to tin foil cups and incinerated them at 430°C for an hour before placing into a desiccator for 2 hours. We then re-weighed samples and calculated the organic content as the difference in mass before and after incineration. Further statistical analyses proved that organic content did not affect hormone concentration (see details in de Bruin et al. 2018).

4.4. Data Analysis

4.4.1. Foraging behaviour

We collected data from July 2014 to April 2016, amounting to 57 ± 29 h mean observation time per individual. For each follow, we calculated foraging rates by dividing the total count of all ingested food items during the follow by the duration (in minutes) of the follow (i.e., items per min). Additionally, we classified food items consumed into different size categories based on measurement estimates (Table 4.1).

Table 4.1. Food size classification of bat-eared fox diet

Food size	**Measurement**	**Order and Class†**
Small	≤ 2 cm	Isoptera (termites) Hymenoptera (ants) Plant seeds Orthoptera (crickets)
Medium	2—4.9 cm	Neuroptera (antlions) Coleoptera (beetles) Lepidoptera (caterpillars) Orthoptera (grasshoppers) Mantodea (mantises) Hemiptera (cicadas) Lepidoptera (moths) Arachnida† (spiders)
Large	5—50 cm	Rodentia (rodents) Diplopoda (millipedes) Lagomorpha (Springhares) Reptilia† (reptiles) Scorpiones (scorpions) Amphibia† (frogs) Other (fungi)

Due to the infrequent consumption of large items by foxes, we combined medium and large food sizes into one category simply termed, large items. A non-significant number (0.0001) was added across all dataset to neutralise any zeroes still present in the dataset even after this merger. We used generalised linear mixed effect models (GLMMs) in R (R Core Team 2019, version 3.5.3) to assess multiple interactions of three traits namely: sex, parental status —parents (n=3) and non-parents (n=17) —and seasonal activity on both foraging rate and food sizes ingested. Food sizes were included in the models as fixed variables while we controlled for austral season (i.e. summer, winter, autumn and spring) as random variable, since previous research showed seasonal effects on foraging behaviour and food availability (see Jumbam et al. 2019). Individual foxes were maintained as random variables and we log-transformed our data to meet normality assumptions and also examined the significance of different models using log-likelihood ratio tests, LRT (see Table 4.2).

4.4.2. Faecal hormone data

We measured faecal glucocorticoid metabolite (fGCM) levels for 332 samples which were expressed per gram organic mass (µg/g organic content). To evaluate the effect of parental status on seasonal activity, we used GLMMs in R to assess the interactions of both parental status and seasonal activity on fGCM levels (the dependent variable). We controlled for austral season (i.e. summer, winter, autumn and spring) as random variable, as previously described. With fGCM level as dependent variable, we set austral season as fixed variable and individual foxes as random variables to evaluate variations in hormone levels across austral season. We log-transformed the hormone data to meet normality assumptions and examined the significance of different models with LRT.

4.5. Results

4.5.1. Daily foraging rate variation

We did not find any significant difference in daily foraging rates between sexes across seasonal activity ($F_{2,560}$=1.08, *P* = 0.34; Figure 4.1 a). Parental status did not affect foraging rates ($F_{2,560}$=0.50, P = 0.61; Figure 4.1 b), but we found a significant interaction between sex and parental status ($F_{1,560}$=5.0, P = 0.03; see Table 4.2) with male parents foraging at much higher rates than non-parental males, mothers, and non-parental females (Figure 4.1 c). We also found significant interactions between sex, seasonal activity and parental status ($F_{2,560}$=3.3, P = 0.04; see Table 4.2).

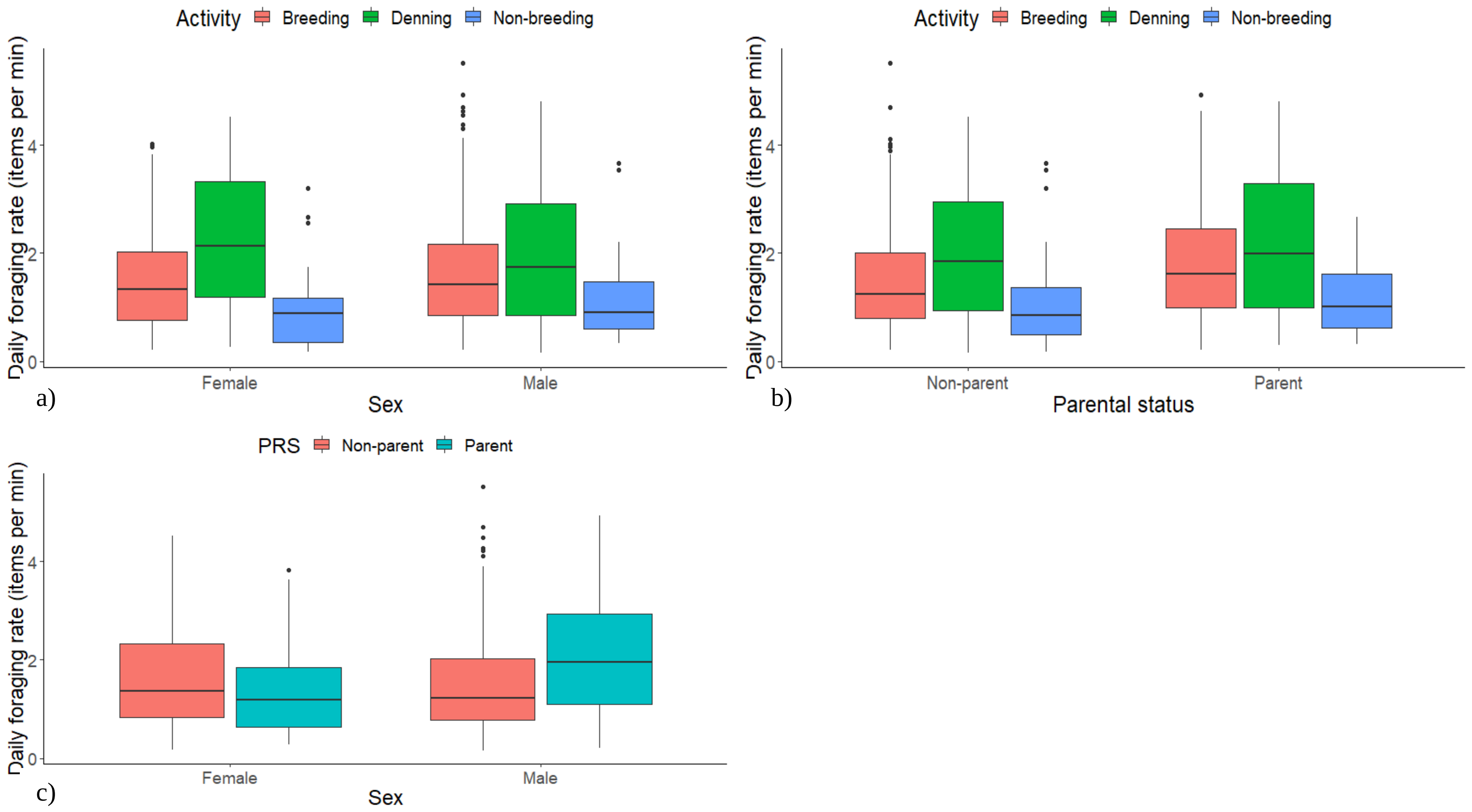


Figure 4.1. Variations in daily foraging rate of bat-eared fox **a**) across seasonal activity between males and females, **b)** across seasonal activity as related to parental status, and **c**) between males and females as related to parental status. Boxplots represent interquartile range (IQR) comprising of lower quartile, median —middle line, and upper quartile. Box shape shows the spread of data, with symmetry denoting normality. Whiskers denote data range outside of IQR, and dots are possible outliers. PRS = Parental status.

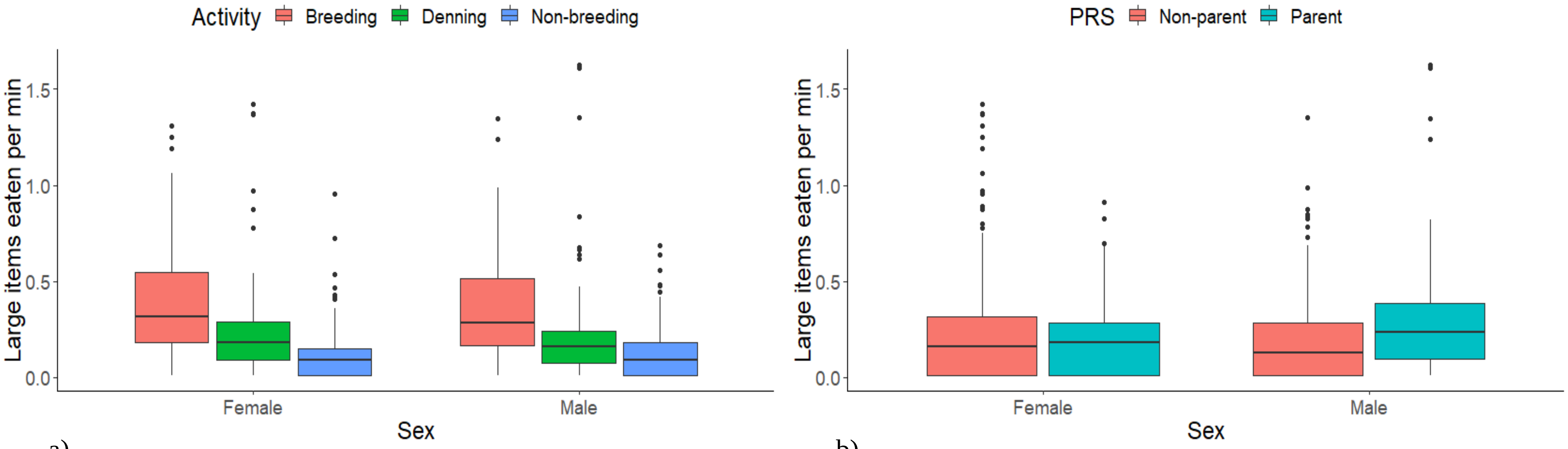
Table 4.2. Generalised linear mixed-effect models (GLMMs) with *daily foraging rate* as the dependent variable, trait interactions as fixed variables, fox identity and austral season as the random variables. We used log-likelihood ratio test (LRT) estimates as a measure of model fit, and significant interactions are in bold.

Models	**LRT**	***df***	**χ^2**	***P***
M1.1: sex+activity+PRS	-1014.9	7.0		
M1.2: "M1.1" + sex*activity	-1011.5	9.0	0.0	1.0
M1.3: "M1.1" + sex*PRS	**-1006.6**	**8.0**	**16.7**	**< 0.001**
M1.4: "M1.1" + activity*PRS	-1014.6	9.0	0.0	1.0
M1.5: "M1.1" + sex*activity*PRS	**-999.3**	**14.0**	**30.7**	**< 0.001**

PRS = Parental status; activity = seasonal activity

4.5.2. Daily foraging rates of large food items

We found seasonal activity was significantly related to foraging rates of large food items (2-50 cm) within this population, with both sexes exhibiting the highest foraging rates in breeding season, followed by denning and non-breeding seasons ($F_{2,178}$=16.5, $P < 0.001$; Fig. 4.2a). Foraging on large items was significantly affected by the interaction between parental status and sex ($F_{1,562}$=4.1, $P < 0.05$) with male parents foraging at much higher rates than non-parent males and females, regardless of parental status (Fig. 4.2b). Interestingly, the foraging pattern of highest foraging rates in breeding season, followed by denning and then non-breeding seasons did not differ significantly between sexes ($F_{2,562}$=2.9, $P > 0.05$) and a similar foraging pattern was also observed for parents and non-parents ($F_{2,562}$=1.1, $P > 0.05$).



a)

b)

Figure 4.2. Variations in daily foraging rates of large items (2 – 50 cm) eaten between males and females as related to **a)** seasonal activity **b)** parental status (PRS). Boxplots represent interquartile range (IQR) comprising of lower quartile, median —middle line, and upper quartile. Box shape shows the spread of data, with symmetry denoting normality. Whiskers denote data range outside of IQR, and dots are possible outliers.

Table 4.3. Generalised linear mixed-effect models (GLMMs) with *large food items* (2-50 cm) as the dependent variable, trait interactions as fixed variables, fox identity and austral season as the random variables. We used log-likelihood ratio test (LRT) estimates as a measure of model fit, and significant interactions are in bold.

Models	**LRT**	***df***	**χ^2**	***P***
M1.1: "sex+activity+PRS"	-1391.2	7.0		
M1.2: "M1.1" + sex*activity	-1388.6	9.0	2.1	0.2
M1.3: "M1.1" + sex*PRS	-1389.7	8.0	3.2	0.1
M1.4: "M1.1" + activity*PRS	-1390.8	9.0	0.0	1.0
M1.5: "M1.1" + sex*activity*PRS	**-1383.2**	**14.0**	**15.2**	**< 0.01**

PRS = Parental status; activity = seasonal activity

4.5.3. Daily foraging rates of small food items

Seasonal activity significantly influenced foraging rates of small items (≤2 cm) within this population, with higher foraging rates during denning season and similar foraging rates between breeding and non-breeding seasons ($F_{2,172}$=3.3, $P < 0.05$; Fig. 4.3a, Table 4.4). We noted significant differences in foraging rates of small items between sexes across parental status with male parents foraging at much higher rates than non-parental males, mothers, and non-parental females ($F_{1,562}$=8.2, $P < 0.05$; Fig. 4.3b).

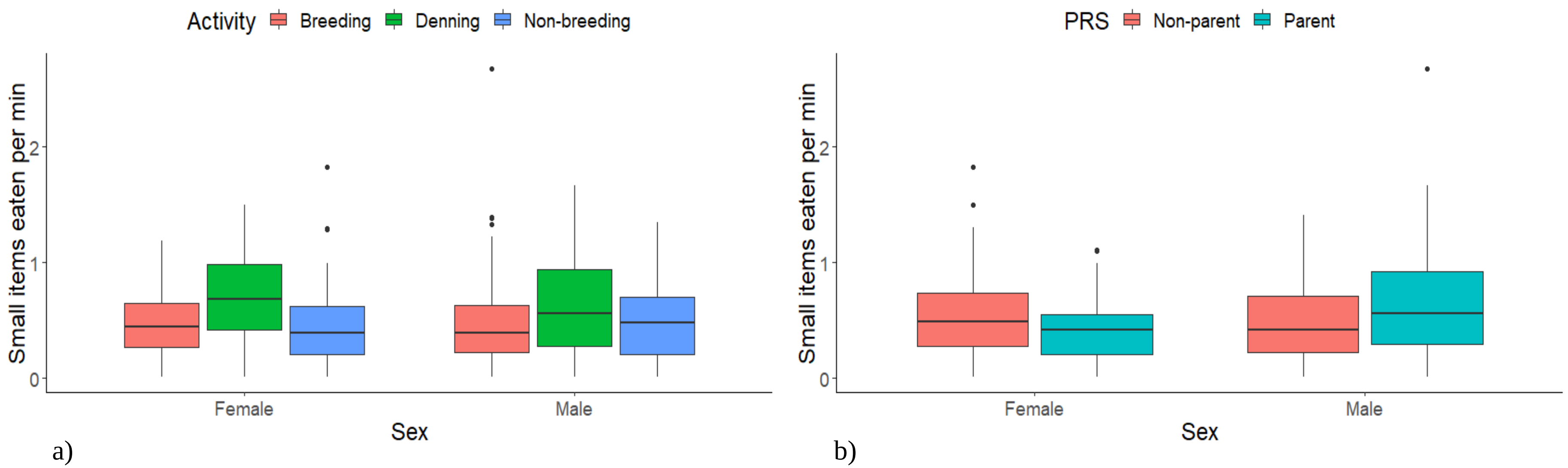


Figure 4.3. Variations in daily foraging rates of small items (≤ 2 cm) eaten between males and females as related to **a)** seasonal activity **b)** parental status (PRS). Boxplots represent interquartile range (IQR) comprising of lower quartile, median —middle line, and upper quartile. Box shape shows the spread of data, with symmetry denoting normality. Whiskers denote data range outside of IQR, and dots are possible outliers.

Table 4.4: Generalised linear mixed-effect models (GLMMs) with *small food items* (≤ 2 cm) as the dependent variable, trait interactions as fixed variables, fox identity and austral season as the random variables. We used log-likelihood ratio test (LRT) estimates as a measure of model fit, and significant interactions are in bold.

Models	**LRT**	***df***	**χ^2**	***P***
M1.1: “sex+activity+PRS”	-1308.0	7.0		
M1.2: “M1.1” + sex*activity	**-1386.5**	**10.0**	**8.8**	**< 0.01**
M1.3: “M1.1” + sex*PRS	**-1304.9**	**8.0**	**6.2**	**0.01**
M1.4: “M1.1” + activity*PRS	-1307.0	9.0	0.0	1.0
M1.5: “M1.1” + sex*activity*PRS	-1301.5	12.0	2.2	0.3

PRS = Parental status; activity = seasonal activity

4.5.4. Caching behaviour in the bat-eared fox

Between dusk on 16th March and dawn on 17th March 2015, the only mother (Bertha) in the study population successfully hunted 21 rodents. On that specific night, Bertha’s pups remained with her for a brief period during the first half of the evening, and thereafter were not seen again until 05:30 the following morning. Bertha hunted and consumed ten mice within the first focal period of the evening and subsequently cached several surplus killings.

We noted the first caching incident at 23:30. The vixen carried a freshly-killed mouse in her jaws for five minutes, before digging a shallow scrape into which she deposited the prey item. She immediately moved it to another area where she once again dug out a scrape and deposited her prey in the open before moving off (Fig. 4.4). Three more such occurrences followed in quick succession (at two, five and three-minutes intervals), where freshly-killed mice were deposited into scrapes she had dug, after which she left the mice unburied. In the third such case, she marked the scrape with urine. At 00:37 Bertha killed another mouse, carried it around for four minutes before abandoning it without digging a scrape. She left this prey behind to immediately pursue another. The elapsed time between the catching and caching of the first item and the fifth in this series of observations was 50 minutes. Bertha successfully hunted and consumed four more mice hereafter, before caching her kills again. At 02:22 she caught another mouse and deposited into a scrape she had just dug out, followed by a second in close succession at 02:27. She marked this scrape with urine before resuming foraging on other prey items. At 02:58 she consumed the head of a newly caught rodent, carried the body for ten minutes and then dug a scrape into which she deposited her kill. She returned two minutes later to the spot and consumed the rest of the body. She caught another mouse at 05:28 and consumed it rapidly, while growling at her approaching pups. At 06:03 Bertha revisited one of her scrapes and consumed the mouse she had cached there. This particular scrape was not any of the new scrapes she had dug that evening but was approximately 20 meters from the closest known caching site from the evening's observations. We lost sight of Bertha at dawn and could not confirmed whether she returned to any of the caching sites she dug that evening. During the entire study period, she consumed the highest number of rodents in the project (n=35) and mostly during the denning season. On average, her foraging rate of rodents was three times higher than for the rest of the population (Bertha: 3 ± 7 —mean ± SD; range 2 – 24 rodents consumed per month. Population: 1 ± 1 —mean ± SD; range 1 – 9 rodents consumed per month).

Fig. 4.4. An example of a rodent cached in a scrape (Photo credit: Samantha Renda)

4.5.5. Physiological stress and seasonal activity

We noted significantly higher fGCM levels in the population in autumn (Figure 4.5 a) but did not find any differences between the sexes ($F_{1,14}$=0.78, $P = 0.39$). Hormone levels differed significantly between parents and non-parents across seasonal activity ($F_{2,19}$=9.0, $P < 0.01$), with all foxes exhibiting higher hormone levels during the denning season, and parents' fGCM levels considerably lower in the breeding season (Figure 4.5 b).

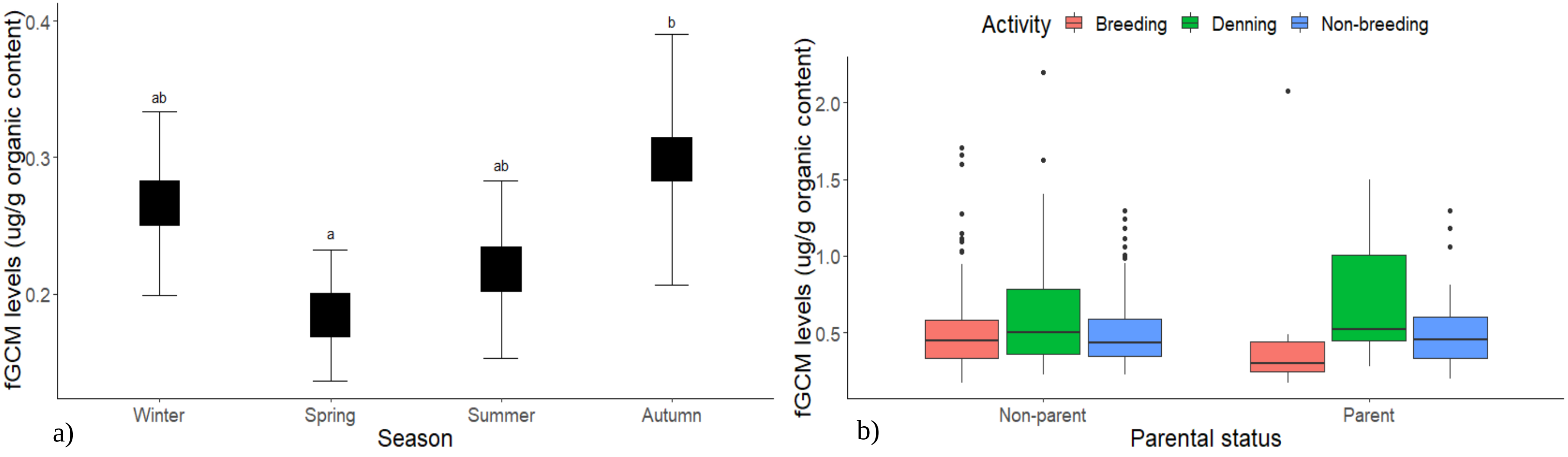


Fig. 4.5. Variations in faecal glucocorticoid hormone (fGCM) levels **a)** across austral season. Boxes indicate means and bars are 95 % confidence intervals. Seasons sharing a letter are not significantly different (Tukey-adjusted comparisons); **b)** between parents and non-parents across seasonal activity. Boxplots represent interquartile range (IQR) comprising of lower quartile, median —middle line, and upper quartile. Box shape shows the spread of data, with symmetry denoting normality. Whiskers denote data range outside of IQR, and dots are possible outliers.

Table 4.5. Generalised linear mixed-effect models (GLMMs) with *faecal glucocorticoid metabolite (fGCM)* levels as the dependent variable, trait interactions as fixed variables, fox identity and austral season as the random variables. We used log-likelihood ratio test (LRT) estimates as a measure of model fit, and significant interactions are in bold.

Models	**LRT**	***df***	**χ^2**	***P***
M1.1: "sex+activity+PRS"	-460.3	7.0		
M1.2: "M1.1" + sex*activity	-459.3	9.0	1.8	0.2
M1.3: "M1.1" + sex*PRS	-460.3	8.0	0.2	0.7
M1.4: "M1.1" + activity*PRS	**-456.1**	**9.0**	**6.4**	**< 0.001**
M1.5: "M1.1" + sex*activity*PRS	-453.6	14.0	5.1	0.4

PRS = Parental status; activity = seasonal activity

4.6. Discussion

4.6.1. Parental status and foraging behaviour

This study provides the first evidence of how bat-eared foxes' foraging behaviour is impacted by parenting roles. Across the population, daily foraging rates were highest during denning season and interestingly, more so for the male parents than for any other subgroup. This effect was particularly prominent for small food items (their primary prey). In canids such as the racoon dog (*Nyctereutes procyonoides*), fathers spend considerably more time (> 75 %) at dens caring for their pups than their female counterparts (Kauhala et al. 1998) and the bat-eared fox is no different (Pauw 2000; Maas and Macdonald 2004; Wright 2006; Wright et al. 2010). We propose that prolonged periods spent with pups at the den significantly constrained foraging time available to fathers. This would explain why fathers foraged at higher rates than any other member of the population, when they had the opportunity to do so. It is possible that during den-intensive babysitting periods, male parents would then focus on small food items such as termite patches closest to the den which are abundant and less energetically costly to attain.

Fathers also consumed large food items more frequently than other adults in the population, although the consumption rates peaked —for the whole population —during breeding season, before pups were present. This could be an intuitive preparatory strategy by male parents for the subsequent denning season where foraging time constraints would force them to switch to small food items while caring for pups. To our knowledge, this is the first time such a behavioural coping mechanism by male parents through food-size transitioning has been documented in the Canidae.

Importantly, analysis of shifts in food-size selection was constrained by the relatively small number of large items that bat-eared foxes consumed, and this lack of statistical strength masked the exceptional hunting behaviour of the only successful mother in this population. Bertha proved to be highly effective in hunting large food items, as she actively hunted and consumed a hare (Jacobs and le Roux 2015) and also caught the highest number of rodents in the population. The caching behaviour that Bertha displayed was the first ever recorded caching behaviour in this species. It was previously assumed that the species did not exhibit surplus killing and caching behaviour as they ate larger food items too rarely (see Clark 2005). Bertha's apparent surplus killing, also observed in other foxes (Kruuk 1972; Endicott et al. 2014), suggests a strategy to stock up on future food supplies either for herself and/or her pups. Indeed, adult red foxes caching turtle eggs have been seen to return to caches on subsequent nights with their young, suggesting that these animals have stored caches with the intent of provisioning their offspring (Macdonald et al. 1994).

We noted two incidents during Bertha's caching behaviour where she marked her scrapes with urine, most likely for easy relocation in the future. Canids are known to use scent marking in the form of rolling against items, faeces and urine (Wells 1981; Gorman and Trowbridge 1989) to serve a variety of roles including courtship, territorial defence, spatial orientation and dominance assertion (Harrington 1981; Wells 1981). Some canids such as the red fox (*Vulpes vulpes*) and coyote (*Canis latrans*) use scent marking while foraging to mark emptied scrapes and thus prevent the energy expense of returning there to search for a cache in future (Henry 1977; Wells 1981). Scent marking is often used for different functional roles between the sexes in canids. For instance, in coyotes, males use scent marking mainly for courtship and territorial defence while females use it for food acquisition particularly at denning season (Wells 1981). However, defaecation is the preferred scent marking method of relocating carrion in coyotes (Wells 1981). Bertha marked two of her scrapes with urine, suggesting that she may indeed return to relocate her cache through scent. Due to lack of territoriality in bat-eared foxes, scent-marking appears not to be a prominent form of communication in the species. Urination in the bat-eared foxes is correlated with androgen hormone levels in males (de Bruin et al. 2018), but Bertha's urine markings of her cache is a novel finding in this species. Pauw (2000) observed instances of bat-eared foxes provisioning large food items to pups upon return to the den. Provisioning with insect-harbouring dung by male parents has also been observed in bat-eared foxes (le Roux et al. 2014). It is possible therefore that the cached mice seen in this study was intended for pup provisioning, thus justifying the energetic costs of continued hunting by the vixen past her apparent satiation phase (e.g. see Kruuk 1972 for illustration on spotted hyaenas).

It is also possible that Bertha's successful hunting skill is a coping mechanism for her physiological dietary needs as a nursing mother. Observational records indicate that she continued to stalk and chase after hares on at least two separate occasions and a rabbit in another instance. Given that the demands of nursing in bat-eared foxes often necessitate allocare (Pauw 2000) and may lead to the relinquishment of maternal care entirely (Ross and MacLarnon 2000), we suspect that her hunting skills and penchant for large mammalian prey are a behavioural mechanism to counteract the dietary needs of her maternal role (see Pauw 2000). The timing of her caching behaviour (denning season) coincides with rains in the Kalahari where increased shrub cover is deemed suitable for rodents such as highveld gerbils (Blaum et al. 2006). Bertha may therefore have been capitalising on rodent availability in this period.

4.6.2. Physiological stress

We used fGCM levels as a proxy for physiological stress, and our findings agree with those of de Bruin et al. (2018) that show overall low fGCM levels in this population, which did not differ significantly between sexes. In other canids such as wolves, their fGCM levels have been shown to be twice as high as in this study, and to vary with the level of aggression within the population (Sands and Creel 2004, Creel 2005, van Kesteren et al. 2012). In this study, stress levels were highest within the population in the austral season of autumn, which incidentally coincides with denning season. The highest foraging rates within the population were also recorded within this season (Chapter 3; Jumbam et al. Under Review), suggesting that high stress levels may have been associated with rapid foraging rates within the population. Of notable interest were the peculiar foraging behaviours of the parents. Given Bertha’s caching behaviour in the denning season, and the result that male bat-eared fox parents had the highest foraging rates of different food categories within this season, suggests that parenting may be impacting on their stress levels. Secondly, social interactions within and between the growing pups and their surroundings with increasing foraging expedition trips would most likely require parental intervention, which could be another source of parental stress. Indeed, a strong correlation between cortisol levels in male adults and pup-feeding rates have been shown in some small carnivores (Carlson et al. 2006), thus providing a strong possibility that food provisioning and pup-rearing could be triggers for stress levels in parents.

4.7. Conclusion

We have showcased coping mechanisms in bat-eared fox parents, with fathers exhibiting the highest foraging rates in the population, and the only mother in the population capitalizing on the hunting —and surplus-killing —of large mammalian prey. This novel finding suggests that parenting demands may be driving unusual foraging adaptations in these canids. These behavioural coping mechanisms by the parents, coupled with limited negative social interactions within this species (de Bruin et al. 2018), likely account for the overall low stress levels observed in this study. Although our sample of parents was very low, we provide the first solid evidence for potentially unique foraging adaptations to the demands of parenting in a non-cooperatively breeding carnivore.

4.8. References

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CHAPTER 5

GENERAL DISCUSSION

5.1. Diet breadth in termite specialists

To date, no study has documented the foraging behaviour of free-living bat-eared foxes on a daily basis over such a long-term period, and explicitly by direct observations. My research provides fine scale foraging data on wild bat-eared foxes monitored daily on foot for two years. Direct behavioural observations provided me several advantages over traditionally indirect methods (e.g. scats and stomach content assessments), such as visually identifying and quantifying most prey items (60%) consumed during follows, thus circumventing processing time employed by traditional methods. Furthermore, direct observations presented the added advantage of discovering and documenting rare foraging events such as the first ever caching behaviour recorded in this canid. My research is the first to have combined direct observations with varied (pitfall and sweep netting) prey availability assessments in this canid, which brought novel insights into the foraging behaviour and prey item choice of this termite-specialist. For example, I demonstrated that these canids were not entirely opportunistic, but would select for larger prey when available, which was more pronounced in summer. I was also able to demonstrate some nuance in their prey choices by showing that their selection for larger prey was not necessarily based on nutritional content. For instance, despite the high nutritional value of some larger prey items such as beetles, their utilisation was lower than what I expected based on their relative abundances in the traps (see Chapter 2). Additionally, I was able to show that these canids consumed more termites in winter when alternative prey was limited. These findings highlight the importance of incorporating invertebrate assessments in broadening our understanding of the foraging behaviour of myrmecophagous mammals. While there’s considerable information on the foraging ecology of other termite specialists such as the aardwolf (*Proteles cristata*) (Cooper and Skinner 1979; de Vries et al. 2011) and the aardvark (Taylor et al. 2002), prey assessments alongside their foraging behaviours are limited, which could markedly improve our understanding of how they navigate seasonal fluctuations in their prey base.

An accurate description of invertebrate prey availability can be attained only by using varied assessment techniques. While pitfall traps are effective for invertebrate assessments and have been used for studies of termite foragers (Kuntzsch and Nel 1992; Willis et al. 1992) better methods such as termite baits are best suited for assessment of termite availability. I also advocate the use of sticky and light traps for phototactic insects such as Lepidoptera (Kuntzsch and Nel 1992), which also constitutes part of bat-eared fox diet (Jumbam et al. 2019).

5.2. Repeatability and behavioural syndromes in foraging and exploration behaviour

To the best of my knowledge, this is the first study to have investigated behavioural syndromes beyond the typical assessed traits of boldness, shyness and aggression (Sih et al. 2004; Dingemanse and Wolf 2010; Petelle et al. 2013; Blumstein et al. 2013; Spiegel et al. 2017). I focused on ecologically important metrics such as foraging (e.g. diet breadth and foraging rates), and movement metrics (e.g. speed, tortuosity, distance and percentage of home range explored), which are traits that remain rarely assessed, possibly because behavioural syndromes are typically determined experimentally or in the laboratory, rather than through long-term behavioural observations of wild animals. These suites of metrics inform what individuals eat, the rate of foraging and their exploratory behaviour in search of food. I was able to demonstrate the inherent lack of behavioural syndromes across all traits examined in this study as well as low repeatability (individual differences in behaviour). My findings describe an extreme foraging specialist, with individuals exhibiting similar behaviours across traits —suggesting limited room for flexibility to develop in these traits and without the constraints of co-varying evolution between the traits. These outcomes have a larger implication with regards to the population's ability to persist through limited flexibility (or inflexible) adaptation in the face of changing environmental conditions (Dingemanse and Wolf 2013).

It is possible that human presence may have impacted both foraging and movement metrics, but previous studies show that humans were not seen as a threat by these canids and that they quickly habituated to human presence (Welch et al. 2017). Further, although tameness varies amongst individual foxes (Petelle et al. 2018), it seems likely that any effect of observers on foraging or exploratory behaviour would have been consistent over time. I therefore don't expect our findings to have been considerably altered by human presence. Importantly, the advantages of direct behavioural observations far surpass the subtle effects of human presence in monitoring such behaviours.

5.3. Parenting in bat-eared foxes

This study provides the first in-depth documentation of how parenting pressures influence both foraging behaviour and stress levels in the bat-eared fox. I have explicitly described the first ever caching behaviour of this canid, a behaviour previously considered non-existent in this species. I show for the first time that fathers (often ignored in studies in favour of absentee mothers) seem to mitigate stress levels though higher foraging rates than all other adults. The overall low cortisol levels in this population and particularly in parents, could have therefore been maintained behaviourally through caching behaviour, exceptional hunting skills of the mother, and through compensatory high foraging rates of fathers. I have equally shown that pup-rearing season seems to be the most stressful period for parents whose hormonal levels were highest in this period, and particularly for the sole mother, who not only successfully hunted a hare, but continued to stalk them.

Considering limited repeatability of foraging behaviour in this species (Chapter 3) and generally narrow diet breadth (Chapter 2), the bat-eared fox seems to demonstrate unusual behaviour (e.g. hunting a hare) only under extreme parenting pressures. Within a narrow range of prey choices, the bat-eared fox alters its foraging rates, prey choices (e.g. choosing larger prey such as beetles) and exhibits innovative behaviour (e.g. caching) to its advantage when time or lactational demands increase. Other species such as the samango monkeys (*Cercopithecus mitis*) have equally been shown to exhibit innovative foraging behaviour in high risk locations, lending support to the ability of some species to implement novel actions under extreme pressure (le Roux et al. 2019). Other extreme termite foragers such as the aardwolf and the aardvark, given their limited dietary breadth which seldom extends beyond the range of termites and ants (Williams et al. 1997; Taylor and Skinner 2000; Taylor et al. 2002), are likely to navigate parental pressures through heightened foraging rates alone —though this remains unexplored.

The novel findings presented in this study should nonetheless be interpreted with caution due to our limited parental sample size (n = 3) partly due to this lack of breeding in the population and rabies outbreak that terminated the project. It is also worth noting that during dispersal season (prior to the breeding season), animals without collars could easily get lost to observers, especially for bat-eared foxes with great dispersal capabilities (Kamler et al. 2013). Furthermore, parents frequently change dens based on proximity to water source, human disturbances, predation pressures, food availability and parasite loads in den (see Boydston et al. 2006). I therefore advocate closer parental monitoring and where possible, a larger sample size over long-term periods.

5.4. New directions in bat-eared fox foraging ecology

One of the primary causes of deaths in bat-eared foxes may be related to when and where they forage. The high rates of animal mortalities on South African national and regional roads as a result of vehicle-wildlife collision is of great concern, with ~2700 fatalities reported within three years (Périquet et al. 2018). Of these casualties, nocturnal species ranked among the top five mortalities, with scrub hares (*Lepus saxatilis*) as the most prevalent roadkill species, followed closely by other mammals, including bat-eared foxes (Périquet et al. 2018). The R360 main road from Twee Rivieren to Upington, in the Northern Cape province has been termed a hot spot for animal road kills, with bat-eared foxes as the primary casualties (Bullock et al. 2011). On this road (~260 km), I noted 37 bat-eared fox carcasses at different stages of decomposition on a single trip to Upington (K. Jumbam, pers. obs.). The principal causes are thought to include: 1) their nocturnal lifestyle 2) a high-speed zone area (Fig. 5.1), and 3) high traffic zone (Bullock et al. 2011). From a behavioural point of view, their nocturnal lifestyle is of interest. Importantly, they are predominantly killed in winter, near duneveld vegetation —seemingly because of their termite diet, and at high speed zones (Bullock et al. 2011). I found that foxes fed predominantly on termites in winter season owing to unavailability of alternate prey (Jumbam et al. 2019; Chapter 2) while Bullock et al. (2011) suggested plausible mortality causes to include a combination of day-time foraging activities in winter, drivers' poor night vision and the paralysing effect of bright headlights on nocturnal animals.

Fig 5.1. Traffic warning signs erected along R360 road to curtail road kills, particularly of bat-eared foxes

These suggestions are yet to be thoroughly tested, especially with regards to the foraging behaviour and movement patterns of these canids along roads, in conjunction with prey availability along the roads. Assessing foraging behaviours and termite availability in duneveld vegetation and high-speed zones would provide crucial information for understanding the contributing factors for high mortality rates. We know from literature that despite previous studies alluding to fox activity correlating with termite activity (Nel 1990; Kuntzsch and Nel 1992), fox space use did not overlap with termite habitats in our study site (Périquet and le Roux 2017). We also know that termites in our study site avoided grass areas in preference to bushy vegetation regardless of season (Périquet and le Roux 2017), despite findings that 93 % of termite diet is dry grass (Symes and Woodborne 2010), and that their populations increase with dry conditions (Bissett et al. 2019). These puzzling discoveries highlight the complexities in space use and exploratory behaviour of bat-eared foxes as well as termite distributions, which should be taken into consideration when assessing their foraging behaviours. To address some of these road mortalities, I recommend a long-term study to 1) assess termite seasonal variability along roadsides and at duneveld vegetation 2) to determine correlations between fox movement patterns and termite availability 3) to ascertain if road kills are linked to fox movement patterns and termite abundance.

Other miscellaneous recommendations for optimal direct behavioural observations include investing in waterproof notebooks to circumvent challenges such as signal interference when using electronic devices in poor weather conditions. Furthermore, whilst I have maintained a standard count for all prey items foraged upon based on forage bouts, a separate measurement metric for clumped prey (e.g. termites) would be more beneficial to avoid counting bias towards small prey items. Some direct observational studies for mesopredators such as meerkats utilise the index “number of chews per prey item and prey size” (Doolan and Macdonald 1996). This method may not be suitable for bat-eared foxes owing to their unique dentition enabling swifter food ingestion rates (Maas and Macdonald 2004). I therefore suggest assigning a pre-determined value (e.g. n = 50) per forage bout based on termite abundance assessments in the locality. Finally, in addition to prey size, handling time of prey and their estimated weights could provide valuable insight into the energetics of foraging.

5.5. Conclusions

In summary therefore, I have improved our understanding of wild bat-eared fox foraging behaviour by providing a foundation of their diet and highlighting their preference for larger prey when available. Furthermore, I have demonstrated their inherent lack of behavioural syndromes suggesting that traits could respond independently to natural selection pressures. I have also shown that there are low individual differences in behaviour within this population, alluding to higher individual plasticity within the species. Finally, I have determined intricate relations between foraging rates, parenting behaviour, and hormone levels in this canid, highlighting novel behavioural strategies employed by parents to potentially mitigate stress levels such as caching, hunting and exceptionally high foraging rates. Importantly, I have outlined future research opportunities and provided guidelines on how to improve on this study together with our general understanding of this ecologically important canid.

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Appendix

Details on the number and duration of follows per individual, including mean and standard deviation of minutes per individual as described in chapter 3 (sections 3.3.3 – 3.3.5). Total number of follows (n = 566) for diet breadth estimates (section 3.3.3) increased to 575 —in table below, with the inclusion of "unknown" prey items in foraging rate assessment (section 3.3.4). Movement metrics assessments (section 3.3.5) began later in the project and has 250 follows.

Fox identity	Sex	Number of follows	Follow duration (min)	Mean ± SD
ANG	M	7	693	99 ± 31
ARI	M	30	4146	138 ± 71
BAI	M^{P}	51	6319	124 ± 51
BAR	F	58	6893	119 ± 36
BEA	F	19	2389	126 ± 52
BEN	M	25	2929	117 ± 26
BER	F^{P}	43	5530	129 ± 61
BLA	M	25	3236	129 ± 73
BRU	M	26	3192	123 ± 52
CAM	F	18	2181	121 ± 32
CAT	F	12	1115	93 ± 50
CYL	M^{P}	26	3064	118 ± 66
DON	F	34	4125	121 ± 58
EDE	F	31	3491	119 ± 42
EMM	M	22	2578	117 ± 48
ERN	M	19	2460	115 ± 43
ESC	M	32	3677	115 ± 31
GAR	F	31	3926	127 ± 58
ILO	M	55	6274	114 ± 57
SCR	M	11	1084	99 ± 35

M = Male, F = Female; ^{P} = Parent