

Foraging Behaviour and Sensory
Ecology of the bat-eared fox (*Otocyon
megalogotis*)

By

Samantha Renda

Dissertation submitted in fulfilment of the
requirements for the degree Magister Scientiae to the
Faculty of Natural and Agricultural Sciences
Department of Zoology and Entomology,
University of the Free State

Supervisor: Prof. A. le Roux

December 2016

Declaration

I, Samantha Renda, the undersigned, hereby declare that the work contained in this dissertation is my own original work and that I have not previously, in its entirety or in part, submitted it at any university for a degree. I furthermore cede copyright of the dissertation in favour of the University of the Free State.

Signature:

Date:

Alice laughed. 'There's no use trying,' she said. 'One can't believe impossible things.'

For the longest time I believed it was impossible that I would ever study further at all, let alone delve into the world of post-graduate study and have the opportunity to wander off to the desert to spend my nights in the company of anything as peculiar as a bat-eared fox. Yet here I am, handing in my thesis on them.

Said the White Queen to Alice: "Why sometimes I've believed as many as six impossible things before breakfast."

Acknowledgements

There have been many people whose assistance has been vital and invaluable during the course of this study. My thanks and appreciation goes out to them all but I would specifically like to mention the following:

Prof. Aliza le Roux – Who encouraged me to pursue this degree and was always available to lend insight and advice regarding how best to proceed with my experiments, analysis and write-up.

Dr. Stephanie Periquét – For looking over my models and drafts and offering invaluable advice. But mostly for her friendship and putting up with me as I bumbled through the complexities of planning, executing and analysing a study.

All my other ‘Battie’ colleagues – you know who you are – living with you all in the desert taught me a great deal about both fieldwork and life in a tiny, self-contained community.

I would like to thank the National Research Foundation for the Scarce Skills Masters Grant (#100317) made available to me, and for a Thuthuka grant (TTK1206041007) to A. le Roux. Additional thanks for field site access goes to the Kalahari Meerkat Project, which has been supported by ERC Grant No 294494 to T.H. Clutton-Brock since 1/7/2012.

And finally, a very special thank you to my ex-husband, Gavin Dollman, who showed me that what I had considered impossible was easily within my reach and who has remained my friend, my sounding board and my staunch supporter through a very strange journey indeed.

Table of Contents

Declaration..... 2

Acknowledgements.....	4
Abstract.....	7
List of Figures	9
List of Tables	10
Chapter 1: Literature Review	11
1.1 A background to the field of sensory ecology	12
1.2 The problem of finding food - sensory challenges faced by foragers.....	14
1.2.1 Environmental factors affecting sensory systems.....	16
1.3 How foragers function: testing the sensory ecology of foraging.....	20
1.3.1 Foraging experiments in the wild.....	22
1.4 Sensory ecology in the Canidae.....	24
1.5 The case for studying sensory ecology in foraging bat-eared foxes	25
Chapter 2: The sensory ecology of prey detection in the bat-eared fox (<i>Otocyon megalotis</i>)	28
2.1 Abstract.....	29
2.2 Introduction	30
2.3 Materials and Methods.....	32
2.3.1 Field site	32
2.3.2 Work sessions	33
2.3.3 Experimental set-up and trials.....	33
2.3.4 Feeder insects	36
2.3.5 Statistical analysis	38
2.4 Results.....	39
2.4.1 Likelihood of same side selection	39
2.4.2 Choice data by sensory type	40
2.4.3 No-choice scenarios and failed trials	42
2.5 Discussion.....	44
Chapter 3: Gone with the wind? The effect of natural ambient noise on an acoustic forager's most salient sense.....	48
3.1 Abstract.....	49
3.2 Introduction	50
3.3 Materials and Methods.....	52
3.3.1 Study location and population.....	52
3.3.2 Focal sessions.....	53
3.3.3 Meteorological data.....	53

3.3.4 Foraging rates and in-patch time	55
3.3.5 Statistical analysis	55
3.4 Results	56
3.4.1 Effect of wind on between-patch foraging rates	56
3.4.2 In-patch time as a function of wind-speed	61
3.5 Discussion.....	63
4. Discussion and conclusion	66
4.1 Determining auditory thresholds.....	67
4.2 Pinnae structure and hearing	67
4.3 Masking and other noise effects.....	68
4.4 Conclusion	70
Appendix A : Wind measurement.....	72
Appendix B: Winter wind speeds.....	73
References	74

Abstract

In the wild, foraging animals face challenges that affect foraging success, including conditions which influence the usefulness of the sensory input they receive from their environment. Nocturnal foragers must cope with diminished light availability and may come to rely on sensory modalities other than vision in order to locate prey. The auditory mode is particularly useful under such conditions; however, various environmental variables may affect this sense as well. Ambient noise for example, may negatively affect foraging success in these hunters. Bat-eared foxes (*Otocyon megalotis*) are small, nocturnal insectivores noted anecdotally to rely primarily on acoustic cues in prey detection, though this has not been empirically tested. The aim of the current study was therefore to determine the relative importance of three common sensory modalities (audition, olfaction and vision) to foraging bat-eared foxes and to examine the effect of naturally occurring ambient noise on the auditory sense in particular. In the first instance, it was predicted that auditory cues would be most salient to foraging foxes while visual cues would be least so. In the second case, it was predicted that wind noise would have a deleterious effect on foraging rate outside termite patches and that foxes would spend a greater amount of time in termite patches under windy conditions. To test sensory perception of prey-generated cues, foxes were presented with a choice experiment in which sensory cues were manipulated. To determine the effect of wind, foraging and meteorological data collected over the course of a year were analysed. The predictions in the first case were proven correct but foxes continued to be able foragers even under windy conditions, thus refuting the predictions in the second. Foxes may therefore be able to exploit the temporal structure of natural noise to overcome foraging challenges imposed or may simply modify their foraging behaviour to avoid the effects of masking noise. Future work on the effect of noise from other sources, such as anthropogenic noise, as well as determination of the

auditory thresholds of these specialised canids will serve to clarify the mechanisms underlying bat-eared fox aural sensitivity.

Key words: audition, bat-eared fox, foraging, olfaction, prey detection, sensory ecology, vision, wind

List of Figures

Figure 1. A bat-eared fox from the Kuruman River Reserve site.....26

Figure 2. Schematic of apparatus for sensory experiments.....35

Figure 3. Modelled probability of success by trial type in sensory experiments.....43

Figure 4. Foraging rate in relation to recorded wind speed.....58

Figure 5. Interaction of wind and season on foraging rate of bat-eared foxes.....60

Figure 6. Time spent in termite patches in relation to wind speed.....62

Figure 7. Winter wind speeds by hour of the day.....74

List of Tables

Table 1. Summary of experimental set-up for sensory trials.....38

Table 2. Parameter estimates for sensory trial GLMM.....41

Table 3. Choices by sensory trial type.....44

Table 4. Parameter estimates for wind and season LMM.....59

Table 5. Parameter estimates for wind and season LMM (reduced data set).....61

Chapter 1: Literature Review

1.1 A background to the field of sensory ecology

It has long been recognized that all species perceive their environment differently, due to factors such as distinct sensory mechanisms and neural processing. This concept, of a differing perceptual world peculiar to each organism, was classically described as that animal's 'umwelt' by the German biologist Jakob von Uexküll (Partan and Marler 2002). An animal's umwelt is not only impacted by its own physiology, but also by the relevance it ascribes to various stimuli in its external environment (Sutrop 2001). The stimuli involved in prey recognition for a creature like a tick (*Ixodes* spp.), for example -- those of heat and carbon dioxide (Oorebeek *et al.* 2009)-- are very different to the stimuli which elicit hunting responses in larger vertebrates relying on visual search images (Anjum *et al.* 2006). The job of the sensory ecologist then is to unravel the umwelt of their particular study species. In its broadest terms, sensory ecology is the study of how an animal perceives its environment and how that perception affects its interactions with the world surrounding it (Martin 2012).

Approaches to the question of animal perception often focus on mechanistic and physiological explanations (Dangles *et al.* 2009). Studies may map brain structures to compare regions of the brain associated with systems such as olfaction, vision and audition (Martin *et al.* 2007). The structure of sensory organs themselves provides further detail regarding the utility of the associated sense. The structure of the eye in water birds, for example, may be used to determine their visual capabilities in both air and water (Sivak *et al.* 1977; Martin and Young 1984). By examining the properties of the eye lens in pursuit-diving birds such as cormorants (*Phalacrocorax* spp.) it may be surmised that vision is the predominant sense guiding underwater activity (Glasser and Howland 1996). Similarly, comparison of brain structures associated with the olfactory sense between different lineages of insectivores and

primates reveal that nocturnal groups exhibit larger olfactory regions (Barton *et al.* 1995), leading to the conclusion that olfaction is of greater use under nocturnal conditions.

Though investigation of senses at the structural and neurological levels grants insight into the utility of different sensory modalities to an organism, this approach does not fully address the ecological context the organism faces (Dangles *et al.* 2009). To understand this, we need to study how an organism's interactions with its environment are affected by the limitations or capabilities of its sensory system as well as by environmental factors. Neural mapping of the olfactory sense, for example, gives few clues as to which chemical cues may be most salient at different times of the day, or what the prey detection range for olfactory foragers may be. Experimental and observational evidence in the laboratory and field are vital to understanding the practical implications of an animal's unique sensory experiences/ systems, as the actual utility of specific senses may differ from predictions based on purely physiological studies (Garber and Hannon 1993; Barton *et al.* 1995; Vincent *et al.* 2005; Dangles *et al.* 2009).

Physiological studies on bats, for example, have high-lighted their extremely sophisticated echo-location and auditory systems as being central to their ability to orient themselves in space and navigate (Ulanovsky and Moss 2008). Though these systems are essential at short-range, in navigating long distances bats have been found to rely heavily on unexpected mechanisms such as sight and even magnetoreception (Holland 2009). In the case of salticid spiders seeking out mates, their keen vision is presumed the most important sense, based on both physiological and behavioural evidence (Land 1985; Elias *et al.* 2005; Li *et al.* 2008). Yet for some of these visual specialists, experimental evidence has shown that vibratory signals are equally as vital to copulation success as visual display (Elias *et al.* 2005).

Another fascinating example of this gap between physiology and behavioural capabilities is found in cephalopods. Animals such as octopi and cuttlefish are masters of camouflage, capable of rapidly matching their body patterns, colouration and texture to nearly any backdrop to escape detection (Hanlon 2007). Physiologically it has been determined that these animals are colour-blind (Brown and Brown 1958; Bellingham *et al.* 1998). Through behavioural sensory studies cues such as contrast, texture and object orientation have been indicated as vital to successful cephalopod crypsis, but the exact means by which they manage to colour match remains to be discovered (Ulmer *et al.* 2013; Chiao *et al.* 2015).

Sensory ecology studies thus allow researchers to investigate a diverse array of topics in ecological contexts: from how birds navigate across oceans (Nevitt 2008); how female spiders differentiate between a mate and a potential meal (Uetz and Roberts 2002) to how the presence of bio-luminescent dino-flagellates influences the prey capture rate of hunting squid (Fleisher and Case 1995). Perhaps the most widely studied ecological context however is how sensory systems affect foraging behaviour and success.

1.2 The problem of finding food - sensory challenges faced by foragers

In order to survive, animals must develop the most efficient strategies for detecting and evaluating potential food items in their environment (Von der Emde and Bleckmann 1998). The challenges encountered by foragers, those of locating food, environmental confounding factors and the reactions of prey are recognised as driving forces behind adaptation, cognition and sensory specialisation (Martin 2012; Clarin *et al.* 2013). In the face of what is often an arms race between predators and prey, foragers must adapt to ever-changing circumstances (Dawkins and Krebs 1979; Hristov and Conner 2005).

Foraging animals use a plethora of sensory information in order to locate food items, from the widely-used channels of vision (Santisteban *et al.* 2002; Nekaris 2005), audition (Klinka and Reimchen 2009; Siemers and Schaub 2011), and olfaction (Bicca-Marques and Garber 2004; Martin 2012), to less common sensory systems such as electroreception (Von der Emde and Bleckmann 1998). Optimising these sensory systems ranges from the specialized development of a single capability, as in many echo-locating bats (Belwood and Fullard 1984; Jones 2013), to benefitting from the synergistic effects of integrating multiple sensory inputs (Piep *et al.* 2008; Hazan *et al.* 2015).

Even when one sense in particular is highly specialised, being able to use multiple modalities is often critical to correct identification of food sources (Piep *et al.* 2008; Campbell and Borden 2009; Rushmore *et al.* 2012). Page *et al.* (2012), in assessing the use of sensory information by fringe-lipped bats (*Trachops cirrhosis*), determined that these bats used not only auditory cues to detect prey but also chemical cues at close range to identify suitable, non-toxic items. Similarly, Rushmore *et al.* (2012) showed that Coquerel's sifakas (*Propithecus coquereli*) exhibited greater likelihood of selecting high quality leaves when both visual and olfactory cues were available to them.

As with other sensory contexts, the senses salient to foragers may also differ from predictions based purely on observation or physiology. Returning to the example of cormorants, White *et al.* (2007) tested great cormorant (*Phalacrocorax carbo*) underwater visual acuity and found it to be decidedly poor. Those authors concluded that cormorant hunting behaviour was rooted more in short-range visual detection of prey and close pursuit strategies than in the ability to clearly distinguish the underwater landscape. A similarly surprising outcome occurred in a study of the visual responsiveness of *Cupiennius* sp. wandering spiders (Fenk *et*

al. 2010). These nocturnal arachnids were thought to respond pre-dominantly to stimulation of their complex mechano-sensory systems across contexts as varied as courtship and hunting (Friedel and Barth 1997). By using visual images on a computer screen however, Fenk *et al.* (2010) demonstrated that these spiders were able to respond to entirely visual stimuli as well, in the absence of mechanical stimulation, and that these stimuli alone elicited attack behaviours.

1.2.1 Environmental factors affecting sensory systems

In addition to the sensory information used by a forager, the impact of environmental variables on the quality of this information can also drastically affect successful foraging, and may result in reduced foraging efficiency (Edut and Eilam 2004; Kelber 2005; Schaub *et al.* 2008; Dangles *et al.* 2009; Klinka and Reimchen 2009; Siemers and Schaub 2011; Bunkley and Barber 2015). The shift from a lit environment to darkness; a quiet situation to one with ambient noise, or between terrestrial and aquatic environments are all situations in which sensory challenges are expected to differ (Klinka and Reimchen 2002; Catania 2006; Siemers and Schaub 2011). Numerous effects of such changing environmental variables occur for animals relying on sensory modes such as vision, olfaction, touch and audition.

In vision-reliant species, foraging ability diminishes rapidly with a loss of reliability of this sense, i.e. nocturnal conditions with low ambient illumination or turbid waters (Kelber 2005; Regular *et al.* 2011; Ranåker *et al.* 2012). Pikes (*Esox lucius*), for example, while able to use alternate information such as chemical cues in prey capture, exhibit greatest efficiency in aquatic environments with high visibility (Ranåker *et al.* 2012). Some, such as bears, may be able to reliably use other senses. Klinka and Reimchen's (2009) study of black bears (*Ursus*

americanus) hunting for salmon demonstrated such a shift, with nocturnally foraging bears switching to reliance on auditory rather than visual cues. Other visually driven species may forgo foraging entirely when conditions preclude the use of this sense (Kelber 2005). Conversely, facultative foraging may occur when ambient night-time light conditions permit or anthropogenic sources of illumination are provided (Davies *et al.* 2013). Regardless, the decline in reliability of their predominant sensory mode often, though not always, predicts lower foraging success for such species (Regular *et al.* 2011).

Similarly, for olfactory foragers deprived of reliable input, foraging success drops dramatically. Kiwis (*Apteryx mantelli*) presented with an experimental situation in which either prey items were distributed in an homogenous prey-scented medium or in plain medium, performed significantly better when discrete olfactory cues were available to them (Cunningham *et al.* 2009). A similar finding in male file snakes (*Acrochordus arafurae*), indicated scent to be a vital component to prey capture behaviours in these reptiles (Vincent *et al.* 2005).

In researching Etruscan shrews (*Suncus etruscus*), Anjum *et al.* (2006) examined tactile prey perception, with the prediction that tactile cues alone would suffice for prey capture, a prediction supported even in the absence of visual or olfactory cues. Interestingly, work on a related species, water shrews (*Sorex palustris*), showed that when foraging aquatically, these animals relied not only on tactile cues, but also olfactory and motion stimuli (Catania *et al.* 2008). Those authors observed that shrews could exhale and re-inhale air bubbles whilst submerged to 'sniff' objects of interest to them, demonstrating the unexpected continued utility certain sensory modes can have even in surprising environmental contexts.

Of relevance to the acoustic forager, are the effects of physical environmental properties, ambient noise and prey movement on their ability to detect prey (Schaub *et al.* 2008; Siemers

and Schaub 2011; Bunkley and Barber 2015). Properties of the environment such as proximity to water, vegetative clutter or the medium through which sound must travel can all play a role in foraging success (Arlettaz *et al.* 2001; Siemers *et al.* 2001; Jensen *et al.* 2011). In some cases, these environmental properties are detrimental, such as the reduced foraging success experienced by bats trawling over water bodies covered with surface vegetation (Boonman *et al.* 1998). Clear water however, provides a perfect reflective surface, even allowing bats to detect prey over greater distances (Siemers *et al.* 2005).

The effect of noise, by comparison, is usually deleterious. Noise has a masking effect and thus obfuscates prey-generated sounds which an acoustic predator would typically use to locate its prey (Schaub *et al.* 2008). Whilst very few studies have examined the effect of noise on foragers, the ones which have done so tend to focus on the effect of anthropogenic noise (Schaub *et al.* 2008). Traffic noises for example have been shown to negatively impact foraging success in hunting bats (Siemers and Schaub 2011; Bunkley and Barber 2015). Other studies on marine organisms such as whales, link human-generated noise to changes in behaviour and impaired foraging success (Aguilar Soto *et al.* 2006; Weilgart 2007).

The ability of a masking noise to affect a hunting acoustic predator lies in both the degree of similarity of that noise with prey-generated noises and with the ability of the predator to process multiple streams of auditory information (Barber *et al.* 2003; Schaub *et al.* 2008). Barber *et al.* (2003) found that pallid bats, (*Antrozous pallidus*), had difficulty in processing two concurrent audio streams when searching for prey items. In another bat experiment conducted by Schaub *et al.* (2008) vegetation noise similar to the effect of wind significantly impacted foraging success in greater mouse-eared bats (*Myotis myotis*). This effect was attributed to the likely high degree of overlap between prey generated noises and natural

background noise created by wind moving through vegetation (Goerlitz *et al.* 2008; Schaub *et al.* 2008). If however, gaps in the masking stimulus occur, the acoustic forager may still be able to hunt successfully (Hübner and Wiegrebe 2003).

Such disruptive challenges exist for organisms with less common sensory systems as well. There is evidence to suggest that Chinese pit vipers (*Gloydius shedaoensis*), for example, have a harder time distinguishing the thermal signatures of their prey in areas where the background temperature is closely aligned with prey animal temperature (Shine *et al.* 2002). Scorpions, which rely on small-scale air movements and vibrations to ambush prey, become active searching hunters when windy conditions hamper their ability to rely on those cues (Bradley 1988). Similarly, for electro-receptive foragers such as paddlefish (*Polyodon spathula*), non-prey sources of electrical signals lead to avoidance behaviours consistent with a disruption of their sensitive prey-detection system (Wilkins and Hofmann 2007).

Predators face the additional challenge that prey items may attempt to evade capture through responses such as 'freezing' or 'fleeing' (Edut and Eilam 2004). By freezing, a prey animal eliminates certain sensory cues, most notably motion and auditory ones (Chelini *et al.* 2009). Prey animal camouflage may also play a role, by making a potential prey item inconspicuous to its predator (Defrize *et al.* 2010). Fleeing, on the other hand, is simply the direct attempt to escape to safety during which visual and auditory cues become highly salient in capture (Fux and Eilam 2009). More dramatic predator evasion behaviours may also occur, with the classic example being the adaptations of tiger moths (Lepidoptera: Arctiidae) to their bat predators (Conner and Corcoran 2012). The ultrasonic clicks produced by these insects are thought either to startle their predators, jam their sensory systems or simply to advertise the toxic nature of the prey (Conner and Corcoran 2012).

The net result for the sensory ecologist of such abundant modalities and challenges is a rich field of study. In addition to the specific senses salient to the study species, the environmental context and its effect on these can also be examined.

1.3 How foragers function: testing the sensory ecology of foraging

Studies of the sensory ecology of foraging have been undertaken for a number of species, ranging from invertebrates such as cephalopods (Fleisher and Case 1995), arachnids (Bleckmann and Lotz 1987) and insects (Goyret and Kelber 2011) to vertebrates such as birds (Clarke 1983; Santisteban *et al.* 2002), snakes (Vincent *et al.* 2005), mammals (Isley and Gysel 1975; Boonman *et al.* 1998; Catania *et al.* 2008; Paukner *et al.* 2009; da Costa and Bicca-Marques 2014) and fish (Fraser and Metcalfe 1997; Von der Emde and Bleckmann 1998).

In order to address the question of which senses are most salient in an experimental context, foragers are often presented with an experimental apparatus in which the availability of sensory cues is manipulated, while rewards are hidden in random locations within an arena. During such experiments the availability of certain sensory cues from food items are restricted and the subsequent success or failure of subjects in detecting food analysed. The set-up of experiments varies widely, but the basic principles remain similar. Subjects are presented with a stimulus and their reactions to or detection of that stimulus are monitored (Vincent *et al.* 2005; Raghuram *et al.* 2009). In the most basic form, studies are designed to simply allow captive animals to forage naturally whilst exposed to certain stimuli (i.e. prey generated sounds or fruit odours) as in the studies by Siemers and Swift (2006), Jones *et al.* (2003) and Raghuram *et al.* (2009).

Jones *et al.* (2003) approached this problem in the following manner. *Mystacina* sp. bats were required to search a darkened arena filled with leaf litter for buried mealworms, both alive and pre-killed (auditory cue), or pre-killed only (olfactory cue). By burying worms under the leaf-litter, these authors ensured that neither echolocation nor vision could be used. Using this approach, it was established that *Mystacina* can use audition and likely also olfaction in prey detection.

Alternately, foragers are presented with a situation in which a choice must be made in order to obtain a food reward (Goerlitz and Siemers 2007; Piep *et al.* 2008; Rushmore *et al.* 2012). In these choice experiments, sensory cues regarding the location of the food item(s) are restricted. Depending on which sensory modalities are to be excluded from the search, the experiment may be modified in various ways. For example, in order to restrict visual cues, opaque containers or lids may be used (Siemers *et al.* 2007; Piep *et al.* 2008). For the restriction of auditory cues from prey, prey animals are often pre-killed (Piep *et al.* 2008; Cunningham *et al.* 2009). Olfactory cues may be minimised through the use of sealed containers or homogenously scented substrates (Piep *et al.* 2008; Cunningham *et al.* 2009; Rushmore *et al.* 2012). Theoretically, if motivated to forage, the forager should always choose the correct (rewarded) option first if the sensory cues available are salient enough to allow this. Through such an experimental approach, the relative utility of various sensory modes to a species can be established, as can the utility of concurrent stimuli (Vincent *et al.* 2005; Piep *et al.* 2008). Experimental evidence supports the idea that synergistic effects trump the individual utility of senses in helping an animal locate food, but the situation varies with context, and of course, with species (Piep *et al.* 2008).

Studies on mouse lemurs (*Microcebus murinus*) provide a good general frame-work for how such a choice-based sensory ecology experiment may be conducted (Siemers *et al.* 2007; Piep *et al.* 2008). In these experiments, lemurs were provided with a scenario of two choices in the form of covered dishes placed at a set distance from one another. The covers of these ceramic dishes were modified to allow or restrict certain sensory cues. Live insects were used to provide auditory stimuli, whereas insects were pre-killed otherwise. Insects were sealed in airtight plastic bags to restrict olfactory information or playbacks with no insect present were conducted. Opaque or transparent lids meanwhile allowed for the transmission of visual cues (from pre-killed insects or insect dummies). Using a combination of these factors, the researchers in those experiments tested cues individually as well as testing between uni- and multi-modal stimuli. The dish associated with a stimulus was usually rewarded (i.e. the insect could be fed upon on discovery) whereas the other dish was an empty decoy. Other studies, such as that done by Rushmore *et al.* (2012) with folivorous lemurs, may utilise more complicated devices; however, the effect is largely the same, with the point being to restrict certain cues and allow access to others, in order to elucidate which cues are most salient.

1.3.1 Foraging experiments in the wild

With a few exceptions, the majority of experimental studies discussed above have been carried out with captive animals under controlled conditions. Sensory ecology studies involving wild animals on the other hand, are often purely observational. In such, researchers record natural foraging occurrences and infer sensory information based on behaviour and

ambient conditions (Klinka and Reimchen 2002, 2009; Nekaris 2005; Cunningham and Castro 2011). Studies on bears, for example, catching salmon under diurnal versus nocturnal conditions have shown that these large omnivores seem to pay greater attention to auditory cues under dark conditions (Klinka and Reimchen 2002, 2009). Nekaris (2005) observed distinctive behaviours in hunting lorises (*Loris lydekkerianus lydekkerianus*) such as focusing the gaze on a prey item (visual detection), pronounced sniffing (olfactory detection) and twitching the ears (auditory detection) and concluded that whilst other sensory modalities did facilitate prey detection the major mode used by these animals was vision.

Not all cases are as clear cut as this however, as evidenced by observational studies on wild kiwis (Cunningham and Castro 2011). Kiwis showed no evidence of visually guided foraging, on occasion missing prey items close by which were visible to the observing researcher (Cunningham and Castro 2011). Instead, these birds showed evidence of combined tactile/olfactory foraging and perhaps the ability to hear invertebrate prey items (Cunningham and Castro 2011). Thus while direct observation and recording of foraging behaviour can provide invaluable insight into which sensory modalities are being utilised, it may also be difficult to disentangle exactly which sensory stimuli are active at different stages of the foraging process. This is particularly problematic, due to the advantage for foragers in paying attention to multiple sensory modes for successful foraging (Piep *et al.* 2008). To control which cues are available however, experimental manipulation is required.

Examples of wild foraging ecology studies including some aspect of experimental manipulation may also be found. Such experimental work has been undertaken with primates, and involves the habituation of animals to feeding platforms where differing options are presented and the subsequent choices made by members of a group evaluated

(Bicca-Marques and Garber 2004; Teichroeb and Chapman 2014). In the experiment conducted by Bicca-marques and Garber (2004) wild monkeys (*Aotus nigriceps*, *Saguinus imperator imperator*, *S. fuscicollis weddelli* and *Callicebus cupreus*) were exposed to feeding platforms in their home ranges which held either real food rewards (bananas) or sham food items (plastic replicas). Using this system and by obscuring the items with leaves, these researchers determined which cues were most salient to each species of primate under study, concluding that whilst visual cues were universally useful, olfactory ones were of salience only to nocturnal species. Similarly, responses to manipulated food items have been studied for wild bats (Bell 1982) and arthropods (Campbell and Borden 2009; Shimasaki *et al.* 2012), amongst others.

1.4 Sensory ecology in the Canidae

Amongst canids, the Umwelt of “man’s best friend,” the domestic dog, has been the subject of detailed study, largely due to the inherent utility of companion animals with well-developed senses distinct from those of humans (Miller and Murphy 1995; Gazit and Terkel 2003; Szetei *et al.* 2003; Gadbois and Reeve 2014). Many working dogs have been bred to enhance specific senses, usually sight or olfaction and thus are divided into ‘sight hounds’ and ‘scent hounds’ (Szetei *et al.* 2003). Dogs have an exquisitely sensitive olfactory sense (100-1000 times better than that of humans), and can be trained to use this across a variety of useful contexts: from sniffing out bombs and narcotics to seeking out disaster victims during rescue efforts (Szetei *et al.* 2003; Browne *et al.* 2006). In the visual realm, dogs are used in activities such as live-stock herding, hunting or trained to act as “seeing eyes” for blind human companions (Miller and Murphy 1995; Fishman 2003).

Amongst large, wild canids the modalities of vision and olfaction are also considered highly salient, particularly for animals such as wolves (*Canis lupus*) when hunting (Gazit and Terkel 2003; Acharya 2007; Lord 2013; Mech *et al.* 2015). Visual cues are important for canids such as wolves and dingos (*Canis lupus dingo*) in tracking the movements of nearby prey (Appleby *et al.* 2015; Mech *et al.* 2015). As canids engaged in such activity must often operate under changing light conditions, their vision is geared towards both low light sensitivity and maintaining good function under brighter conditions (Jacobs *et al.* 1993). The use of olfaction meanwhile lies in tracking prey over greater distance or ferreting out stationary prey or other items (Gazit and Terkel 2003; Appleby *et al.* 2015; Mech *et al.* 2015).

A few studies have examined the umwelt of small nocturnal canids such as foxes experimentally (Österholm 1964; Isley and Gysel 1975; Cervený *et al.* 2011). The nocturnal hunting behaviour of these animals results in the decreased utility of visual stimuli and an increase in the value of olfactory and particularly auditory cues (Österholm 1964; Lareviere 2002; Clark *et al.* 2009). Österholm (1964) for example, found that the red fox (*Vulpes vulpes*), though able to rely on visual cues to detect prey when light allows, pays greater attention to auditory and olfactory cues as light levels diminish. A similar pattern was seen in coyotes (*Canis latrans*), with vision relied upon when possible, followed by auditory and finally olfactory cues (Wells and Lehner 1978).

1.5. The case for studying sensory ecology in foraging bat-eared foxes

“My, what big ears you have!” exclaimed Red Riding Hood.

“All the better to hear you with, my dear,” the Wolf replied grinning.



Figure 1: A young bat-eared fox (“Bentley”) from the Kuruman River Reserve study site.

The question of how bat-eared foxes (*Otocyon megalotis*) find food would seem to be, on the surface, an easy one. Amongst canids, bat-eared foxes have one of the largest ear-to-body size ratios, second only to the fennec foxes (*Vulpes zerda*) of the Sahara desert (Sillero-Zubiri *et al.* 2004). There is, furthermore, plenty of anecdotal evidence for these diminutive canids using their enlarged pinnae in the detection and localisation of prey (Malcolm 1986; Lourens and Nel 1990; Nel 1990). Bat-eared foxes are primarily – though not exclusively –

insectivorous predators, with termites forming the bulk of their prey base (Malcolm 1986; Nel 1990). Foraging foxes are often seen binaurally pin-pointing prey item locations (Malcolm 1986), and in cases where these items are below ground, there is little question over which modality is being used to find them, particularly when digging is preceded by exaggerated cocking of the head.

Above ground, the situation may be more complicated. Presumably, additional information will be available from surface prey items in terms of motion and other visual stimuli, as well as olfactory or even tactile cues. This being the case, it would be expected that other sensory modalities become important in detecting food items, particularly if those items are stationary (Piep *et al.* 2008) or suddenly cease movement (a common prey tactic: Eilam 2005).

Similarly, auditory cues are of little use when searching for items such as fruit (Bicca-Marques and Garber 2004; Piep *et al.* 2008; Raghuram *et al.* 2009) or fungi, both of which form part of the bat-eared fox diet (pers. obs: present study, Kuntzsch and Nel 1992). Furthermore, it has been shown that in cases where 'noisy' prey are abundant, these items do not necessarily form the bulk of the foxes diet (Grant and Samways 2015). Thus, bat-eared fox reliance on auditory cues may not be as clear-cut as anecdotal reports would suggest.

No experimental study has yet been conducted to test the salience of different sensory cues to foraging bat-eared foxes. During the present study the relative importance of prey-generated auditory, olfactory and visual cues to foraging foxes is examined experimentally. The salience of individual and multiple modalities is tested in repeated experiments with individual foxes. In addition, the impact of a potentially disruptive/ masking abiotic factor on bat-eared fox foraging behaviour is investigated. Specifically, a long-term dataset of individual-specific foraging behaviour under different wind speeds is assessed.

Chapter 2: The sensory ecology of prey detection in the bat-eared fox (*Otocyon megalotis*)

S. Renda and A. le Roux

Department of Zoology and Entomology, University of the Free State, Qwaqwa
campus, Phuthaditjhaba 9866, South Africa

Submitted to *Behaviour* – currently in review

2.1 Abstract

In the absence of direct sunlight, nocturnal animals face sensory challenges different to those affecting their diurnal counterparts whilst foraging. Anecdotal observations have led to the general prediction that the auditory sensory mode is the most prominent for the bat-eared fox (*Otocyon megalotis*), a nocturnal, insectivorous canid. The present study aimed to clarify the relative importance of different sensory modes to foraging bat-eared foxes by conducting sensory trials with individuals belonging to a habituated population in the Kuruman River Reserve in South Africa. Foxes were tested in repeated trials controlling for particular sensory stimuli using live or pre-killed prey. Auditory cues proved significant ($p \leq 0.01$) predictors of fox foraging success with olfactory and visual cues indicated as being of secondary

importance. This study thus provides empirical confirmation for anecdotal reports that the bat-eared fox is predominantly reliant on auditory cues to determine hunting success.

Keywords: audition, bat-eared fox, foraging, olfaction, prey detection, sensory ecology, vision

2.2 Introduction

Nocturnal foragers experience a sensory environment that is distinct from the context faced by their diurnal counter-parts (Klinka and Reimchen 2009). Diurnal foragers, for example, are typically able to rely on visual cues (Dominy *et al.* 2001; Bicca-Marques and Garber, 2004; Martin 2012). For predominantly diurnal, vision-reliant species, foraging success drops when they switch to finding food under cover of darkness (Fraser and Metcalfe 1997; Klinka and Reimchen 2009; Regular *et al.* 2011). Whilst some nocturnal hunters are successful visual predators (Nekaris 2005; Piep *et al.* 2008; Martin 2012), in the absence of sunlight visual cues often become less useful than those available through other sensory means and their utility is often reliant on prey movement (Barton *et al.* 1995; Klinka and Reimchen 2002). For nocturnal species therefore, non-visual means of prey detection are often not only their

preferred modalities but are also more effective in detection of prey items over distance (Goerlitz and Siemers 2007; Jones 2013).

Acoustic cues play an important role in the nocturnal foraging activity of species as diverse as lemurs, *Microcebus murinus* and *Daubentonia madagascariensis* (Siemers *et al.* 2007; Ramsier and Dominy 2012), bears, *Ursus americanus* (Klinka and Reimchen 2009) and bats, *Myotis myotis* and *Otonycteris hemprichii* (Schaub *et al.* 2008; Holderied *et al.* 2011). By listening for prey-generated sounds, nocturnal hunters can locate prey in spatially cluttered environments and light conditions that lessen the chances of detection through visual means (Goerlitz and Siemers 2007; Goerlitz *et al.* 2008). Whilst this tactic is effective when prey are in motion, prey animals may freeze in response to predation threat, thereby eliminating both acoustic and motion cues (Eilam 2005). Localisation of prey animals then falls to short-range visual (Nekaris 2005), tactile (Anjum *et al.* 2006) or olfactory detection (Jones 2003).

Olfaction is thus a similarly vital tool in the repertoire of many nocturnal foragers, allowing them to locate non-moving prey or fragrant food items such as fruit in near darkness (Bicca-Marques and Garber 2004; Korine and Kalko 2005; Raghuram *et al.* 2009). Scent is thought to play a role in the detection of malodorous arthropod prey for animals such as pottos, *Perodicticus potto* (Garber and Hannon 1993) as well as in general prey detection, as seen in kiwis, *Apteryx mantelli* (Cunningham *et al.* 2009) and some bats, *Mystacina tuberculata* (Jones *et al.* 2013). Though studies on such species demonstrate that olfactory cues can be used in locating prey, such cues are likely useful at relatively short ranges (Goerlitz and Siemers 2007) and more salient for frugivorous foragers (Barton *et al.* 1995; Raghuram *et al.* 2009). Sensory ecology studies generally indicate that the utility of each sensory mode is context specific, with some being more useful under certain conditions or at specific ranges. Perhaps more

importantly, foragers may switch sensory modalities to best suit their particular foraging context (Klinka and Reimchen 2009).

Canids are a group often noted for the use of exceptional olfactory and visual abilities in locating food (Wells and Lehner 1978; Bender *et al.* 1996; Szetei *et al.* 2003; Gadbois and Reeve 2014). Within this group, bat-eared foxes, *Otocyon megalotis*, are highly specialised insectivores thought to locate insect prey using their over-sized ears instead. Studies on the sensory ecology of red foxes, *Vulpes vulpes*, suggest that similar small canids rely on audition, rather than olfaction or vision, to locate prey when light levels are low (Österholm 1964; Isley and Gysel 1975; Červený *et al.* 2011; Malkemper *et al.* 2015). Despite many anecdotal descriptions of bat-eared foxes locating prey through binaural detection (Malcolm 1986; Grant and Samways 2015), the importance of this and other sensory modes to foraging bat-eared foxes has not been tested.

The aim of the present study was to determine the importance of auditory, olfactory and visual stimuli to foraging bat-eared foxes. Based on field observations of their foraging behaviour, the following predictions were tested:

- (1) Auditory cues would be more salient than either olfactory or visual cues, and
- (2) Vision would likely be the least important mode to nocturnally foraging bat-eared foxes.

2.3 Materials and Methods

2.3.1 Field site

All experimental work was done with individuals ($n = 4$; 3 male, 1 female) from a habituated bat-eared fox population in the Kuruman River Reserve (28°580 S, 21°490 E) in the Northern Cape province of South Africa. Foxes in this population were habituated to being followed for 2-hour observational sessions with handheld spotlights. During habituation, observers noted locations where unhabituated foxes were frequently seen and these were baited with food rewards (raisins) in the presence of a human observer to acclimatise foxes. Once subjects became comfortable with human presence and movement, observational sessions commenced. The length of time between initial human encounter and being followed varied by individual but was typically within a month. Individual animals were dye-marked for identification.

2.3.2 Work sessions

For the purposes of this study, the typical nightly protocol was followed, by tracking study subjects on foot using radio telemetry and proffering a small food reward for responding to a conditioned signal (dog whistle) at the start of a session. The experimental apparatus (Figure 2) and a Bushnell Equinox Z night-vision camera were then set up with the fox in the nearby vicinity (typically 5-10 m from the apparatus), and the animal allowed to approach whilst the researcher (S.R.) filmed their interactions with the apparatus. No artificial light was provided during trials.

2.3.3 Experimental set-up and trials

The experimental apparatus consisted of two plastic cups placed rim-down 10 cm apart and modified according to trial type to allow or restrict certain sensory cues (Table 1). Similar methodologies have been used for sensory testing in lemurs (*Microcebus murinus*, *Propithecus coquereli*, *Varecia* spp., *Lemur catta*) (Siemers *et al.* 2007; Piep *et al.* 2008; Rushmore *et al.* 2012). Availability of visual cues was manipulated by using clear or opaque containers and olfactory cues were made available by perforating containers. In order to prevent the production of auditory cues, prey animals were pre-killed (similar to Jones 2003; Piep *et al.* 2008; Cunningham *et al.* 2009).

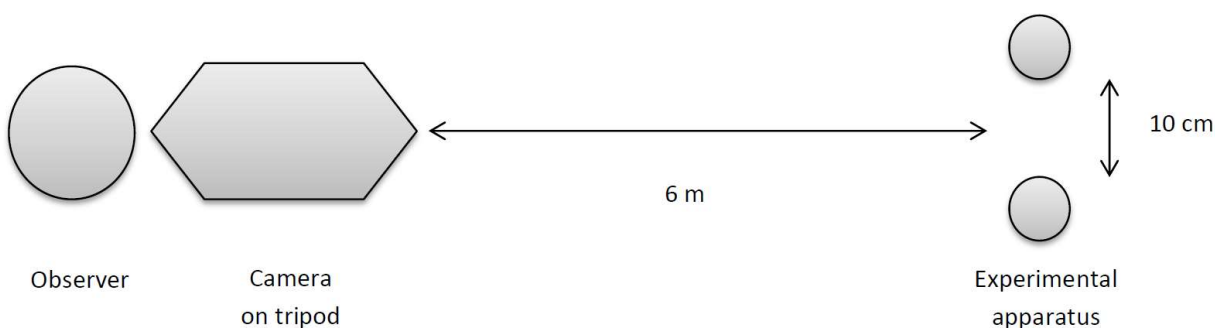


Figure 2: Top-down schematic drawing of the set-up for sensory experiments (not to scale).

Subjects were free to approach the apparatus from any direction.

The initial two trials in a session were reinforcement trials, in which two perforated, clear cups were used, one of which contained a pre-killed insect and the other, a live, moving insect of the same type which thus provided an auditory stimulus in addition to visual and olfactory stimuli. The trials served a similar function to the three-modality task used by Piep *et al.* (2008) in determining engagement of the animals in the task prior to further sensory testing. Whilst both cups contained a food reward in reinforcement trials, only one rewarded option was present in the other trial types, similar to the experimental procedures of Piep *et al.* (2008), Siemers *et al.* (2007) and da Costa and Bicca-Marques (2014). The side an insect was assigned to was determined randomly, with no more than three consecutive trials being allowed with the insect on the same side. If randomisation indicated the insect should be placed on the same side for a fourth trial, this was switched instead.

After these initial engagement trials, six further sensory trials were administered in random order. These trials were of the olfactory, visual or auditory condition. Both cups were modified identically according to trial type in all cases. Foxes were considered to have made a choice when they dug under a cup, seized it in their jaws or, most commonly, flipped the cup over with a paw. Trials were spaced three minutes apart to maintain the interest of the foxes during a test session. The duration of a typical work session was therefore less than an hour.

Once all eight trials were completed in this manner, the fox was not tested again until a minimum of five days had passed. Where possible, all animals were given three such test sessions. This was the case for all but one of the subjects, which only completed a single session and could not be relocated thereafter. Subsequent video analysis of all trials was conducted to determine the number of correct versus incorrect choices made by animals during trials of each type.

2.3.4 Feeder insects

The majority of insects used in trials were woolly chafers (Coleoptera: Scarabaeidae) or, more rarely, cicadas (Hemiptera: Cicadidae). However on two occasions (2 trials of the 80 conducted) other species, specifically red ant drones (Hymenoptera: Formicidae) and katydids (Orthoptera: Tettigoniidae), were used when other live specimens were not available. Prior field observations indicated that these large insects were a usual part of the foxes' diet at this site, and foxes were noted to prey upon these items whenever they became available. Scarabaeid beetles specifically have also been noted as a component of fox diet at

other sites (Kuntzsch and Nel 1992; Stuart *et al.* 2003). Pre-killed chafer specimens were produced by freezing live beetles for later use.

The willingness of foxes to eat pre-killed insects, as well as their ability to detect them after thawing, was tested by dropping newly thawed beetles in the vicinity of foraging foxes and allowing them to search for and consume these insects. Foxes showed no reluctance in eating the thawed insects once discovered and displayed typical canine sniffing behaviour whilst searching for them. Similarly in trials, foxes would immediately consume pre-killed insects upon discovery.

Table 1: Summary of experimental set-up for sensory trials. In each trial except for the reinforcement trials, only one cup was associated with a stimulus whilst the other was an empty decoy. Thus, only in the reinforcement condition would either choice be potentially rewarded.

Trial type	Cup type	Sensory modes tested	Prey item status
Reinforcement	Clear, perforated	All in one cup, olfactory and visual only in the second cup	One live, One pre-killed
Auditory	Opaque, Non-perforated	Auditory only	Live

Olfactory	Opaque, perforated	Olfactory only	Pre-killed
Visual	Clear, non-perforated	Visual only	Pre-killed

For auditory trials and the live condition of reinforcement trials, live specimens were used, thus testing periods were restricted to times when live insects were available. Auditory stimulation was provided by the movement of these live insects under the cups during auditory and live reinforcement trials. Woolly chafers would generally attempt to burrow once placed beneath a cup, providing a clear auditory stimulus to foxes.

2.3.5 Statistical analysis

Statistical analyses were conducted using the statistical program R (version 3.3.0). A Generalized Mixed Effects Model (GLMM) with a binomial error structure (with logit link) using the 'glmer' function from the 'lme4' package (Bates *et al.* 2015), was used to test

whether the likelihood of a fox selecting a cup on the same side as its initial approach was affected by trial type (reinforcement, auditory, olfactory, visual). This model controlled for fox identity as a random effect and used trial type (with auditory as reference level) as a fixed effect. All cases where no choice was made or a fox's approach could not be clearly attributed to a side were excluded.

Sensory choice data was analysed in a separate GLMM (binomial error structure, logit link). Success was used as the response variable in this model, and fox identity as a random effect. Fixed effects in the model were trial type (reinforcement, auditory, olfactory, visual – auditory was once more used as the reference level) and trial number. Trials of each sensory mode were numbered 1-6 for each fox. All cases where no choice was made were excluded from the model. Success probabilities in each trial type were obtained by back-transformation of model coefficients. Post-hoc pair-wise analysis was conducted using the 'lsmeans' package (Lenth 2016) in R. To determine goodness-of-fit, the full model was tested against a restricted model excluding trial type in a likelihood ratio test.

Analysis of how sensory modality affected choice for a given trial was undertaken by means of a chi-square test for association between stimulus type (auditory component/ no auditory component) and whether a choice was made. Scenarios where foxes failed to choose an option were included in this analysis only.

2.4 Results

2.4.1 Likelihood of same side selection

Selection of the first cup encountered during a trial presented a potential confounding factor in this study. A GLMM indicated that the likelihood of a fox picking the cup on the same side as its initial approach was non-significant ($p > 0.05$) for all trial types.

2.4.2 Choice data by sensory type

The likelihood ratio test indicated that the model including trial type was a significantly better fit than a model excluding this factor ($\chi^2 = 19.491$, $df = 3$, $p < 0.001$). Parameter estimates and significance levels for the factor trial type, from the model of best fit are presented in Table 2.

Table 2: Parameter estimates for the factor ‘trial type’ (reference level was Auditory). Actual estimates for each variable are given in brackets as the difference between the reference level and the coefficient for that variable. Significance was determined using z-score values. NS = non-significant.

Variable	Estimate	SE	z-value	p-value
Auditory	3.47	1.36	2.56	= 0.01
Reinforcement	-0.19 (3.28)	1.46	-0.13	NS
Olfactory	-2.78 (0.69)	1.18	-2.35	< 0.05

Visual	- 3.34 (0.13)	1.18	-2.82	< 0.01
--------	---------------	------	-------	--------

In this model, trial number did not influence successful choices, indicating the absence of learning across trials. Probability of successful choices did differ between trial types, with foxes performing significantly better in trials that included auditory cues ($p \leq 0.01$), compared to trials involving non-auditory stimuli (Figure 3).

Post-hoc pairwise comparisons, however, showed non-significance for the difference between pure auditory and olfactory conditions ($p = 0.09$), with the reinforcement condition emerging as statistically indistinguishable from olfactory trials. The likelihood of making correct choices during visual trials was significantly lower compared to both auditory ($p < 0.05$) and reinforcement ($p < 0.05$) trial conditions. As per the GLMM, no significant difference was found between reinforcement and auditory conditions, nor did visual and olfactory conditions differ significantly ($p = 0.9$).

2.4.3 No-choice scenarios and failed trials

There was a significant relationship between inclusion of an auditory component in trials and whether a choice was made ($\chi^2 = 6.6$, $df = 1$, $p = 0.01$): no-choice scenarios occurred more frequently than expected in non-auditory trials and less frequently than expected in trials including an auditory component. Similarly, the highest percentages of failed trials occurred in the visual and olfactory conditions (Table 3).

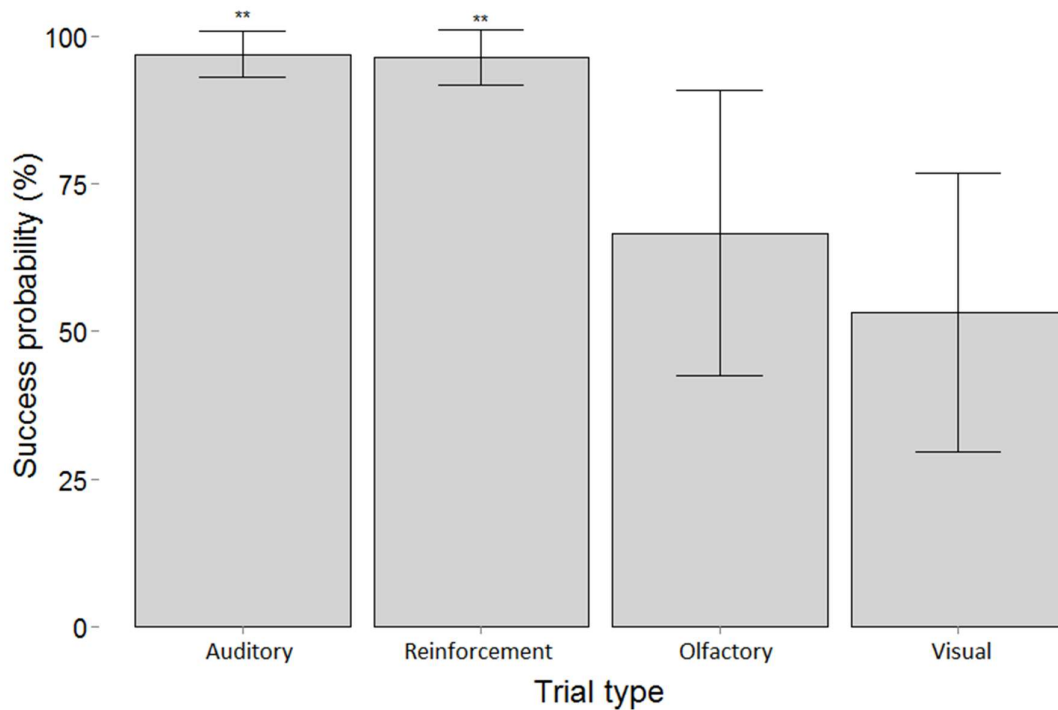


Figure 3: Modelled probability of success by trial type. Success probabilities in each trial type were obtained by back-transformation of model coefficients. Columns indicate success

probability with error bars representing estimated SE. Significance is indicated as: ** ($p \leq 0.01$) for trial types which are significant predictors of a successful choice.

Table 3: Choices by trial type including 'no choice' scenarios. A successful choice in reinforcement conditions was regarded as one where the fox selected the cup with sensory information of all modalities available.

Trial type	Success (%)	Failure (%)	No Choice (%)
Visual	30	45	25
Olfactory	40	30	30
Auditory	95	5	0
Reinforcement	85	5	10

2.5 Discussion

The present study aimed to clarify the relative importance of various sensory stimuli to foraging bat-eared foxes, with the prediction that auditory cues should be most salient. Experimental results clearly indicated that auditory components are the best predictors of successful choices by these foxes. In addition, the presence of an auditory stimulus was almost always associated with a correct choice regardless of the original approach angle of the test subject. These findings confirm that bat-eared foxes, primarily hunters of invertebrate prey, are similar to many other nocturnal foragers in terms of sensory ecology. Nocturnally foraging bears for example, have been noted to orient to prey using auditory cues when visual cues are not available (Klinka and Reimchen 2009). Similarly, in species which hunt exclusively at night such as gleaning bats (Jones, 2003; Siemers and Swift 2006), tawny owls, *Strix aluco* (Martin 2012) and some lemurs (Siemers *et al.* 2007) auditory cues are often the initial cue type used to pin-point prey locations.

Bat-eared foxes are noted for their over-sized ears. Whilst to some extent, these may serve a thermoregulatory function and aid in communication, their primary purpose, as with other insectivores with enlarged pinnae, seems to lie in detecting prey (Clark 2005; Siemers *et al.* 2007). Evidence from field observations of bat-eared foxes supports a dominant role of auditory cues in informing their hunting strategy (Nel 1990; Grant and Samways 2015). The same anecdotal observations were made in this present study. For example, foxes clearly located burrowed prey items such as scorpions, ants or grubs by listening intently, cocking the head and binaurally pin-pointing prey before digging them out (S. R. - pers. obs.). Similar behaviour has been noted for red foxes when tracking prey through auditory means (Červený *et al.* 2011).

Post-hoc tests suggested that olfactory cues may also aid bat-eared foxes in locating prey. As with other nocturnal insectivores however, it is likely that olfactory cues are primarily useful at short range (Jones 2003; Cunningham *et al.* 2009), and serve to locate prey items employing a 'freeze' strategy in the face of predation. These types of cues are also likely to be useful in locating aromatic food items such as fruit as seen for mouse lemurs, night monkeys, *Aotus* spp. and frugivorous bats (Bicca-Marques and Garber 2004; Korine and Kalko 2005; Siemers *et al.* 2007). Observations of foxes searching for fragrant 'Kalahari truffles' (*Kalaharituber* sp.), for example, a delicacy appearing after the rains, indicate that they are able to detect these fungi with minimal visual input, as they must often dig them out from the sand (S. R. - pers. obs.). Other arthropod hunters such as lorises, *Loris lydekkerianus lydekkerianus* and pottos (Garber and Hannon 1993; Nekaris 2005) also employ olfaction when seeking out pungent beetles. It is possible then, that bat-eared foxes are more likely to utilise odour cues in

searching for specific types of food. Less attention may be paid to odour cues of food items that could typically be located through auditory means.

The use of pre-killed and thawed insects during the current study may have influenced the ability of foxes to detect these items. It is likely that thawed beetles produce odour cues different from those of a live insect. The willingness of foxes to consume these items when offered suggests that they were not avoiding the prey as a result of it being pre-killed. Whilst it cannot be ruled out that foxes would perform differently in olfactory trials given fresh, immobile prey items, olfaction is likely more important when foxes are foraging for vegetable matter such as berries or truffles.

Vision appeared to play a lesser role in bat-eared fox foraging success than the two modes discussed above, however this was statistically significant only in the case of the difference between visual trials and trials including an auditory component. The overall failure rate in detecting prey items however was highest when only visual cues were available to foxes. Nocturnal foragers which rely heavily on sight, such as owls, tend to have large eyes in relation to their skull (Martin 2012). Even so, their ability to locate prey may be heavily influenced by ambient light availability in the form of moon or star light (Clarke 1983). For nocturnal visual hunters, movement also plays a vital role in prey detection (Barton *et al.* 1995). In the coyote, *Canis latrans*, sensory trials conducted by Wells and Lehner (1978), as well as in Österholm's (1964) red fox experiments, moving prey stimulated a more rapid capture response than non-moving visual targets. The challenge inherent to providing a visually stimulating moving target without accompanying sound under field conditions meant that the importance of visual movement cues from a prey item could not be explicitly tested during the current study. It is

likely that, dependent on ambient light, vision would play a stronger role in prey detection when prey items are moving.

Despite experience with obtaining food from the experimental apparatus, foxes appeared less likely to search for food items without a prior auditory stimulus. This is in keeping with evidence from other nocturnal insectivores such as long-eared bats, which were observed to search for prey only when prompted by an auditory cue (Holderied *et al.* 2011). Similarly, in early experiments on the red fox, Österholm (1964) found that under dark conditions responsiveness to auditory stimuli was far greater than that to olfactory or visual stimuli when locating prey. A similar observation has been made for coyotes, though capture times for these typically visual hunters were far longer when having to rely on auditory cues (Wells and Lehner 1978).

In conclusion, the present study provides empirical support for anecdotal observations that bat-eared foxes detect prey primarily through auditory means. Future experimental work focusing on the role of ambient light, detection ranges and food item type would serve to further clarify the respective roles of vision, audition and olfaction in bat-eared fox foraging behaviour.

Chapter 3: Gone with the wind? The effect of natural ambient noise on an acoustic forager's most salient sense

S. Renda, S. Periquét and A. le Roux

Department of Zoology and Entomology, University of the Free State, Qwaqwa
campus, Phuthaditjhaba 9866, South Africa

3.1 Abstract

Under natural conditions, foraging animals must contend with a number of environmental variables that affect foraging success, including conditions which diminish the usefulness of particular sensory modes. Ambient noise in particular is expected to influence foraging success in pre-dominantly acoustic foragers. The present study aimed to examine the effects of natural ambient noise -- in the form of wind -- on foraging rates in the insectivorous bat-eared fox (*Otocyon megalotis*). Recent experimental research indicated that these foxes rely predominantly on hearing for prey detection, and it was therefore predicted that increasing wind disturbance would negatively impact their foraging success by masking or interfering with the acoustic cues available from small prey. The foraging behaviour of eighteen bat-eared foxes from a habituated population in the Kuruman River Reserve, South Africa, was monitored over the course of a year under different wind conditions. Foraging rates between patches of termites and time within patches were examined. In contrast to expectations, foraging rates of foxes outside termite patches did not decline with increasing wind speed as predicted. Furthermore, foraging bouts in patches -- potentially richer foraging areas where

the importance of auditory information would decrease -- were not significantly longer during observations of increased wind speed. Taken together, this evidence indicates that, within the wind speeds observed, foraging behaviour in bat-eared foxes is not significantly negatively impacted by ambient wind noise. It is likely that these acoustically-driven insectivores are able to target prey by either filtering prey noises from background noise or by exploiting gaps in the masking noise, similar to some gleaning bats.

Keywords: audition, bat-eared fox, foraging, prey detection, sensory ecology, wind noise

3.2 Introduction

In order to successfully detect prey, predators must be able to rely on sensory cues from their prey items. The salience of different types of cues varies both with the ecology of the particular predator (Klinka and Reimchen 2009), and with ambient environmental conditions. Changes in factors such as illumination, vegetation density or noise levels, for example, affect the utility of sensory cues (Klinka and Reimchen 2002; Goerlitz *et al.* 2008; Barber *et al.* 2010; Regular *et al.* 2011). In terms of commonly used sensory modes such as vision, audition or olfaction, such changes may result in reduced foraging efficiency (Bicca-Marques and Garber 2004; Siemers and Schaub 2011; Ranåker *et al.* 2012; Luo *et al.* 2015).

While diurnal hunters are typically vision reliant, their nocturnal counter-parts often glean more information from their olfactory or auditory senses (Dominy *et al.* 2001; Goerlitz and Siemers 2007; Martin 2012; Jones 2013). For many nocturnal insectivores, acoustic cues in particular are of paramount importance in prey detection (Goerlitz and Siemers 2007; Goerlitz

et al. 2008; Schaub *et al.* 2008, Renda and le Roux, submitted). The auditory sense enables such hunters to locate prey not only over distance but also in spatially cluttered environments (Goerlitz and Siemers 2007). Visually inconspicuous prey may still be detected through pinpointing their location aurally, often with the aid of over-sized pinnae (Ramsier and Dominy 2012). Foragers reliant on this sense are also subject to ambient interference. Noise, both of anthropogenic and natural origin, plays a role in obfuscating prey-generated sounds (Schaub *et al.* 2008) and reduces the efficiency of predators such as greater mouse-eared bats (*Myotis myotis*) in detecting prey (Siemers and Schaub 2011).

The majority of investigations into the effects of noise on wildlife have focused on the anthropogenic disturbance of behaviours such as communication, mating or vigilance (Reijnen *et al.* 1997; Quinn *et al.* 2006; Barber *et al.* 2010). There is less information available regarding how noise affects foraging behaviour. Studies undertaken on this topic tend to focus on aquatic organisms (Croll *et al.* 2001; Aguilar Soto *et al.* 2006; Weilgart 2007; Purser and Radford 2011; Wale *et al.* 2013). With regard to noise effects on terrestrial, acoustically-driven hunters, only bats have been studied in any detail (Schaub *et al.* 2008; Siemers and Schaub 2011; Bunkley and Barber 2015). In the majority of studies, noise interference has been found to have a deleterious effect on foraging. Hunting bats are noted to avoid high noise areas such as highways and may avoid foraging altogether in such unfavourable situations (Schaub *et al.* 2008; Bunkley *et al.* 2015). Schaub *et al.* (2008) revealed an effect of both anthropogenic noise and natural ambient noise on greater mouse-eared bat (*Myotis myotis*) foraging success. For these aural hunters, noise interference resulted in both lower foraging success and avoidance behaviours. Interestingly, the greatest deleterious effect was

not as a result of anthropogenic noise. Rather, for gleaning bats, it was simulated wind-generated noise which resulted in greater impairment of their prey detection abilities.

Bat-eared foxes (*Otocyon megalotis*) -- foxes hereafter -- are nocturnal insectivores that feed primarily on termites, though their reliance on these as a food source varies seasonally (Malcolm 1986; Nel 1990). A large variety of other prey items are consumed as and when they become available (Malcolm 1986; Kuntzsch and Nel 1992, pers. obs: present study). Anecdotally, these canids have been noted to rely predominantly on auditory stimuli when seeking prey (Malcolm 1986; Grant and Samways 2015); however, as termites often occur in high density patches, fox reliance on auditory detection once within a patch is likely lowered. Empirical testing of their sensory capabilities supports observations, with the auditory sense shown as being of greatest salience to foxes when seeking prey (Renda and le Roux, submitted). Given their reliance on audition in finding prey, a similar effect of wind noise as that seen in bats might be expected for foxes. In this current study, we used individual-based observational data as well as meteorological information to examine the following two predictions:

- 1) The foraging rate of foxes between termite patches would decline with increasing wind speed and this change in rate would differ between seasons.
- 2) Foxes would spend more time feeding in termite patches under windy conditions due to lower profitability of out-of-patch searches as a result of impaired audition.

3.3 Materials and Methods

3.3.1 Study location and population

Observations of fox behaviour were undertaken on individuals ($n = 18$) from a wild population in the Kuruman River Reserve (28°580 S, 21°490 E), Northern Cape province, South Africa. Foxes were habituated to being followed on foot for 2-hour observational sessions with handheld spotlights, usually on a weekly basis. Foxes were observed eating a wide range of prey items including termites (Isoptera: Hodotermitidae), ants (Hymenoptera: Formicidae), beetles (Coleoptera: Carabidae; Tenebrionidae; Scarabaeidae), adult ant-lions (Neuroptera: Myrmeleontidae), adult and larval Lepidoptera (various families), Arachnida (various families) and some vertebrates (Rodentia: Muridae, as well as occasional amphibians or reptiles).

3.3.2 Focal sessions

The typical nightly protocol for focal sessions involved tracking study subjects on foot using radio telemetry and proffering a small food reward for responding to a dog whistle at the start of a session. Fox behavioural data was recorded using the program Cybertracker loaded on a Samsung Galaxy tablet. The GPS coordinates of each foraging instance was recorded, including a description of the item(s) eaten, when clearly visible to the observer. As foxes became very wary of human observers during daylight hours, attempts to follow them at these times were unsuccessful. As a result, it was not possible to collect comparative data on foraging rates during daytime.

3.3.3 Meteorological data

Weather data collected from the Kuruman River Reserve field station was used to determine average wind speeds and temperature per hour of focal. During the present study, maximum

recorded wind speeds were 22 km/h, corresponding to a 'moderate breeze' on the Beaufort scale (see Appendix A). According to this same scale, wind speeds of 6 km/h upwards would start generating noise would through light leaf rustling, up to more pronounced noise produced by moving branches and grasses.

In considering the effects of wind, the effect on the activity of arthropods eaten by foxes also had to be taken into account. Overall, wind speeds in the range recorded during this study have been shown to have little effect on the activity of many arthropods, including ants, beetles and termites (Briese and Macauley 1980; Curtis 1985; Heatwole 1996; Adam *et al.* 2008; Geerts *et al.* 2016), however this can change on a taxon by taxon basis. In some cases, wind effects may be stimulatory, negligible, or (most commonly in flying taxa) inhibitory (Henwood 1975; Tucker 1983; Bradley 1988; McGeachie 1989; Heatwole 1996; Yela and Holyoak 1997; Holyoak *et al.* 1997; Szentkirályi *et al.* 2007; Adam *et al.* 2008; Jonason *et al.* 2014; Geerts *et al.* 2016). Though the impact of wind on *Hodotermes* worker activity has not been quantified, studies on harvester termites with similar foraging ecology have revealed little effect of this factor on activity levels. Workers of *Trinervitermes*, for example, were found to continue foraging at wind speeds in excess of 21.6 km/h (Adam *et al.* 2008). Similarly, wind was found to have little effect on the foraging behaviour of *Baucaliotermes* workers (Geerts *et al.* 2016). In general, the effect of wind on the primarily terrestrial arthropod prey of foxes was assumed to be minimal.

As temperature is a factor known to affect arthropod activity (Heatwole 1996), all data corresponding to temperatures below 10 °C were cut from the data set, based on the thermal limits of foraging *Hodotermes* workers (Mitchell *et al.* 1993).

3.3.4 Foraging rates and in-patch time

Foraging bouts on termites were defined as at least 15 consecutive foraging records (typically with multiple termites eaten per record). Bouts within 20 meters and 5 minutes of one another were grouped into larger, contiguous patches. Individual bouts and termite patches were treated as discrete foraging events for the purposes of analysis, as foxes were presumed to be less reliant on audition when foraging on termites in this manner. In-patch time was the elapsed time between the start of a fox foraging in a termite patch (or start of a bout) and the end of in-patch foraging (or end of the bout). Foraging rates between termite patches or bouts were calculated as the number of items eaten per minute.

3.3.5 Statistical analysis

All data analysis was undertaken using the statistical program R (version 3.3.0). Linear Mixed Effects Models (LMMs) using the 'lmer' function from the package 'lme4' (Bates *et al.* 2015) were used to assess the effect of wind on foraging rate within and between termite patches. The foraging rate and in-patch time variable were log-transformed in all models to meet assumptions of normality. Models were compared with one another and a null model using likelihood ratio tests (LRTs) to select the best model. The most parsimonious model (in terms of least covariates) was chosen as the best in each case.

Two initial models were run for between-patch foraging rate. The first included the interaction of wind and season as fixed effects and focal session nested within fox identity as random effect. The second was identical, with the addition of temperature as a covariate.

Once a best model had been selected, the same model was run using a sub-set of this data, including only wind speeds above 6 km/h, corresponding to Beaufort-scale wind levels at which masking noises such as leaf rustling would occur.

As fewer focal sessions during which foxes foraged in patches were available seasonal data was pooled for the in-patch time analysis. Two models were run and again compared with a null model. Models thus used wind or wind and temperature as covariates with the same random effect as above. As for between patch foraging rate, once a best model had been selected, the same model was run using a sub-set of the data that excluded wind-speeds below 6 km/h.

3.4 Results

3.4.1 Effect of wind on between-patch foraging rates

A total of 790 instances of fox foraging success were included in the initial foraging- rate/wind-speed analysis. At speeds between 0-20 km/h (Figure 4), fox foraging rate was only significantly affected by wind in winter (Table 4). The best model in this case was the model incorporating the wind and season interaction (Figure 5), which was a significantly better fit than the null model ($\chi^2 = 45.416$, $df = 7$, $p < 0.001$), but not significantly different from the model including temperature ($\chi^2 = 2.727$, $df = 1$, $p = 0.1$). During winter fox foraging rates increased significantly ($p < 0.001$) with wind, with an approximate 9 % increase in foraging rate per unit wind increase, resulting in a predicted additional item per minute at the highest wind levels near 15 km/h. An analysis of a subset of this data including only wind speeds above

6 km/h (n = 179 observations across all seasons, n = 34 winter observations: Table 5), showed no significant correlations between wind speed and foraging rate.

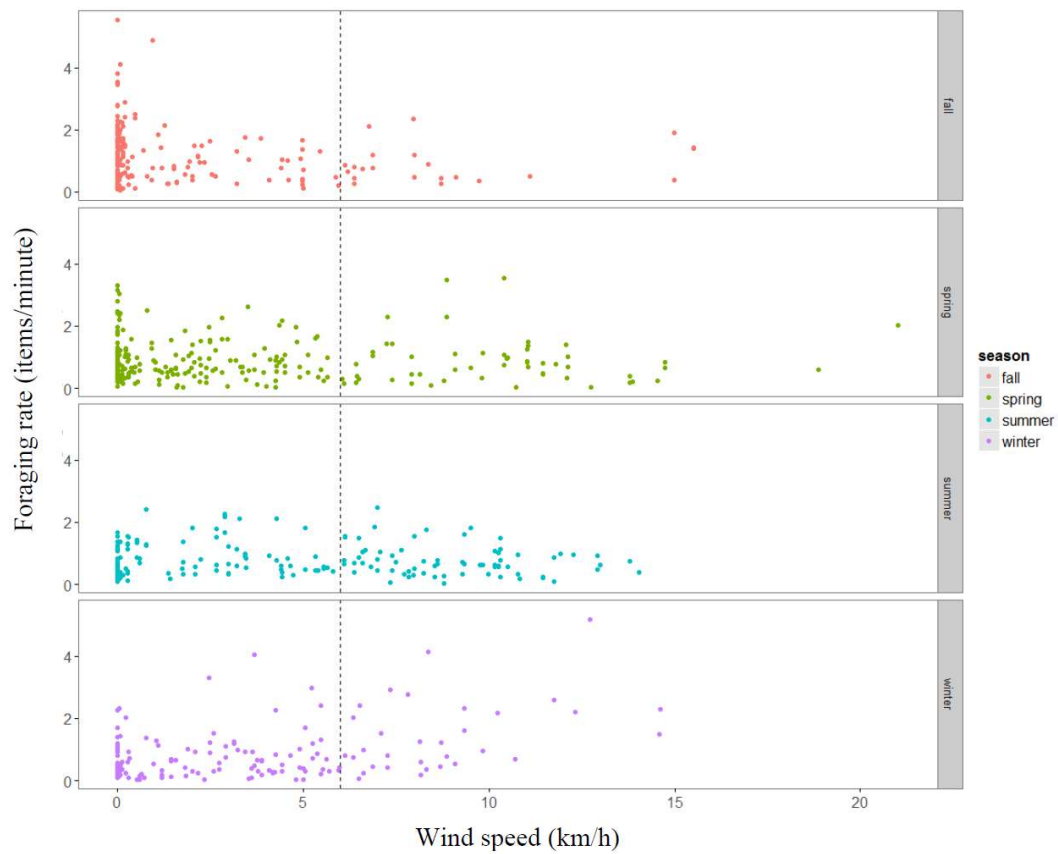


Figure 4: Foraging rate in relation to recorded wind speed. The dashed line represents a wind speed of 6 km/h above which masking noise would begin to occur.

Table 4: Parameter estimates for wind and season calculated from the LMM using log (foraging rate) as the response variable and the full data set. Interaction effects (X 100) may be interpreted as percentage change in foraging rate for increase of one unit of wind. NS = non-significant.

Variable	Estimate	SE	t-value	<i>p</i> -value
Fall	-0.121	0.120	-1.007	NS
Spring	-0.288	0.137	-2.095	<0.05
Summer	-0.281	0.150	-1.880	NS
Winter	-0.930	0.151	-6.166	<0.01
Wind:Fall	-0.034	0.020	-1.645	NS
Wind:Spring	0.010	0.025	0.388	NS
Wind:Summer	0.015	0.027	0.554	NS
Wind:Winter	0.129	0.029	4.399	< 0.001

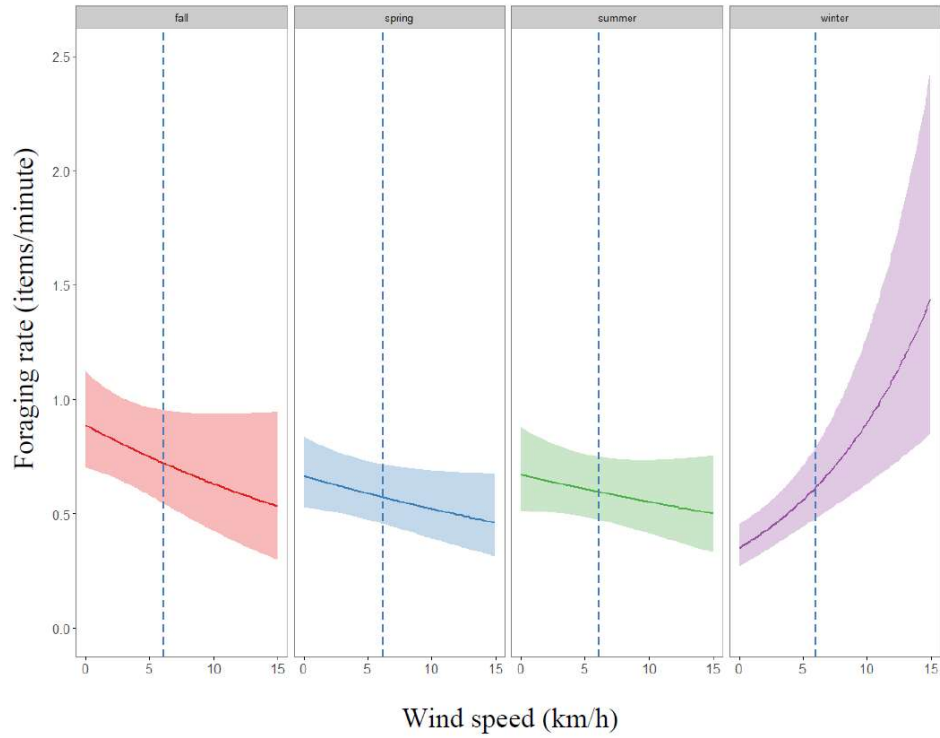


Figure 5: Interaction of wind and season on foraging rate of bat-eared foxes. Values are predicted from the LMM with 95 % confidence intervals. The effect in winter is significant ($p < 0.001$), however becomes non-significant when only ‘noisy’ wind-speeds above 6 km/h (represented by the dashed lines) are included in the analysis.

Table 5: Parameter estimates for wind and season calculated from the LMM using log (foraging rate) as the response variable and the reduced data set (wind speeds above 6 km/h only). NS = non-significant.

Variable	Estimate	SE	t-value	<i>p</i> -value
Fall	-0.580	0.625	-0.930	NS
Spring	-0.054	0.745	-0.073	NS
Summer	1.000	0.756	1.323	NS
Winter	-0.7523	0.837	-0.864	NS
Wind:Fall	0.025	0.067	0.375	NS
Wind:Spring	-0.021	0.077	-0.266	NS
Wind:Summer	-0.124	0.081	-1.529	NS
Wind:Winter	0.114	0.091	1.247	NS

3.4.2 In-patch time as a function of wind-speed

A total of 204 observations of foxes foraging in termite patches were recorded. The amount of time foxes spent in patches was not significantly affected by wind (Figure 6, wind parameter estimate = -0.002, SE = 0.013, $p = 0.935$). In this case the model did not differ significantly from a null model ($\chi^2 = 0.011$, df = 1, $p = 0.917$) or a model incorporating temperature ($\chi^2 = 4.927$, df = 2, $p = 0.085$). A further LMM analysis of a subset of this data comprising only observations above 6 km/h wind-speeds (n = 42 observations) also revealed no significant effect (wind parameter estimate = 0.045, SE = 0.049, $p = 0.362$) of wind on time spent in patches.

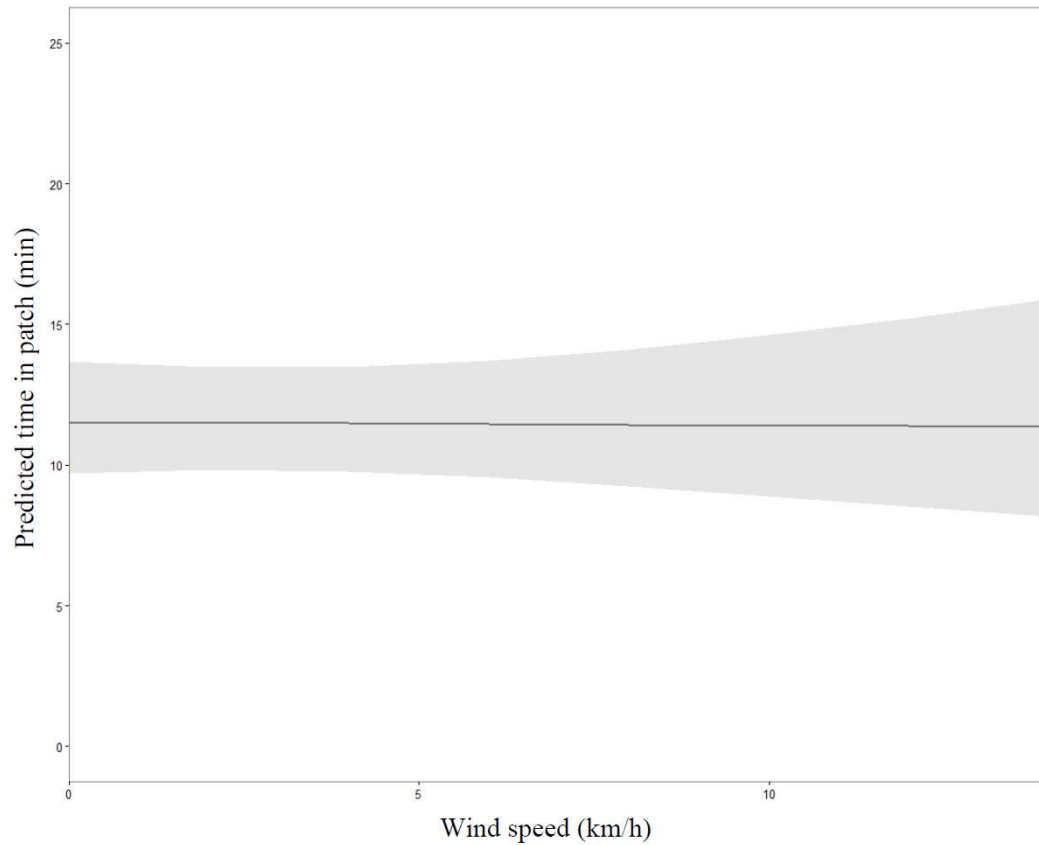


Figure 6: Time spent in termite patches in relation to wind speed. Values are predicted from the full data LMM with 95 % confidence interval. No significant effect of wind speed on in-patch time was found and this model did not differ significantly from a null model.

3.5 Discussion

The wind speeds recorded during the current study, whilst within the lower range of the Beaufort scale, would still have produced potentially disruptive background noise through the movement of vegetation (Boersma 1997; Bolin 2009). Contrary to predictions, fox foraging rate did not decline with this increase in ambient noise due to wind. Interestingly, although a significant change of foraging rate did occur in winter, the change was positive, with fox foraging rate increasing as wind speed increased. This effect may have been mediated by a shift in fox ecology peculiar to the winter season.

For Southern African foxes, winter is the season during which foraging activity often occurs diurnally (Lourens and Nel 1990; Nel 1990). This is primarily dictated by a shift in activity of a prime food source, the Harvester termite (*Hodotermes mossambicus*), from nocturnal to diurnal foraging (Nel 1990). Desert day-time wind speeds are typically higher and foxes have been noted to decrease diurnal foraging as winds increase beyond 12 km/h, with activity often ceasing altogether at high speeds (Lourens and Nel 1990). Windy days during the current study followed this trend, with winter wind speeds typically higher earlier in the day and tapering off by evening (see Appendix B). It is likely, therefore, that foxes in the present study missed diurnal foraging opportunities more frequently during windy winter days, therefore exhibiting higher motivation to forage in the evenings.

In the second prediction of this study, foxes were expected to spend more time in patches under windy conditions if wind noise increased the difficulty of finding alternate patches or food items. As arthropod activity was not expected to be negatively affected by wind at the speeds recorded for this study, termite patch quality was also not expected to diminish with

wind. Any change in the amount of time foxes spent in patches could therefore be attributed to fox behavioural responses rather than prey availability.

Studies on the how the availability of sensory information affects patch use tend to focus on predation risk. Foragers in patches where sensory inputs are restricted, for example sandpipers (*Calidris pusilla*) foraging near a visual barrier, have been found to increase vigilance behaviours (Beauchamp 2015). These authors are aware of no studies detailing how availability of sensory information about potential prey affects patch residence time in vertebrates, however this factor is known to influence time spent in patches in some invertebrates such as Lycosid spiders (Persons and Uetz 1996). As the amount of time foxes spent in termite patches did not show the predicted increase, there appeared to be no greater value to remaining in patches as wind speeds rose. These results align with the findings of between-patch foraging rates, suggesting that wind has no meaningful impact on foxes' foraging success, at least up to the levels studied here.

The combined results of this study suggest that foxes do not suffer from impaired hearing due to ambient wind noise at the levels recorded during the present study. This finding is surprising in light of documented noise effects on other acoustic predators such as gleaning bats (Schaub *et al.* 2008; Siemers and Schaub 2011; Bunkley and Barber 2015). However, Hübner and Wiegand (2003) demonstrated that when acoustic gaps were present in a masking noise, bat detection of prey-generated rustling sounds improved. Those authors concluded that through a combination of exploiting gaps in the masking stimulus and the ability to segregate prey sounds from background noise, bats were able to continue foraging successfully under noisy conditions.

For foxes foraging under conditions of ambient wind noise both cases may hold true. Like gleaning bats, foxes use their large ears in the detection and localisation of prey (Malcolm 1986; Grant and Samways 2015). The benefit of having enlarged pinnae is that the masking effect of background noise is reduced whilst prey movement sounds are amplified (Obrist *et al.* 1993; Hübner and Wiegrebe 2003). Foxes are likely also able to exploit naturally occurring gaps in ambient wind noise to locate prey or at lower wind levels may simply be able to filter prey generated sounds from background noise. Whilst the present study provides a compelling glimpse into the aural sensitivity of foxes in the wild, future studies using captive subjects are required to determine thresholds of aural sensitivity. Such an approach would allow the questions of exactly how these animals detect and pinpoint prey-generated sounds under differing noise regimes to be addressed.

A further consideration in the wild is that foxes may also simply alter their foraging behaviour in the presence of noise, as seen in foraging bats (Schaub *et al.* 2008), e.g., by moving from a dense scrub area to one with less vegetation to avoid noise effects. Further study of fox movement during foraging in the presence and absence of background noise is needed to ascertain whether this type of behavioural response is employed to mitigate the effects of natural ambient noise.

4. Discussion and conclusion

The present study constitutes both the first experimental investigation into bat-eared fox sensory ecology and the first study on the species examining the role of ambient environmental effects on that ecology. Bat-eared foxes have long been viewed as primarily acoustic predators and in the second chapter of this thesis, that assumption was confirmed experimentally. The validation of a significant role for auditory stimuli in pin-pointing prey meant that these diminutive canids might be susceptible to disturbance from environmental noise, which was investigated in chapter three. Wind-generated noise did not exert a deleterious effect on foraging success, nor did it cause foxes to spend more time in patches, foraging areas where reliance on audition would be lessened. Thus, within the limits tested, foxes are highly capable of detecting prey under windy conditions. Whether this is by filtering background noise, exploiting gaps in noise or through behavioural means, remains to be determined.

In working with a wild population, certain restrictions came into effect. The overall auditory sensitivity of bat-eared foxes for example, could not be tested under field conditions. The field setting also precludes the possibility of controlling levels of back ground noise, the duration of such stimuli and the presence or absence of prey items during natural foraging. By controlling these factors, a clearer picture of the limits of sensitivity experienced by the foxes could be determined along with how this relates to prey capture. The structure and nature of noise may also play a role, as may factors such as substrate (sand versus harder ground), the size of prey items and the distance at which the prey item is moving relative to the animal (Hübner and Wiegrebe 2003; Goerlitz *et al.* 2008). Future studies incorporating these effects would undoubtedly have to work with captive foxes. Under the controlled

conditions of a captive setting, a far more nuanced investigation of fox auditory abilities would become possible. Such a study would include the determination of auditory thresholds and a more detailed investigation into the effects of masking stimuli on fox hearing.

4.1 Determining auditory thresholds

No audiogram yet exists detailing the limits of bat-eared fox hearing or the peaks of sensitivity experienced by these animals. In order to generate a bat-eared fox audiogram, foxes would need to be tested at a series of frequencies to determine:

- a) whether they respond to a particular frequency and
- b) the reduction in sound intensity (in dB SPL) at a particular frequency required for no further response to be seen

Determining peaks of sensitivity in this manner would shed further light on the results of the current study with regard to how foxes are able to detect prey under 'noisy' conditions, as the overlap between peak prey-generated noise, masking noise and fox peak frequency sensitivity could be examined. To date, behavioural audiograms have been generated for only two fox species, arctic and kit foxes (*Vulpes lagopus* and *V. macrotis*), both of which exhibited peak sensitivity at 2-4 kHz (Stansbury *et al.* 2014). Both the afore-mentioned species are hunters of vertebrates however (Egoscue 1962; Elmhagen *et al.* 2000), and may not be as reliant on auditory cues as a specialist, acoustic insectivore such as the bat-eared fox.

4.2 Pinnae structure and hearing

Though detailed study of bat-eared fox ear morphology has not been undertaken, such studies have been conducted for other, acoustic insectivores: gleaning bats (Obrist *et al.* 1993). In these animals enlarged pinnae provide the benefits of prey noise amplification and a reduction in the impact of masking sound (Obrist *et al.* 1993). Despite the benefits conferred by such sensitive auditory systems (or perhaps because of their very sensitivity) such animals are prone to disturbance effects from noise (Schaub *et al.* 2008; Bunkley and Barber 2015). Barber *et al.* (2003) also showed that pallid bats (*Antrozous pallidus*) were unable to process two simultaneous auditory streams. If the same case holds true for bat-eared foxes, the strategy of exploiting gaps in noise to find prey seems highly likely.

4.3 Masking and other noise effects

The current study examined only natural ambient noise and its effect on an acoustic hunter. A further consideration for future studies may be the effects of introduced noise, specifically that generated by anthropogenic sources. If bat-eared fox hearing sensitivity peaks concur with those of kit and arctic foxes, these would be well within range to be affected by anthropogenic noise (Barber *et al.* 2010). The impact of anthropogenic noise on wildlife has recently attracted a great deal of attention (Weilgart 2007; Morley *et al.* 2013; Luo *et al.* 2015). Potential impacts of such noise for bat-eared foxes are just as numerous and extend beyond foraging impacts alone.

Studies looking into the effects of such noise on aquatic organisms and on calling behaviour in birds and other organisms have found such animals alter their behaviour in the presence of noise (Weilgart 2007; Wignall *et al.* 2011; Bunkley *et al.* 2015). Noise has also been found to increase bird vigilance rates (Quinn *et al.* 2006) as their risk of predation increases.

Conversely, some studies have found that prey animals become more susceptible to predation due to the distracting effect of noise (Chan *et al.* 2010). Acoustic foragers such as bats have been noted to avoid roads, and are averse to traffic noise when subjected to such in a laboratory situation (Schaub *et al.* 2008; Siemers and Schaub 2011; Bennett *et al.* 2013). Noise can effectively reduce habitat for such species with the associated problems this causes (Bunkley *et al.* 2015).

Though no effect of natural noise was found in the present study, future studies on fox movements in noisy areas near roads or other human activity could well add to the growing body of evidence for deleterious effects of anthropogenic noise on wildlife. During the present study, it was observed that large numbers of bat-eared foxes are killed on roads near the study site (pers. obs). Bat-eared foxes have also been noted to comprise a large proportion of road kills recorded in South Africa (S. Périquet, pers. comm.). The possibility of a link between the sensitive auditory ecology of this species and susceptibility to being killed on roads is a topic open for further investigation.

In addition to the captive setting there is still much room for building on the results presented in the current study *in situ*. The question of fox movements and anthropogenic noise, for example, could be investigated both in the field and in captive, choice-based experiments. Questions to be addressed in such studies include whether foxes avoid roads during 'noisy' times or if they are perhaps attracted there for some other reason despite noise. Similarly to the current study, the effects of anthropogenic noise on foraging success may be examined. It is possible that due to the structure of anthropogenic noise, this factor exerts a negative impact where natural ambient noise did not. If, on the other hand, foxes are found to be

tolerant of anthropogenic noise, as seen for some bats (Bunkley *et al.* 2015), the mechanisms underlying this would be of interest.

4.4 Conclusion

In summary, the present study provides experimental confirmation of the importance of auditory cues to bat-eared foxes in a foraging context. This study further shows that even under conditions of ambient noise, fox foraging is not negatively impacted and these canids are still capable of locating prey at rates consistent with less noisy conditions. Noise impact near areas such as busy roads may reveal a different picture and fox foraging may indeed be negatively impacted. In order to build on the findings of the current study, the following points should be addressed with regards to fox audition:

- a) Generation of a behavioural audiogram for the bat-eared fox.
- b) Captive experimental testing of the effects of sequential noise levels and different noise types on the ability of these animals to detect prey.
- c) Captive testing of the effects of gaps in masking noise on fox prey detection.
- d) Further *in situ* studies of fox foraging behaviour, including behaviour near roads.
- e) Studies of behaviour near other sources of anthropogenic noise .
- f) Fox movement patterns when subjected to ambient noise with specific reference to time spent between different vegetation types.

Appendix A : Wind measurement

BEAUFORT SCALE OF WIND

BEAUFORT NUMBER	DESCRIPTIVE TERM	VELOCITY EQUIVALENT AT A STANDARD HEIGHT OF 10 METRES ABOVE OPEN FLAT GROUND				SPECIFICATIONS			Probable wave height* in metres	Probable wave height* in feet
		Mean velocity in knots	m s ⁻¹	km h ⁻¹	m.p.h.	Land	Sea	Coast		
0	Calm	< 1	0–0.2	< 1	< 1	Calm; smoke rises vertically	Sea like a mirror	Calm	—	—
1	Light air	1–3	0.3–1.5	1–5	1–3	Direction of wind shown by smoke drift but not by wind vanes	Ripples with the appearance of scales are formed, but without foam crests	Fishing smack just has steerage way	0.1 (0.1)	¹ / ₄ (¹ / ₄)
2	Light breeze	4–6	1.6–3.3	6–11	4–7	Wind felt on face; leaves rustle; ordinary vanes moved by wind	Small wavelets, still short but more pronounced; crests have a glassy appearance and do not break	Wind fills the sails of smacks which then travel at about 1–2 knots	0.2 (0.3)	¹ / ₂ (1)
3	Gentle breeze	7–10	3.4–5.4	12–19	8–12	Leaves and small twigs in constant motion; wind extends light flag	Large wavelets; crests begin to break; foam of glassy appearance; perhaps scattered white horses	Smacks begin to careen and travel about 3–4 knots	0.6 (1)	2 (3)
4	Moderate breeze	11–16	5.5–7.9	20–28	13–18	Raises dust and loose paper; small branches are moved	Small waves, becoming longer; fairly frequent white horses	Good working breeze, smacks carry all canvas with good list	1 (1.5)	3 ¹ / ₂ (5)
5	Fresh breeze	17–21	8.0–10.7	29–38	19–24	Small trees in leaf begin to sway; crested wavelets form on inland waters	Moderate waves, taking a more pronounced long form; many white horses are formed (chance of some spray)	Smacks shorten sail	2 (2.5)	6 (8 ¹ / ₂)
6	Strong breeze	22–27	10.8–13.8	39–49	25–31	Large branches in motion; whistling heard in telegraph wires; umbrellas used with difficulty	Large waves begin to form; the white foam crests are more extensive everywhere (probably some spray)	Smacks have double reef in mainsail; care required when fishing	3 (4)	9 ¹ / ₂ (13)
7	Near gale	28–33	13.9–17.1	50–61	32–38	Whole trees in motion; inconvenience felt when walking against wind	Sea heaps up and white foam from breaking waves begins to be blown in streaks along the direction of the wind	Smacks remain in harbour and those at sea lie to	4 (5.5)	13 ¹ / ₂ (19)
8	Gale	34–40	17.2–20.7	62–74	39–46	Breaks twigs off trees; generally impedes progress	Moderately high waves of greater length; edges of crests begin to break into the spindrift; the foam is blown in well-marked streaks along the direction of the wind	All smacks make for harbour, if near	5.5 (7.5)	18 (25)
9	Strong gale	41–47	20.8–24.4	75–88	47–54	Slight structural damage occurs (chimney pots and slates removed)	High waves; dense streaks of foam along the direction of the wind; crests of waves begin to topple, tumble and roll over; spray may affect visibility	—	7 (10)	23 (32)
10	Storm	48–55	24.5–28.4	89–102	55–63	Seldom experienced inland; trees uprooted; considerable structural damage occurs	Very high waves with long overhanging crests; the resulting foam, in great patches, is blown in dense white streaks along the direction of the wind; on the whole, the surface of the sea takes on a white appearance; the tumbling of the sea becomes heavy and shock-like; visibility affected	—	9 (12.5)	29 (41)
11	Violent storm	56–63	28.5–32.6	103–117	64–72	Very rarely experienced; accompanied by widespread damage	Exceptionally high waves (small and medium-sized ships might be for a time lost to view behind the waves); the sea is completely covered with long white patches of foam lying along the direction of the wind; everywhere the edges of the wave crests are blown into froth; visibility affected	—	11.5 (16)	37 (52)
12	Hurricane	64 and over	32.7 and over	118 and over	73 and over	—	The air is filled with foam and spray; sea completely white with driving spray; visibility very seriously affected	—	14 (—)	45 (—)

* This table is only intended as a guide to show roughly what may be expected in the open sea, remote from land. It should never be used in the reverse way; i.e., for logging or reporting the state of the sea. In enclosed waters, or when near land, with an offshore wind, wave heights will be smaller and the waves steeper. Figures in brackets indicate the probable maximum height of waves.

(Source: World Meteorological Organisation)

Appendix B: Winter wind speeds

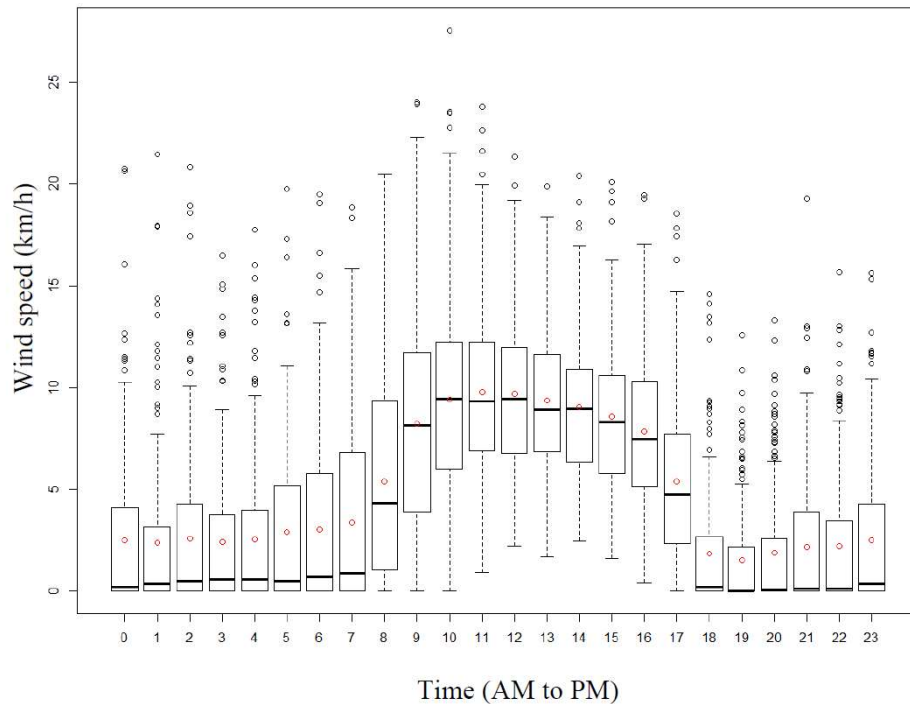


Figure 7: Winter wind speeds by hour of the day. Red points indicate mean wind speed for a particular hour for the entire winter season.

Note: Though day-time wind-speeds shown here do not generally exceed speeds at which no foraging impact was seen to occur nocturnally, the effects of wind are likely to be different diurnally, both in terms of prey activity and in fox perception of risk while foraging. Foxes were noted to be far more nervous around human observers during daylight hours (pers. obs.) than nocturnally, and have been noted to slow or cease diurnal foraging at speeds above 12 km/h (Lourens and Nel 1990).

References

- Acharya BB. 2007. The ecology of the Dhole or Asiatic wild dog (*Cuon alpinus*) in Pench tiger reserve, Madhya Pradesh. Gujarat: Saurashtra University.
- Adam RA, Mitchell JD, van der Westhuizen MC. 2008. Aspects of foraging in the harvester termite, *Trinervitermes trinervoides* (Sjöstedt) (Termitidae: Nasutitermitinae). *African Entomology* 16: 153–161.
- Aguilar Soto N, Johnson M, Madsen PT, Tyack PL, Bocconcelli A, Fabrizio Borsani J. 2006. Does intense ship noise disrupt foraging in deep-diving Cuvier's Beaked Whales (*Ziphius cavirostris*)? *Marine Mammal Science* 22: 690–699.
- Anjum F, Turni H, Mulder PG, van der Burg J, Brecht M. 2006. Tactile guidance of prey capture in Etruscan shrews. *Proceedings of the National Academy of Sciences* 103: 16544–16549.
- Appleby R, Johnson C, Marrant D, Savolainen P, Watson L. 2015. *The dingo debate: origins, behaviour and conservation*. CSIRO publishing.
- Arlettaz R, Jones G, Racey MH. 2001. Effects of acoustic clutter on prey detection by bats. *Nature* 414: 742–744.
- Barber JR, Crooks KR, Fristrup KM. 2010. The costs of chronic noise exposure for terrestrial organisms. *Trends in Ecology and Evolution* 25: 180–189.
- Barber JR, Razak KA, Fuzessery ZM. 2003. Can two streams of auditory information be processed simultaneously? Evidence from the gleaning bat *Antrozous pallidus*. *Journal of Comparative Physiology A: Sensory, Neural, and Behavioral Physiology* 189: 843–855.
- Barton RA, Purvis A, Harvey PH. 1995. Evolutionary radiation of visual and olfactory brain systems in primates, bats and insectivores. *Philosophical Transactions of the Royal Society B: Biological Sciences* 348: 381–392.
- Bates D, Mächler M, Bolker B, Walker S. 2015. Fitting Linear Mixed-Effects Models Using **lme4**. *Journal of Statistical Software* 67: 1–48.
- Beauchamp G. 2015. Visual obstruction and vigilance: a natural experiment. *Journal of Avian Biology* 46: 476–481.
- Bell GP. 1982. Behavioral and ecological aspects of gleaning by a desert insectivorous bat *Antrozous pallidus* (Chiroptera: Vespertilionidae). *Behavioral Ecology and Sociobiology* 10: 217–223.
- Bellingham J, Morris AG, Hunt DM. 1998. The rhodopsin gene of the cuttlefish *Sepia officinalis*: sequence and spectral tuning. *Journal of Experimental Biology* 201: 2299–2306.
- Belwood JJ, Fullard JH. 1984. Echolocation and foraging behaviour in the Hawaiian hoary bat, *Lasiurus cinereus semotus*. *Canadian Journal of Zoology* 62: 2113–2120.
- Bender DJ, Bayne EM, Brigham RM. 1996. Lunar condition influences coyote (*Canis latrans*) howling. *American Midland Naturalist*: 413–417.
- Bennett VJ, Sparks DW, Zollner PA. 2013. Modeling the indirect effects of road networks on the foraging activities of bats. *Landscape Ecology* 28: 979–991.
- Bicca-Marques JC, Garber PA. 2004. Use of spatial, visual, and olfactory information during foraging in wild nocturnal and diurnal anthropoids: A field experiment comparing *Aotus*, *Callicebus*, and *Saguinus*. *American Journal of Primatology* 62: 171–187.
- Bleckmann H, Lotz T. 1987. The vertebrate-catching behaviour of the fishing spider *Dolomedes triton* (Araneae, Pisauridae). *Animal Behaviour* 35: 641–651.

- Boersma HF. 1997. Characterization of the natural ambient sound environment: Measurements in open agricultural grassland. *The Journal of the Acoustical Society of America* 101: 2104–2110.
- Bolin K. 2009. Prediction Method for Wind-Induced Vegetation Noise. *Acta Acustica united with Acustica* 95: 607–619.
- Boonman AM, Boonman M, Bretschneider F, van de Grind WA. 1998. Prey detection in trawling insectivorous bats: duckweed affects hunting behaviour in Daubenton's bat, *Myotis daubentonii*. *Behavioral Ecology and Sociobiology* 44: 99–107.
- Bradley RA. 1988. The influence of weather and biotic factors on the behaviour of the scorpion (*Paruroctonus utahensis*). *The Journal of Animal Ecology* 57: 533.
- Briese DT, Macauley BJ. 1980. Temporal structure of an ant community in semi-arid Australia. *Austral Ecology* 5: 121–134.
- Brown PK, Brown PS. 1958. Visual pigments of the octopus and cuttlefish. *Nature* 182: 1288–1290.
- Browne C, Stafford K, Fordham R. 2006. The use of scent-detection dogs. *Irish Veterinary Journal* 59: 97.
- Bunkley JP, Barber JR. 2015. Noise Reduces Foraging Efficiency in Pallid Bats (*Antrozous pallidus*). *Ethology* 121: 1116–1121.
- Bunkley JP, McClure CJW, Kleist NJ, Francis CD, Barber JR. 2015. Anthropogenic noise alters bat activity levels and echolocation calls. *Global Ecology and Conservation* 3: 62–71.
- Campbell SA, Borden JH. 2009. Additive and synergistic integration of multimodal cues of both hosts and non-hosts during host selection by woodboring insects. *Oikos* 118: 553–563.
- Catania KC. 2006. Olfaction: underwater 'sniffing' by semi-aquatic mammals. *Nature* 444: 1024–1025.
- Catania KC, Hare JF, Campbell KL. 2008. Water shrews detect movement, shape, and smell to find prey underwater. *Proceedings of the National Academy of Sciences* 105: 571–576.
- Červený J, Begall S, Koubek P, Novakova P, Burda H. 2011. Directional preference may enhance hunting accuracy in foraging foxes. *Biology Letters* 7: 355–357.
- Chan AAY-H, David Stahlman W, Garlick D, Fast CD, Blumstein DT, Blaisdell AP. 2010. Increased amplitude and duration of acoustic stimuli enhance distraction. *Animal Behaviour* 80: 1075–1079.
- Chelini M-C, Willemart RH, Hebets EA. 2009. Costs and benefits of freezing behaviour in the harvestman *Eumesosoma roeweri* (Arachnida, Opiliones). *Behavioural Processes* 82: 153–159.
- Chiao C-C, Chubb C, Hanlon RT. 2015. A review of visual perception mechanisms that regulate rapid adaptive camouflage in cuttlefish. *Journal of Comparative Physiology A* 201: 933–945.
- Clarín TMA, Ruczyński I, Page RA, Siemers BM. 2013. Foraging Ecology Predicts Learning Performance in Insectivorous Bats. *PLoS ONE* 8: e64823.
- Clark HO, Murdoch JD, Newman DP, Sillero-Zubiri C. 2009. *Vulpes corsac* (Carnivora: Canidae). *Mammalian Species* 832: 1–8.
- Clark Jr HO. 2005. *Otocyon megalotis*. *Mammalian Species* 766: 1–5.
- Clarke JA. 1983. Moonlight's influence on predator/prey interactions between short-eared owls (*Asio flammeus*) and deermice (*Peromyscus maniculatus*). *Behavioral Ecology and Sociobiology* 13: 205–209.
- Conner WE, Corcoran AJ. 2012. Sound Strategies: The 65-Million-Year-Old Battle Between Bats and Insects. *Annual Review of Entomology* 57: 21–39.

- Da Costa RS, Bicca-Marques JC. 2014. Owl Monkeys (*Aotus nigriceps* and *A. infulatus*) Follow Routes Instead of Food-Related Cues during Foraging in Captivity. *PloS one* 9: e115188.
- Croll DA, Clark CW, Calambokidis J, Ellison WT, Tershy BR. 2001. Effect of anthropogenic low-frequency noise on the foraging ecology of Balaenoptera whales. *Animal Conservation* 4: 13–27.
- Cunningham SJ, Castro I. 2011. The secret life of wild brown kiwi: studying behaviour of a cryptic species by direct observation. *New Zealand Journal of Ecology*: 209–219.
- Cunningham SJ, Castro I, Potter MA. 2009. The relative importance of olfaction and remote touch in prey detection by North Island brown kiwis. *Animal Behaviour* 78: 899–905.
- Curtis BA. 1985. Activity of the Namib Desert dune ant, *Camponotus detritus*. *South African Journal of Zoology* 20: 41–48.
- Dangles O, Irschick D, Chittka L, Casas J. 2009. Variability in sensory ecology: expanding the bridge between physiology and evolutionary biology. *The Quarterly Review of Biology* 84: 51–74.
- Davies TW, Bennie J, Inger R, Gaston KJ. 2013. Artificial light alters natural regimes of night-time sky brightness. *Scientific Reports* 3.
- Dawkins R, Krebs JR. 1979. Arms Races between and within species. *Proceedings of the Royal Society B: Biological Sciences* 205: 489–511.
- Defrize J, Thery M, Casas J. 2010. Background colour matching by a crab spider in the field: a community sensory ecology perspective. *Journal of Experimental Biology* 213: 1425–1435.
- Dominy NJ, Lucas PW, Osorio D, Yamashita N. 2001. The sensory ecology of primate food perception. *Evolutionary Anthropology: Issues, News, and Reviews* 10: 171–186.
- Edut S, Eilam D. 2004. Protean behavior under barn-owl attack: voles alternate between freezing and fleeing and spiny mice flee in alternating patterns. *Behavioural Brain Research* 155: 207–216.
- Egoscue HJ. 1962. Ecology and life history of the kit fox in Tooele County, Utah. *Ecology* 43: 481–497.
- Eilam D. 2005a. Die hard: A blend of freezing and fleeing as a dynamic defense—implications for the control of defensive behavior. *Neuroscience and Biobehavioral Reviews* 29: 1181–1191.
- Eilam D. 2005b. Die hard: A blend of freezing and fleeing as a dynamic defense—implications for the control of defensive behavior. *Neuroscience and Biobehavioral Reviews* 29: 1181–1191.
- Elias DO, Hebets EA, Hoy RR, Mason AC. 2005. Seismic signals are crucial for male mating success in a visual specialist jumping spider (Araneae: Salticidae). *Animal Behaviour* 69: 931–938.
- Elmhagen B, Tannerfeldt M, Verucci P, Angerbjörn A. 2000. The arctic fox (*Alopex lagopus*): an opportunistic specialist. *Journal of Zoology* 251: 139–149.
- Fenk LM, Hoinkes T, Schmid A. 2010. Vision as a third sensory modality to elicit attack behavior in a nocturnal spider. *Journal of Comparative Physiology A* 196: 957–961.
- Fishman GA. 2003. When your eyes have a wet nose: the evolution of the use of guide dogs and establishing the seeing eye. *Survey of Ophthalmology* 48: 452–458.
- Fleisher KJ, Case JF. 1995. Cephalopod predation facilitated by dinoflagellate luminescence. *The Biological Bulletin* 189: 263–271.
- Fraser NHC, Metcalfe NB. 1997. The costs of becoming nocturnal: feeding efficiency in relation to light intensity in juvenile Atlantic salmon. *Functional Ecology* 11: 385–391.

- Friedel T, Barth FG. 1997. Wind-sensitive interneurons in the spider CNS (*Cupiennius salei*): directional information processing of sensory inputs from trichobothria on the walking legs. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology* 180: 223–233.
- Fux M, Eilam D. 2009. How barn owls (*Tyto alba*) visually follow moving voles (*Microtus socialis*) before attacking them. *Physiology and Behavior* 98: 359–366.
- Gadbois S, Reeve C. 2014. Canine olfaction: scent, sign, and situation. In: Horowitz A (ed), *Domestic Dog Cognition and Behavior*. Berlin, Heidelberg: Springer Berlin Heidelberg. pp. 3–29.
- Garber PA, Hannon B. 1993. Modeling monkeys: a comparison of computer-generated and naturally occurring foraging patterns in two species of neotropical primates. *International Journal of Primatology* 14: 827–852.
- Gazit I, Terkel J. 2003. Domination of olfaction over vision in explosives detection by dogs. *Applied Animal Behaviour Science* 82: 65–73.
- Geerts S, van der Linden J, van der Linden E. 2016. The ecology and foraging behaviour of the harvester termite, *Baicaliotes hainesi* in semi-arid grasslands in the northwestern interior of South Africa. *Insectes Sociaux* 63: 457–465.
- Glasser AH, Howland HC. 1996. A history of studies of visual accommodation in birds. *Quarterly review of biology*: 475–509.
- Goerlitz HR, Greif S, Siemers BM. 2008. Cues for acoustic detection of prey: insect rustling sounds and the influence of walking substrate. *Journal of Experimental Biology* 211: 2799–2806.
- Goerlitz HR, Siemers BM. 2007. Sensory ecology of prey rustling sounds: acoustical features and their classification by wild Grey Mouse Lemurs. *Functional Ecology* 21.
- Goyret J, Kelber A. 2011. How does a diurnal hawkmoth find nectar? Differences in sensory control with a nocturnal relative. *Behavioral Ecology* 22: 976–984.
- Grant PBC, Samways MJ. 2015. Acoustic prey and a listening predator: interaction between calling katydids and the bat-eared fox. *Bioacoustics* 24: 49–61.
- Hanlon R. 2007. Cephalopod dynamic camouflage. *Current Biology* 17: R400–R404.
- Heatwole H. 1996. *Energetics of Desert Invertebrates*. Berlin, Heidelberg: Springer Berlin Heidelberg.
- Henwood K. 1975. A field-tested thermoregulation model for two diurnal Namib desert Tenebrionid beetles. *Ecology* 56: 1329–1342.
- Holderied M, Korine C, Moritz T. 2011. Hemprich's long-eared bat (*Otonycteris hemprichii*) as a predator of scorpions: whispering echolocation, passive gleaning and prey selection. *Journal of Comparative Physiology A* 197: 425–433.
- Holland R. 2009. Blind as a bat? The sensory basis of orientation and navigation at night. In: Berthoz A, Christen Y (eds), *Neurobiology of 'Umwelt': How Living Beings Perceive the World*. Berlin, Heidelberg: Springer Berlin Heidelberg. pp. 125–139.
- Holyoak M, Jarosik V, Novak I. 1997. Weather-induced changes in moth activity bias measurement of long-term population dynamics from light trap samples. *Entomologia Experimentalis et Applicata* 83: 329–335.
- Hristov NI, Conner WE. 2005. Sound strategy: acoustic aposematism in the bat–tiger moth arms race. *Naturwissenschaften* 92: 164–169.
- Hübner M, Wiegand L. 2003. The effect of temporal structure on rustling-sound detection in the gleaning bat, *Megaderma lyra*. *Journal of Comparative Physiology A* 189: 337–346.

- Isley TE, Gysel LW. 1975. Sound-source localization by the red fox. *Journal of Mammalogy* 56: 397–404.
- Jacobs GH, Deegan JF, Crognale MA, Fenwick JA. 1993. Photopigments of dogs and foxes and their implications for canid vision. *Visual Neuroscience* 10: 173.
- Jensen FH, Perez JM, Johnson M, Soto NA, Madsen PT. 2011. Calling under pressure: short-finned pilot whales make social calls during deep foraging dives. *Proceedings of the Royal Society B: Biological Sciences* 278: 3017–3025.
- Jonason D, Franzén M, Ranius T. 2014. Surveying moths using light traps: effects of weather and time of year. *PloS one* 9: e92453.
- Jones G. 2003. Mysterious Mystacina: how the New Zealand short-tailed bat (*Mystacina tuberculata*) locates insect prey. *Journal of Experimental Biology* 206: 4209–4216.
- Jones G. 2013. Sensory Biology: Listening in the dark for echoes from silent and stationary prey. *Current Biology* 23: R249–R251.
- Kelber A. 2005. Light intensity limits foraging activity in nocturnal and crepuscular bees. *Behavioral Ecology* 17: 63–72.
- Klinka DR, Reimchen TE. 2002. Nocturnal and diurnal foraging behaviour of brown bears (*Ursus arctos*) on a salmon stream in coastal British Columbia. *Canadian Journal of Zoology* 80: 1317–1322.
- Klinka DR, Reimchen TE. 2009. Darkness, twilight, and daylight foraging success of bears (*Ursus americanus*) on salmon in coastal British Columbia. *Journal of Mammalogy* 90: 144–149.
- Korine C, Kalko EKV. 2005. Fruit detection and discrimination by small fruit-eating bats (Phyllostomidae): echolocation call design and olfaction. *Behavioral Ecology and Sociobiology* 59: 12–23.
- Kuntzsch V, Nel JAJ. 1992. Diet of bat-eared foxes ; *Otocyon megalotis*; in the Karoo. *Koedoe* 35.
- Land MF. 1985. The morphology and optics of spider eyes. In: Barth FG (ed), *Neurobiology of Arachnids*. Berlin, Heidelberg: Springer Berlin Heidelberg. pp. 53–78.
- Lareviere S. 2002. *Vulpes zerda*. *Mammalian Species* 714: 1–5.
- Lenth RV. 2016. Least-Squares Means: The R Package **lsmeans**. *Journal of Statistical Software* 69: 1–33.
- Li J, Zhang Z, Liu F, Liu Q, Gan W, Chen J, Lim MLM, Li D. 2008. UVB-based mate-choice cues used by females of the jumping spider *Phintella vittata*. *Current Biology* 18: 699–703.
- Lord K. 2013. A comparison of the sensory development of wolves (*Canis lupus lupus*) and dogs (*Canis lupus familiaris*). *Ethology* 119: 110–120.
- Lourens S, Nel JAJ. 1990. Winter activity of bat-eared foxes *Otocyon megalotis* on the Cape West coast. *South African Journal of Zoology* 25: 124–132.
- Luo J, Siemers BM, Koselj K. 2015. How anthropogenic noise affects foraging. *Global Change Biology* 21: 3278–3289.
- Malcolm JR. 1986. Socio-ecology of Bat-eared foxes (*Otocyon megalotis*). *Journal of Zoology* 208: 457–469.
- Malkemper EP, Topinka V, Burda H. 2015. A behavioral audiogram of the red fox (*Vulpes vulpes*). *Hearing Research* 320: 30–37.
- Martin GR. 2012. Through birds' eyes: insights into avian sensory ecology. *Journal of Ornithology* 153: 23–48.
- Martin GR, Wilson K-J, Wild JM, Parsons S, Kubke MF, Corfield J. 2007. Kiwi forego vision in the guidance of their nocturnal activities. *PLoS ONE* 2: e198.

- Martin GR, Young SR. 1984. The eye of the Humboldt penguin, *Spheniscus humboldti*: visual fields and schematic optics. *Proceedings of the Royal Society B: Biological Sciences* 223: 197–222.
- McGeachie WJ. 1989. The effects of moonlight illuminance, temperature and wind speed on light-trap catches of moths. *Bulletin of Entomological Research* 79: 185–192.
- Mech LD, Smith DW, MacNulty DR. 2015. *Wolves on the Hunt: The Behavior of Wolves Hunting Wild Prey*. University of Chicago Press.
- Miller PE, Murphy CJ. 1995. Vision in dogs. *Journal-American Veterinary Medical Association* 207: 1623–1634.
- Mitchell JD, Hewitt PH, Van Der Linde TDK. 1993. Critical thermal limits and temperature tolerance in the harvester termite *Hodotermes mossambicus* (Hagen). *Journal of Insect Physiology* 39: 523–528.
- Morley EL, Jones G, Radford AN. 2013. The importance of invertebrates when considering the impacts of anthropogenic noise. *Proceedings of the Royal Society B: Biological Sciences* 281: 20132683–20132683.
- Nekaris KAI. 2005. Foraging behaviour of the slender loris (*Loris lydekkerianus lydekkerianus*): implications for theories of primate origins. *Journal of Human Evolution* 49: 289–300.
- Nel JAJ. 1990. Foraging and feeding by bat-eared foxes; *Otocyon megalotis*; in the southwestern Kalahari. *Koedoe* 33.
- Nevitt GA. 2008. Sensory ecology on the high seas: the odor world of the procellariiform seabirds. *Journal of Experimental Biology* 211: 1706–1713.
- Obrist MK, Fenton MB, Eger JL, Schlegel PA. 1993. What ears do for bats: a comparative study of pinna sound pressure transformation in Chiroptera. *Journal of Experimental Biology* 180: 119–152.
- Oorebeek M, Sharrad R, Kleindorfer S. 2009. What attracts larval *Ixodes hirsti* (Acari: Ixodidae) to their host? *Parasitology Research*. 104(3): 623–628.
- Österholm H. 1964. The significance of distance receptors in the feeding behaviour of the fox, *Vulpes vulpes* L. *Acta Zoologica Fennica*: 3–31.
- Page RA, Schnelle T, Kalko EKV, Bunge T, Bernal XE. 2012. Sequential assessment of prey through the use of multiple sensory cues by an eavesdropping bat. *Naturwissenschaften* 99: 505–509.
- Partan S, Marler P. 2002. The Umwelt and its relevance to animal communication: introduction to special issue. *Journal of Comparative Psychology* 116: 116.
- Paukner A, Huntsberry ME, Suomi SJ. 2009. Tufted capuchin monkeys (*Cebus apella*) spontaneously use visual but not acoustic information to find hidden food items. *Journal of Comparative Psychology* 123: 26–33.
- Persons MH, Uetz GW. 1996. The influence of sensory information on patch residence time in wolf spiders (Araneae: Lycosidae). *Animal Behaviour*: 1285–1293.
- Piep M, Radespiel U, Zimmermann E, Schmidt S, Siemers BM. 2008. The sensory basis of prey detection in captive-born grey mouse lemurs, *Microcebus murinus*. *Animal Behaviour* 75: 871–878.
- Purser J, Radford AN. 2011. Acoustic noise induces attention shifts and reduces foraging performance in three-spined sticklebacks (*Gasterosteus aculeatus*). *PLoS ONE* 6: e17478.
- Quinn JL, Whittingham MJ, Butler SJ, Cresswell W. 2006. Noise, predation risk compensation and vigilance in the chaffinch *Fringilla coelebs*. *Journal of Avian Biology* 37: 601–608.

- Raghuram H, Thangadurai C, Gopukumar N, Nathar K, Sripathi K. 2009. The role of olfaction and vision in the foraging behaviour of an echolocating megachiropteran fruit bat, *Rousettus leschenaulti* (Pteropodidae). *Mammalian Biology - Zeitschrift für Säugetierkunde* 74: 9–14.
- Ramsier MA, Dominy NJ. 2012. Receiver bias and the acoustic ecology of aye-ayes (*Daubentonia madagascariensis*). *Communicative and Integrative Biology* 5: 637–640.
- Ranåker L, Jönsson M, Nilsson PA, Brönmark C. 2012. Effects of brown and turbid water on piscivore-prey fish interactions along a visibility gradient: Predator-prey interactions in reduced visibility. *Freshwater Biology* 57: 1761–1768.
- Regular PM, Hedd A, Montevicchi WA. 2011. Fishing in the Dark: A pursuit-diving seabird modifies foraging behaviour in response to nocturnal light levels. *PLoS ONE* 6: e26763.
- Reijnen R, Foppen R, Veenbaas G. 1997. Disturbance by traffic of breeding birds: evaluation of the effect and considerations in planning and managing road corridors. *Biodiversity and Conservation* 6: 567–581.
- Rushmore J, Leonhardt SD, Drea CM. 2012. Sight or scent: lemur sensory reliance in detecting food quality varies with feeding ecology. *PLoS ONE* 7: e41558.
- Santisteban L, Sieving KE, Avery ML. 2002. Use of sensory cues by fish crows *Corvus ossifragus* preying on artificial bird nests. *Journal of Avian Biology* 33: 245–252.
- Schaub A, Ostwald J, Siemers BM. 2008. Foraging bats avoid noise. *Journal of Experimental Biology* 212: 3036–3036.
- Shimasaki L, Kitagawa K, Hernandez M, Blumstein DT. 2012. Are blue land crabs (*Cardisoma guanhumi*) attracted to falling fruit? *acta ethologica* 15: 159–164.
- Shine R, Sun L-X, Kearney M, Fitzgerald M. 2002. Thermal correlates of foraging-site selection by Chinese pit-vipers (*Gloydius shedaoensis*, Viperidae). *Journal of thermal Biology* 27: 405–412.
- Siemers BM, Baur E, Schnitzler H-U. 2005. Acoustic mirror effect increases prey detection distance in trawling bats. *Naturwissenschaften* 92: 272–276.
- Siemers BM, Goerlitz HR, Robsomanitrndrasana E, Piep M, Ramanamanjato J-B, Rakotondravony D, Ramilijaona O, Ganzhorn JU. 2007. Sensory Basis of Food Detection in Wild *Microcebus murinus*. *International Journal of Primatology* 28: 291–304.
- Siemers BM, Schaub A. 2011. Hunting at the highway: traffic noise reduces foraging efficiency in acoustic predators. *Proceedings of the Royal Society B: Biological Sciences* 278: 1646–1652.
- Siemers BM, Stitz P, Schnitzler H-U. 2001. The acoustic advantage of hunting at low heights above water: behavioural experiments on the European ‘trawling’ bats *Myotis capaccinii*, *M. dasycneme* and *M. daubentonii*. *Journal of Experimental Biology* 204: 3843–3854.
- Siemers BM, Swift SM. 2006. Differences in sensory ecology contribute to resource partitioning in the bats *Myotis bechsteinii* and *Myotis nattereri* (Chiroptera: Vespertilionidae). *Behavioral Ecology and Sociobiology* 59: 373–380.
- Sillero-Zubiri C, Hoffmann M, Macdonald DW (eds). 2004. *Canids: foxes, wolves, jackals and dogs: status survey and conservation action plan*. Gland, Switzerland and Cambridge, UK: IUCN/SSC Canid Specialist Group.
- Sivak JG, Lincer JL, Bobier W. 1977. Amphibious visual optics of the eyes of the double-crested cormorant (*Phalacrocorax auritus*) and the brown pelican (*Pelecanus occidentalis*). *Canadian journal of zoology* 55: 782–788.

- Stansbury AL, Thomas JA, Stalf CE, Murphy LD, Lombardi D, Carpenter J, Mueller T. 2014. Behavioral audiogram of two Arctic foxes (*Vulpes lagopus*). *Polar Biology* 37: 417–422.
- Stuart, C.T.; Stuart, T. & Pereboom, V. 2003. Diet of the bat-eared fox (*Otocyon megalotis*), based on scat analysis, on the Western-Escarpment, South Africa. *Canid News*. 6(2): [online].
http://www.stuartonnature.com/resources/Scientific_papers/Diet_of_the_bat-eared_fox.pdf
- Sutrop U. 2001. Umwelt: Word and concept: Two hundred years of semantic change. *Semiotica* 134 (1/4): 447–462.
- Szentkirályi F, Kazinczy L, Kádár F, Bernáth B, Barabás S. 2007. Monitoring of Antlions (Neuroptera Myrmeleontidae) by light trapping: influence of weather elements on daily and seasonal flight patterns. *Ann. Mus. civ. St. nat. Ferrara Vol* 8: 167–172.
- Szetei V, Miklósi á, Topál J, Csányi V. 2003. When dogs seem to lose their nose: an investigation on the use of visual and olfactory cues in communicative context between dog and owner. *Applied Animal Behaviour Science* 83: 141–152.
- Teichroeb JA, Chapman CA. 2014. Sensory information and associative cues used in food detection by wild vervet monkeys. *Animal Cognition* 17: 517–528.
- Tucker MR. 1983. Light-trap catches of African armyworm moths, *Spodoptera exempta* (Walker)(Lepidoptera: Noctuidae), in relation to rain and wind. *Bulletin of Entomological Research* 73: 315–319.
- Uetz GW, Roberts JA. 2002. Multisensory cues and multimodal communication in spiders: insights from video/audio playback studies. *Brain, Behavior and Evolution* 59: 222–230.
- Ulanovsky N, Moss CF. 2008. What the bat's voice tells the bat's brain. *Proceedings of the National Academy of Sciences* 105: 8491–8498.
- Ulmer KM, Buresch KC, Kossodo MM, Mäthger LM, Siemann LA, Hanlon RT. 2013. Vertical visual features have a strong influence on cuttlefish camouflage. *The Biological Bulletin* 224: 110–118.
- Vincent SE, Shine R, Brown GP. 2005. Does foraging mode influence sensory modalities for prey detection in male and female filesnakes, *Acrochordus arafurae*? *Animal Behaviour* 70: 715–721.
- Von der Emde G, Bleckmann H. 1998. Finding food: senses involved in foraging for insect larvae in the electric fish *Gnathonemus petersii*. *The Journal of experimental biology* 201: 969–980.
- Wale MA, Simpson SD, Radford AN. 2013. Noise negatively affects foraging and antipredator behaviour in shore crabs. *Animal Behaviour* 86: 111–118.
- Weilgart LS. 2007. A brief review of known effects of noise on marine mammals. *International Journal of Comparative Psychology* 20.
- Wells MC, Lehner PN. 1978. The relative importance of the distance senses in coyote predatory behaviour. *Animal Behaviour*: 251–258.
- White CR, Day N, Butler PJ, Martin GR. 2007. Vision and foraging in cormorants: more like herons than hawks?
- Wignall AE, Jackson RR, Wilcox RS, Taylor PW. 2011. Exploitation of environmental noise by an araneophagic assassin bug. *Animal Behaviour* 82: 1037–1042.
- Wilkens LA, Hofmann MH. 2007. The paddlefish rostrum as an electrosensory organ: a novel adaptation for plankton feeding. *BioScience* 57: 399–407.

Yela JL, Holyoak M. 1997. Effects of moonlight and meteorological factors on light and bait trap catches of noctuid moths (Lepidoptera: Noctuidae). *Environmental Entomology* 26: 1283–1290.