The influence of foraging habitat on acoustic signal source levels in two bat species, *Neoromicia capensis* (Vespertilionidae) and *Tadarida aegyptiaca* (Molossidae)

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DECLARATION

I, **Itani Victor Mutavhatsindi**, know the meaning of Plagiarism and declare that the work on which this dissertation is based, is my original work (except where acknowledgements indicate otherwise) and that neither the whole work nor any part of it has been, is being, or is to be submitted for another degree in this or any other University. I authorise the University to reproduce for the purpose of research either the whole or any portion of the contents in any manner whatsoever.

Signed by candidate

Signature: Signature removed   Date: **30 August 2017**.

DEDICATION

This research is dedicated to my parents (Mr Ramashiya Petrus Mutavhatsindi and Mrs Mudifho Sarah Mutavhatsindi) and siblings (Takalani Marcus Mutavhatsindi, Tshililo Enny Mutavhatsindi, Azwinndini Prudence Mutavhatsindi, Lufuno Confidence Mutavhatsindi and Dilgent Rendani Mutavhatsindi) for their unconditional love and support.

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LIST OF ABBREVIATIONS

3-D	three-dimensional
CF	constant frequency
cm	Centimeter
dB	decibel
DHNR	De Hoop Nature Reserve
FFT	Fast Fourier Transformation
FM	frequency modulated
HDC	High-duty cycle
Hz	hertz
kHz	Kilohertz
km	Kilometer
LDC	Low-duty cycle
m	meter
ms	milliseconds
N. capensis	*Neoromicia capensis*
NRF	National Research Foundation
pe	peak equivalent
PI	pulse interval
QCF	quasi-constant frequency
RMS	root mean square
SL	source level
SNR	signal to noise ratio
SPL	sound pressure level

SR	sampling rate
T. aegyptiaca	*Tadarida aegyptiaca*
TOAD	time of arrival difference

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ABSTRACT

The source level of echolocation pulses is an essential parameter because it has an impact on the range at which bats perceive their environment and, most importantly, at which they detect prey. Echolocation pulse source level is under the control of the echolocator and its operational range is likely to vary with body size and foraging habitat because these determine the operational range needed by the bat. This study thus attempted to answer the following questions; (1) is the source levels of animal acoustic signals different in different situations? (2) Does body size and foraging habitat affect the source levels of animal acoustic signals? There are only a few studies that report on the source levels of echolocation pulses of free-ranging bats because of the difficulty of measuring the distance of the bat from the recording microphone. This distance is essential in calculating source levels of echolocation pulses. I used multiple microphone array system to investigate the echolocation sound signals, three-dimensional (3-D) acoustic flight paths and source levels of echolocation pulses at 10 cm standard reference distance from the mouth of a free-flying frequency-modulated (FM) bat, *Neoromicia capensis* and quasi-constant frequency (QCF) bat, *Tadarida aegyptiaca*. The two bat species differ in body size and foraging habitat. I found as predicted, that *T. aegyptiaca*, the larger of the two species and an open-air aerial hawker, emitted echolocation pulses of higher source levels and therefore had greater maximum detection distances than the smaller, clutter-edge aerial hawker, *N. capensis*. *Tadarida aegyptiaca* emitted echolocation pulses with an average of 146.9±4.6 (range 137.7 – 154.8) dB peSPL during emergence from the roost and an average of 143.0±4.9 (range 136.4 – 153.3) dB peSPL during foraging, extending the known range of free-flying bats. *Neoromicia capensis* emitted echolocation pulses with an average of 129.3±4.0 (range 119.3 – 138.7) dB peSPL during emergence from the roost and average of 132.8±5.0 (range 117.8 – 142.9) dB peSPL during foraging. As anticipated, I found *N. capensis* to be emitting echolocation pulses of higher source levels during foraging than when it emerged from the roost. However, there was no significant difference in the source levels of *T. aegyptiaca* between emergence from the roost and foraging habitat. The estimated maximum detection distances for the three insect size categories i.e. small, medium and large was greater for *T. aegyptiaca* than *N. capensis*. My data therefore suggests that bats might adjust their echolocation pulse source levels to suit their foraging habitat and situation.

Keywords: Source level, detection distance, microphone array, sensory ecology, flight path.

CHAPTER 1

Introduction

Sensory ecology deals with how animals receive, process and respond to information from their surrounding environment, and the sensory systems which they use to do so (Dusenbery, 1992). According to Dusenbery (1992) the subject of sensory ecology addresses questions such as what kind of information is available in the environment and how the information is passed on to animals. Information has a significant function for the existence of animals both from the evolutionary and behavioral perspective. Such information is acquired by animals through direct interaction with the environment—*personal information,* and also through observation of other animal's behavior either of the same species or different species—*socially acquired information* (Dall *et al*., 2005). Sensory systems vary widely in terms of their size and complexity. And in the field of sensory ecology, most researchers have given more attention to sensory systems such as magnetic field reception in rodents and birds (Kimchi *et al*., 2004), hearing in insects and frogs (Wilczynski and Ryan, 1988) echolocation in dolphins and bats (Thomas *et al*., 2002), mechanoreception in arthropods (Barth, 2002) and electroreception in fish (Bullock *et al*., 2005).

Sensory systems play important roles in the daily lives of animals as they encounter a wide range of situations which are linked with both animate and inanimate aspects of their environment. Within this environmental context they have to complete a variety of activities such as foraging, orientation, locating roosts, attraction of mate, establishment of territories and avoidance of predation. To successfully complete such activities animals have to make decisions based on their estimation of whether their immediate environmental conditions are favorable (Phelps, 2007). Depending on the reliability of information obtained from the environment by sensory systems, an animal is able to make a decision that favours its survival and reproduction. To achieve that, an animal's brain is responsible for processing the stimuli received by the sensory systems from the environment. The animal then responds to the situation based on the decision taken by the brain. An animal's sense organs are mostly located close to or on the surface of its body thus making it easier to gather information from the environment. Sensory drive, a process in which sensory conditions and sensory systems are responsible for driving evolution in a particular direction influences the adaptability of sensory systems (Endler, 1992). The understanding of sensory ecology thus brings an insight into how an animal's behavior can be managed, reinforced and constrained by the information it obtains from its natural habitat (Martin, 2011). Due to anthropogenic activities such as light pollution (Cinzano, 2000; Cinzano *et al*., 2001; Cinzano, 2003) which have altered the environment and continues to do so in unsustainable ways, studying the sensory ecology of animals is of great importance. It will improve our understanding of the sensory challenges that animals face in a rapidly changing environment. Such understanding may enable us to minimize extinction rates.

In comparison with studies conducted on visual systems, animal acoustics has received less attention due to the difficulties in detecting and recording acoustic signals (Frick, 2013). Particularly if they are outside of human auditory range, because they are mostly used by animals in habitats where vision is of minimal use i.e. at night or in dark roosts (e.g. caves). Various animal species such as bats, frogs, birds and insects produce an abundance of complex acoustic signals. The different kinds of acoustic signals play important roles in reproduction and survival of animals. Insects such as crickets are able to produce songs which are used to attract potential mating partners from a distance (Martin, 2011). The production of calling songs on these insects is accomplished by rubbing a toothed vein which is located on the left forewing with a plectrum on the right forewing (Hummel *et al*., 2014). The variability of songs in birds is very high and the songs are used mainly for species recognition, attraction of mates, establishment of territories and defense (Brumm *et al*., 2011). Bats mostly depend on the process referred to as echolocation for orientation and food acquisition (Griffin, 1958; Simmons *et al.,* 1979 and Neuweiler, 1989). Echolocation may also be used as a communication signal (Fenton *et al*., 1995; Schnitzler *et al*., 2003; Siemers and Schnitzler, 2004, Siemers *et al*., 2005).

All bats are capable of flight but not all bats utilize echolocation. Approximately 184 species depends mostly on vision (Novick, 1958; Griffin, 1958; Holland *et al*., 2004 & Yovel *et al*., 2011). Approximately 70% of all bats (Order: Chiroptera) are insectivorous (Lawrence, 1982 and Altringham, 1996). Others feed on a variety of food types such as frogs, fish, blood, nectar, scorpions, fruits and spiders (Bates and Harrison, 1997). Bats obtain their various kinds of food by employing different strategies which involve echolocation suited to the task at hand. Foraging modes employed by bats include aerial hawking, gleaning, perch-hunting and trawling, each requiring different echolocation strategies. Perch-hunting bats obtain their food by hanging from a perch and intercepting passing prey detected with their echolocation while aerial hawkers catch their prey while in flight either in open space, clutter edges or within vegetation (Neuweiler, 1984; Schnitzler and Kalko, 2001). Gleaners are able to detect and capture prey resting on the substrate including the ground and vegetation, and mostly rely on sounds generated by the prey (Tuttle and Ryan, 1981; Ryan *et al*., 1982; Belwood and Morris, 1987; Schnitzler and Kalko, 2001; ter Hofstede *et al*., 2008 and Jones *et al*., 2011), sometimes vision (Bell, 1985; Ekloef and Jones, 2003) and some would use ensonfying potential prey from various angles to overcome the masking effects of background echoes

(Geipel *et al*., 2013). Those that use trawling find their prey normally above water surfaces by detecting and classifying acoustic signals from prey (Neuweiler, 1984; Schnitzler and Kalko, 2001). The echolocation pulses emitted by trawling bats are usually reflected away from the bat because the water surfaces act as an acoustic mirror thus creating an echo-image with low or no clutter echoes which then enable efficient search of prey (Siemers *et al*., 2001; Siemers *et al*., 2005)

Bat foraging habitats are characterized by clutter conditions (i.e. obstacles such as tree branches and trunks, ground, foliage, water and vegetation) and these are the most significant ecological constraints. Foraging habitats are mainly categorized into three types based on the degree of clutter; open space (uncluttered space), edges of vegetation (background-cluttered space) and within/between vegetation (highly cluttered space) (Aldridge and Rautenbach, 1987; Neuweiler, 1989; Fenton, 1999, Schnitzler and Kalko, 1998; Schnitzler and Kalko, 2001). Various authors categorize bat foraging habitats slightly different. Aldridge and Rautenbach (1987) divided foraging habitat into seven different types viz. open areas, 0.5 m above water, over pasture, 0.5 m away from canopy, between trees, surface of vegetation and within vegetation. Neuweiler (1989) classified foraging habitat into six types namely; above canopy, open spaces between canopy, over water surfaces, close to and within foliage, foliage and ground. Fenton (1990) characterized foraging habitat into three main categories viz. open habitat, edge habitats and closed habitats while Schnitzler and Kalko (1998, 2001) also classified foraging habitat into three categories viz. Uncluttered or open space, background cluttered space or edge space and highly cluttered or narrow space.

Bats that hunt prey in open-space foraging habitats experience limited difficulties as they forage far away from obstacles and the returning echoes from the emitted sound signal are usually from a potential prey. They mostly receive interpretable acoustic information from the returning echoes of each emitted sound pulse (Brinklov *et al.*, 2011) Most of those bats adapted to foraging in open space habitats cannot hunt prey in other foraging habitat types i.e. highly cluttered environments (Aldridge and Rautenbach, 1987). The frequency of sound pulses emitted by bat species foraging in open-space habitat is low, travels far and the duration is long as the prey of interest are usually at a far distance (Jones, 1999). Low frequency calls are most suitable for detecting prey of larger size as the long wavelengths of these sound pulses are unlikely to generate echoes of sufficient intensity from small targets.

Species foraging in cluttered environments experience more difficulties as they receive a cascade of echoes from the background in which is embedded the echoes from the target (Moss and Surlykke, 2010). High frequency sound pulses are mostly used by bat species foraging in the edge space near or within vegetation (Pevey *et al.*, 2001; Siemers and Schnitzler, 2004 and Jung *et al.*, 2007). Bats foraging close to vegetation and therefore within high clutter face challenges as they have to discriminate between the echoes from prey and those from the background. Those that forage within or between vegetation clutter encounter more difficulties as they also have to avoid colliding with the obstacles. Foraging habitat therefore acts as the main determinant of echolocation signal structure in bat species (Neuweiler, 1989).

Bat species foraging in different habitats use different spectral and temporal parameters i.e. duration, peak frequency, inter-pulse interval (see Table 2.1) and duty cycle among others to increase resolution and maximum detection distance. The percentage of time (the duration of the echolocation pulse + time to the next echolocation pulse) in which bats emit their sound pulses is referred to as Duty Cycle (Fenton, 1999) and they are divided into Low Duty Cycle

(LDC) and High Duty Cycle (HDC) bats. LDC bats emit echolocation pulses that are of short duration relative to the interval between the current and the preceding sound pulse, while HDC bats emit echolocation pulses that are of long duration relative to the silent period between the echolocation pulses (Fenton, 1999). Aerial hawking bats such as *T. aegyptiaca* adapted to forage in open space habitats use echolocation pulses of long duration, narrowband with low frequency to increase maximum detection distance. Detection and classification of targets is crucial in open space habitats unlike in vegetation clutter where resolution is more important. The sensitivity of the inner ear make it likely to be damaged by echolocation pulses emitted at high enough source levels to generate an echo. Bats therefore employ two broad strategies to avoid masking. Some species avoid masking by separating echolocation pulse and echo in frequency (i.e. HDC bats) while others separate them in time (i.e. LDC bats). Low Duty Cycle bats contract the middle ear muscles during the emission of each echolocation pulse to protect the inner ear and relax the muscles between the pulses to restore sensitivity of the ear for the perception of the returning echoes (Wever and Vernon, 1961; Henson, 1965; Suga and Jen, 1975).

High Duty Cycle bats have an “acoustic fovea” a region of the auditory cortex (Schuller and Pollak, 1979). HDC bats adjust their echolocation pulse frequency due to the sensitivity of the neurons located in the acoustic fovea for unique and narrow range of frequencies referred to as reference frequency (Schuller and Pollak, 1979). During flight, as a result of bats velocity relative to a target, the echoes from the target return to the bat at a slightly higher frequency than the emitted echolocation pulse because of the “Doppler effect”. The bat thus lowers the frequency of its pulse so that the echo from the target returns at the reference frequency of its acoustic fovea, a phenomenon known as Doppler-shift compensation. Bat species in the family Molossidae and Vespertilionidae, of which the focal species for this study are members, use LDC echolocation pulses of narrow to broad bandwidth.

Atmospheric attenuation in the air has a significant effect on the operational range of bat echolocation. It depends mostly on atmospheric pressure, relative humidity, temperature and the frequency of sound (Lawrence and Simmons, 1982; Stilz and Schnitzler, 2012; Luo *et al.*, 2014). Atmospheric attenuation is the reduction or absorption of the energy in a sound as the sound propagates through the atmosphere, it increases with the distance over which the sound is propagated (Lawrence and Simmons, 1982). Atmospheric attenuation thus decrease the energy in an echolocation pulse as it travels away from the bat and also decreases the energy in the echoes, reflected off objects, as they return to the bat (Lawrence and Simmons, 1982). Low frequency pulses are less attenuated and travel a long distance compared to high frequency sound pulses which are severely attenuated (Lawrence and Simons, 1982; Luo *et al.*, 2014). Atmospheric attenuation of sound pulses at a temperature between 15 and 30˚C is weak while an increase in relative humidity results in an increase of atmospheric attenuation particularly for frequencies from 30 kHz to over 100 kHz (Lawrence and Simons, 1982). The magnitude of atmospheric attenuation decreases for sound pulses with a frequency below 30 kHz. The frequency composition of echolocation pulses has an effect on the bat's detection distance. The wavelengths of low frequency signals are long and are emitted by bat species which are relatively large. So the echolocation pulses frequency also varies with the body size and high frequency pulses are generally emitted by smaller bats.

The nature of the echoes that return to the bat is dependent on various acoustic conditions amongst others; target distance, frequency composition, size of the target, atmospheric attenuation and most importantly source levels of the emitted sonar waveform (Lawrence and Simons, 1982). Source levels of the echolocation pulses influence the maximum detection distance of bat’s potential prey and enable’s the return of audible echoes. Echolocation pulse source level is an important parameter for understanding the bat’s acoustic signal strength, the range at which bats can detect prey and background targets, and is usually expressed in decibels (dB) peSound Pressure Level (peSPL) at a standard reference distance of usually ten centimetres (10 cm) from the source (Holderied & von Helversen, 2003; Parsons, 2010). There is limited data on the echolocation pulse source levels of bats living freely in the natural environment presumably due to the technical difficulties particularly for bat species foraging high in open spaces. Most previous studies have investigated the role of bat echolocation pulse source levels in laboratory conditions rather than in their natural habitat, either hand held at a stationary known distance from the recording microphone or flying in the flight room. Studies conducted on echolocation pulse source levels of bat species flying freely in their natural habitats appear to yield higher source levels than handheld or stationary bats in lab environments.

The work conducted by Griffin (1958) and Novick (1958) on bat echolocation pulse source levels were mostly limited by the technological equipment available at that time, but importantly they provided data on echolocation pulse source levels between bat species. Griffin (1958) classified bats into two groups using the sound recordings obtained from hand-held bats viz. whispering bats (producing source levels of around 70 dB SPL) and loud aerial insectivores (generating source levels of up to 110 dB SPL) at a 10 cm reference distance from the mouth of the bat. Recent advances in technology allow the use of multi-microphone arrays to study how bats vary the source levels of their echolocation pulses in the wild while pursuing prey or when echolocating in different foraging habitats. Although the source levels of most bat species are not known, studies reporting source levels for different bat species are accumulating gradually and show that bats are using much higher source levels than previously suspected. For example Holderied and von Helversen (2003), of all species in their study i.e. *Nyctalus lasiopterus*, *Eptesicus nilssoni*, *Hypsugo savii*, *Pipistrellus kuhli*, *Nyctalus leisleri*, *Nactalus noctula*, *Eptesicus serotinus*, *Pipistrellus pipistrellus*, *Pipistrellus nathusii*, *Pipistrellus pygmaeus* and *Miniopterus schreibersi* were found to be emitting intense echolocation pulses of at least 124 dB peSPL. They found *N. lasioperus,* the heaviest and *P. pygmaeus*, the lightest bat species to be emitting echolocation pulses with the maximum SL of 133 dB peSPL and 128 dB peSPL respectively. Holderied *et al.* (2005) found *Eptesicus bottae* to be emitting echolocation pulses with a maximum source level of 133 dB peSPL during the search phase. Jensen and Miller (1999) calculated the source level of the range between 121 and 125 dB peSPL for *Eptesicus serotinus*. Surlykke *et al.* (1993) recorded source levels ranging from 100 to 115 dB peSPL for two species of bat belonging to the superfamilies Emballonuroidea (*Craseonycteris thonglongyai*) and Vespertilionoidea (*Myotis siligorensis*). Surlykke and Kalko (2008) have also recorded considerably higher source ranging from 122 - 134 dB SPL for Emballonuridae (*Saccopteryx bilineata*, *Saccopteryx leptura*, *Cormura brevirostris* and *Centronycteris centralis*), Mormoopidae (*Pteronotus gymnonotus*), Molosidae (*Molossus molossus*) and Vespertilionidae (*Lasiurus ega*, *Myotis albescenes* and *Myotis nigricans*) levels compared to predictions made by Griffin (1958) in several aerial hawking bat species. Two bat species in the family Noctilionidae (*Noctilio albiventris* and *Noctilio leporinus*) were recorded emitting echolocation calls with an average source level of 137 dB SPL and maximum levels above 140 dB SPL the loudest recorded for any bat (Surlykke and Kalko, 2008) . All the above examples of echolocation pulse source levels reported in previous studies were conducted at a 10 cm standard reference distance from the bat mouth.

Echolocation pulse source levels play a crucial role in the maximum detection distances of foraging bats. However, the maximum detection distances are also affected by the dynamic range, frequency of the echolocation pulses, atmospheric conditions (i.e. temperature, relative humidity, atmospheric pressure) and target size (i.e. small, medium or large). The dynamic range, the amplitudinal range of a bat's sonar system between sound emission level and auditory threshold (Stilz & Schnitzler, 2012), affects maximum detection distances because an echolocation pulse with greater amplitude would be louder to the bat than those with small amplitude depending on the bat's auditory threshold. A study by Stilz and Schnitzler (2012) found that frequency is a dominant factor influencing a bat's detection distance with atmospheric attenuation having a major impact comparable to Generalized Geometric attenuation (GGA). GGA is a model used to calculate attenuation of bat's echolocation pulse as a result of energy absorption by the target, geometric spreading and scattering and to compensate for the effects of such attenuation on the distance at which the bat detects targets (Stilz and Schnitzler, 2012).

However, despite the importance of source levels to bat foraging source levels of echolocation pulses are only known for a handful of bats globally and there is limited data on the source levels for African bats. This study therefore aimed to record echolocation pulses of two of the most common LDC echolocating, insectivorous South African bat species, the Cape serotine, *Neoromicia capensis* (Family Vespertilionidae), and the Egyptian free-tailed bat, *Tadarida aegyptiaca* (Family Molossidae, Figure 2.1). These recordings were used to measure the temporal and spectral parameters (Table 2.1) of the echolocation pulses of these species for use in the calculation of echolocation call source levels and maximum detection distances in different situations. Both species are aerial hawkers but hunt in different habitats.

The study will contribute to the accumulation of data on the echolocation source levels of free-flying bats and will improve our knowledge of how bats adjust pulse parameters to increase their operational range. The acoustic signal data will assist in monitoring and managing programmes which aims at assessing the use of habitat, diversity and abundance of the aerial insectivore's species of bats. Insectivorous bats are adapted to hunt prey in various foraging habitats. These foraging habitats play a role in the design of various bat echolocation call parameters such as frequency and source levels. The knowledge of how foraging habitat affect bats can be used in the protection of foraging habitats thus contributing to the conservation of these bat species. This research study aims to investigate the effect of body size and foraging habitat on echolocation pulse of small, clutter-edge forager (*N. capensis*) and a large open-space forager (*T. aegyptiaca*) and to measure the echolocation pulse source levels of both species in two different situations, emerging from the roost and foraging.

In summary, this study has attempted to answer the following questions; (1) are source levels of animal acoustic signals different in different situation? (2) are source levels influenced by body size and foraging habitat? The study hypothesized that the echolocation pulse source levels will vary in different situation and the source levels of animal acoustic signals would be influenced by foraging habitat and body size. I predicted that; (1) the echolocation pulse source levels would be higher in the bat's respective foraging habitats than when emerging from the roosts. (2) *T. aegyptiaca*, a bat species with a larger body size and an open air aerial hawker would have higher echolocation pulse source levels in their acoustic signals and therefore have greater detection distances than *N. capensis*, a bat species with a small body size and clutter edge aerial hawker.

CHAPTER 2

Materials and Methods

Ethical statement

The study didn't involve capturing or handling of bat species in the field. No ethical clearance was required and license/permit (Permit no 0028-AAA043-ooo11) was granted by Cape Nature to work in a protected areas.

Study area

Field work for this study was conducted at De Hoop Nature Reserve (30˚26'S 20˚37'E) in the Western Cape Province, South Africa (Figure 2.1) from the 22nd to the 31st March 2016 and 17th March 2017 to the 7th April 2017. The DHNR receives an annual rainfall of the range 250-530 mm (Mucina and Rutherford, 2006), and the amount of rainfall is slightly higher during winter and autumn compared to the months of December, January and February where it is at its lowest point (Mucina and Rutherford, 2006). Mucina and Rutherford (2006) classified the vegetation type in the DHNR as De Hoop Limestone Fynbos. The reserve also contains one of the largest areas of the rare lowland Fynbos and Sclerophyllous vegetation. The De Hoop Nature Reserve is a home to South Africa's largest known bat colony comprising of approximately 200000- 300000 individuals in the De Hoop Guano Cave (McDonald *et al*., 1990).

The following seven species of bats are known to occur at the De Hoop Nature Reserve in the Western Cape Province, South Africa viz. *Myotis tricolor* (Temminck's myotis), *Rhinolophus capensis* (Cape horseshoe bat), *Rhinolophus clivosus* (Geoffroy's horseshoe bat), *Miniopterus natalensis* (Natal long-fingered bat), *Nycteris thebaica* (Egyptian slit-faced bat), *Tadarida aegyptiaca* (Egyptian free-tailed bat) and *Neoromicia capensis* (Cape serotine).

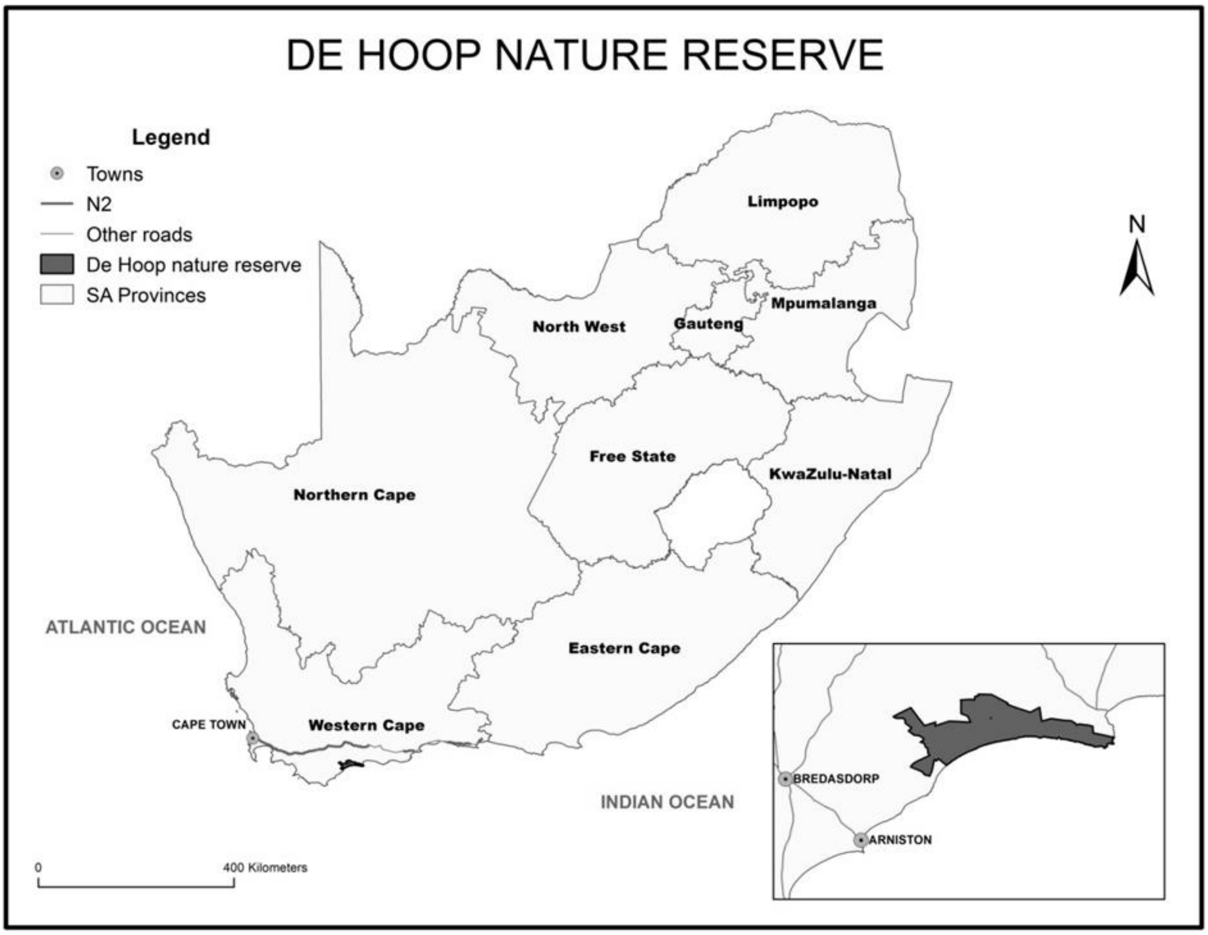

Figure 2.1: Map showing the location of the De Hoop Nature Reserve situated in the Western Cape Province of South Africa where echolocation sound pulses were recorded.

Study animals

Neoromicia capensis (Figure 2.2 b) is a small bat belonging to the most diverse family of bats, the Vespertilionidae, with a mass of approximately 7 grams. It is wide spread and abundant in the sub-Saharan Africa (Barnett and Prangley, 1997; Jacobs *et al*., 2014), occupying a range of habitats, from forests to deserts and savannah to montane grasslands. It has been found to be roosting in man-made structures such as the crevices in roofs of houses, in the base of leaves of mainly aloe plants and in trees particularly under the bark and in hollows in the tree trunk. *Neoromicia capensis* forages on the edges of vegetation and its diet consists mainly of the following Orders of insects; Diptera, Hemiptera, Neuroptera and

Coleoptera. *Neoromicia capensis* use high frequency pulses as it forages on the edges of vegetation where the main focus is on resolution and less on increasing detection range. The diet of *N. capensis* is influenced by seasonal changes and geographic variation (Schoeman and Jacobs, 2003). *Neoromicia capensis* emits Low Duty Cycle-Frequency Modulated (LD-FM) sound pulses with an intermediate duration (5.1±1.3 ms, n=10), intermediate peak frequency (39.4±1.6 kHz, n=10) and narrow bandwidth (14.4±3 kHz, n=10) (Schoeman and Jacobs, 2003)

Tadarida aegyptiaca (Figure 2.2 a) is an open-space forager flying high above the ground and vegetation clutter, covering extensive distances and large areas during foraging. They are recognized as the fastest flyers (Neuweiler, 1984) amongst free-tailed bats (Family Molossidae). The body mass of *T. aegyptiaca* is approximately 16 grams and has a widespread distribution throughout the Southern Africa. Studies conducted on the altitude at which echolocating bats forage have provided evidence that many species of bats particularly of the family Molossidae forage for prey at altitudes as high as 100-3000 m (Davis, 1962; Williams *et al.*, 1973). This species roosts in caves, cavities in trees, rock crevices and in the roofs of man-made structures such as buildings (Shortridge, 1934; Herselman and Norton, 1985; Skinner and Chimimba, 2005).

Tadarida aegyptiaca feeds mainly on the Coleoptera, Diptera and Hemiptera (Fenton and Thomas, 1980; Fenton, 1985; Schoeman and Jacobs, 2003; Schoeman, 2006). *Tadarida aegyptiaca* produces low frequency pulses to maximize detection distance it forages in open space habitats. The echolocation signals are Low Duty Cycle, quasi-constant frequency (LDC-QCF) in structure; the energy is mainly focused on a narrow bandwidth to maximize detection distance.

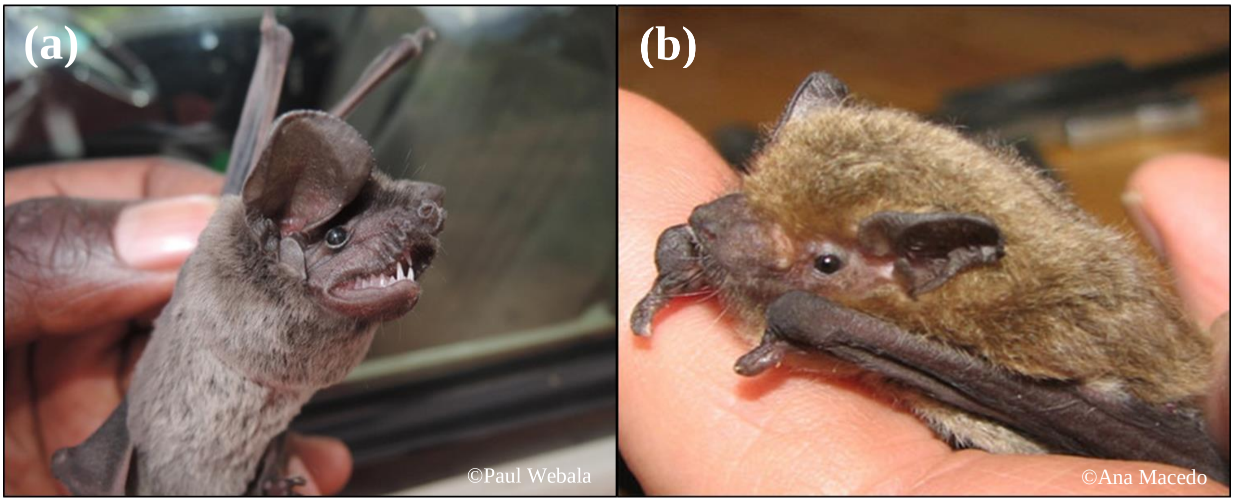

Figure 2.2: The two focal species of bat used in this study, *Tadarida aegyptiaca* (a) and *Neoromicia capensis* (b).

We recorded *N. capensis* and *T. aegyptiaca* as they emerged from their respective roosts and at various foraging sites, both roosts and foraging sites were identified previously by David Jacobs. The presence of feeding buzzes, marked by rapid call rates and decreased bandwidths (Balcombe and Fenton, 1988), at the identified foraging sites was taken as an indication that bats were in fact foraging. The echolocation calls of most of the other species that occurred at DHNR are very different to those of the two focal species. However, there was as at least one other species for each of our focal species that could be confused with one or the other of our focal species. The echolocation pulses of *T. aegyptiaca* and *N. capensis* were however very different from each other. Roosts for the two bat species were known because these species has previously been captured and their echolocation pulses recorded by David Jacobs in the study area. The bats sound pulses were recorded in several locations within the DHNR i.e. open spaces, man-made structures (House buildings), cave (Hothole cave) and in the edges of the vegetation clutter close to water source. The roosts in the man-made structures were visually identified by the presence of bat droppings on the walls and brown discoloration from the body oil of the bat on the sides of crevices between the wall and roofs of the buildings used by the bats. In the present study, both species were recorded as they left their respective roosts and either foraging at the edge of vegetation (*N. capensis*) or in open space (*T. aegyptiaca*). To avoid damaging the microphones and getting poor quality pulse recordings, recording was only done on rainless nights with low winds and areas of high bat activity were avoided.

Data collection

To record the echolocation pulses emitted by free-flying insectivorous bats, *N. capensis* and *T. aegyptiaca,* a state-of-the-art multiple microphone arrays (Figure 2.3 and Figure 2.4) custom built at the University of Cape Town, South Africa was used. Depending on the target species, the microphone arrays were placed at a known distance from each other and height. For recording *N. capensis,* the microphone array (Figure 2.3) was set at a height and distance of approximately 0.8 m and 2 m, respectively from the roost. The system records bat echolocation pulses as it arrive at each microphone and depending on the position of the bat relative to the arrays, echolocation pulses arrive at each of the microphones at different times (Holderied and von Helversen, 2003). The time of arrival differences (TOADs) at each microphone are used to determine the position of the bat relative to the centre microphones (microphones 1 and 5 in Figure 2.3 and Figure 2.4). These TOADs are accurately determined by using a cross correlation function as described by Holderied and von Helversen (2003) using custom scripts in MATLAB 8.1 (The Math Works Inc., Natick, MA, USA) written by Marc Holderied.

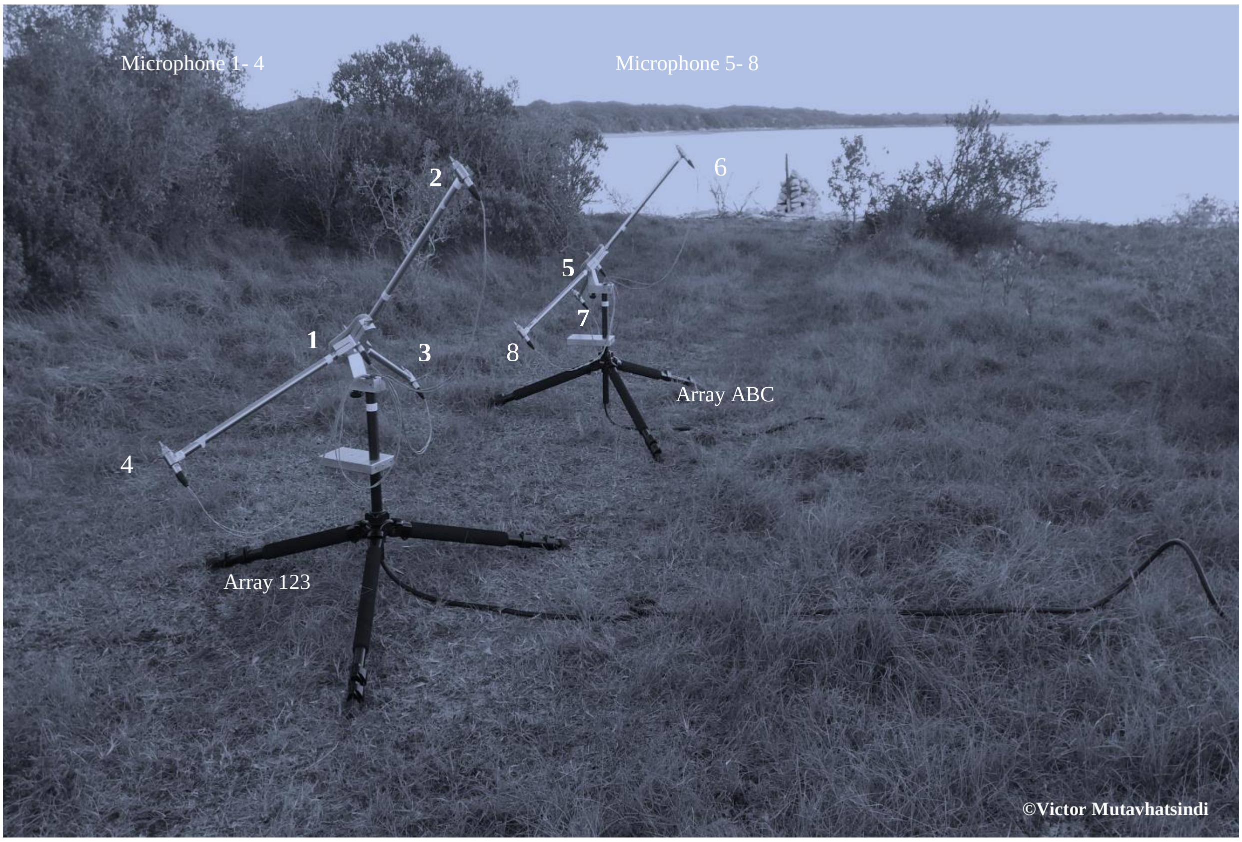

Figure 2.3: Multiple microphones array setup at the edge of a vegetation clutter targeted to record a clutter-edge aerial hawker, *Neoromicia capensis.*

The use of multiple microphone arrays is one of the recent technological advances which allow new insights into adaptive bat echolocation call structure (Jones and Holderied, 2007). The multiple microphone array system used in this study consisted of two arrays, each having four microphones arranged in a symmetrical star (Figure 2.3 and Figure 2.4). In total the microphone array system consisted of eight Knowles FG-O omnidirectional electret ultrasound microphones (Avisoft Bioacoustics, Knowles FG-O, Berlin, Germany). The centre piece of both arrays was covered with high frequency sound absorbing foam. The height and distance (Figure 2.4) measurements for the microphone array targeted to record *T. aegyptiaca* were set at approximately 1.9 m and 3 m, respectively.

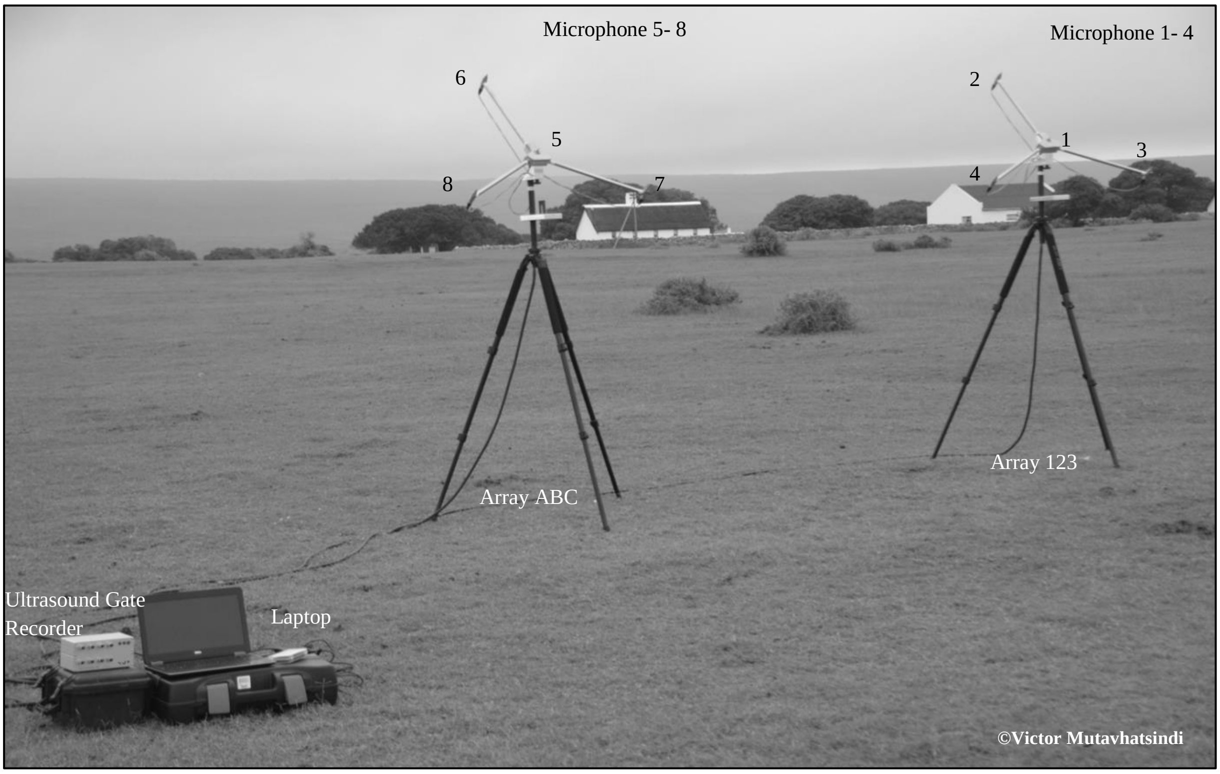

Figure 2.4: Multiple microphone array setup in an open space habitat targeted to record an open-air aerial hawker, *Tadarida aegyptiaca*.

The data for the two arrays were recorded i.e. angle (˚/degrees) of the arrays relative to each other, distance (meters) of the arrays from each other, height (metres) of each array measured from the ground to the centre microphone and the middle height, the height measured from the ground in the middle of distance between the arrays to the point of the centre stage of the array. A weather station (Professional Weather Centre, Model WMR200A, Oregon Scientific Inc., Tualatin, Oregon, USA) was set-up (Figure 2.5) on each site whenever echolocation pulses were recorded to continuously record atmospheric pressure (kPa), Temperature (˚C), humidity (%), wind speed and direction ($m.s^{-1}$).

The weather data were recorded each time echolocation pulse was being recorded and allowed the documentation of actual atmospheric conditions when each pulse was recorded. This allowed the more accurate adjustment of source levels with respect to atmospheric attenuation.

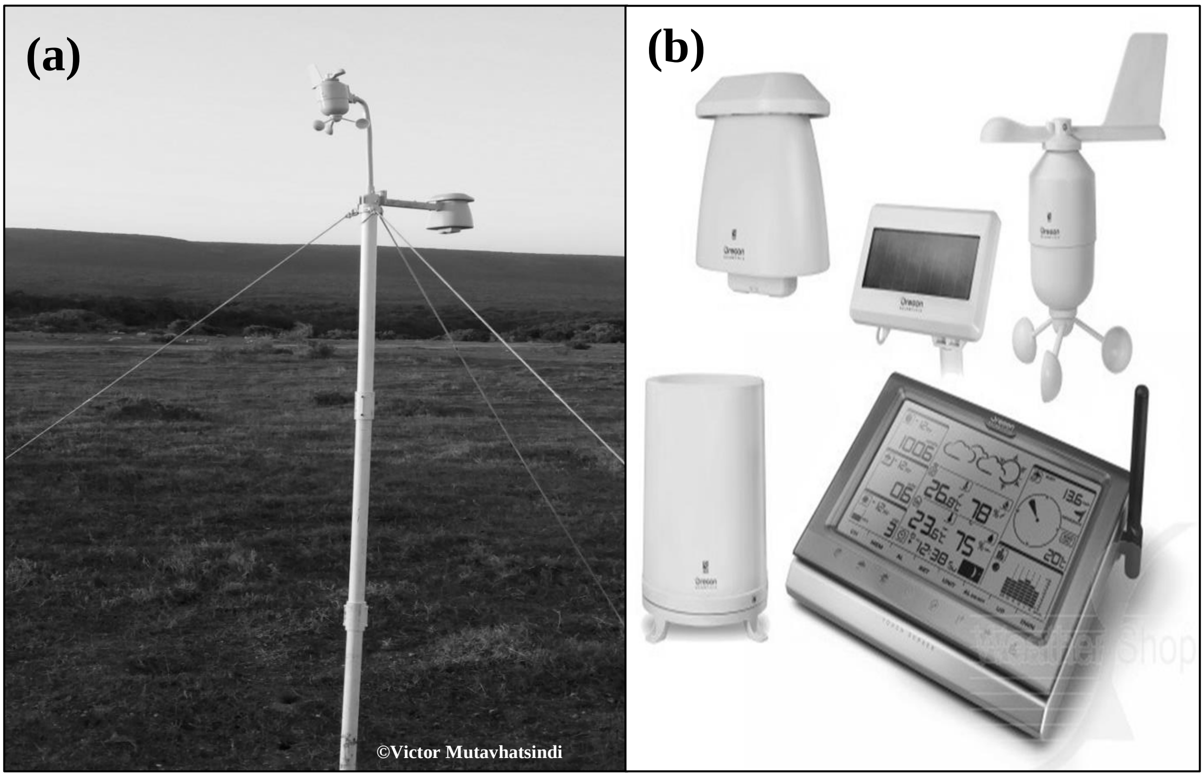

Figure 2.5: The weather station used in the field (a) and the components of the weather station (b) to measure weather conditions (i.e. temperature ˚C, relative humidity %, atmospheric pressure Pa, wind speed m/s and wind direction.

The microphone arrays were placed roughly perpendicular to known bat flight routes, within a distance of not less than 5 meters from their roost to ensure that they flew more or less straight towards the microphone arrays. Bat sounds were recorded using a real-time 8-channel recorder, Avisoft UltraSoundGate 816H (Avisoft Bioacoustics, Germany) at a sampling rate of 300 kHz and a resolution of 16 bits connected to the omnidirectional electret ultrasound microphones (Avisoft Bioacoustics, Knowles FG-O). The UltraSoundGate was connected to the Dell Laptop (Model: Vosstro 14 5000 series, serial number: 134067774078, Dell, South Africa) and the recordings were manually triggered when high quality pulse sequences were observed on the laptop’s real time spectrogram. The power to the UltraSoundGate Recorder was supplied by the Laptop used during the recording. The echolocation signals were recorded via Avisoft recording software (Avisoft-SASLAB Pro Version 5.2.09, Germany) installed on the same Dell Laptop. All the echolocation pulse recordings were automatically stored in a laptop's hard drive during recording and were then copied and stored in multiple external hard drives.

The echolocation pulses recording were started immediately after dusk each day and recorded for a minimum of one hour to a maximum of three hours. The echolocation pulses were not recorded for more than 3 hours to avoid recording the bats that might be returning to the roost several times. The bats usually emerged from their roosts at about 19h00 each day. Analyses were based on passes rather than numbers of bats so pseudo-replication could not be completely avoided, although observations when there was still enough light and sequence of bat pulses on the screen of the laptop suggested multiple bats. Calibration of each microphone was conducted 360˚ in the vertical and horizontal planes in the laboratory (Marc Holderied's lab, Bristol University) at different ranges of temperature and relative humidity to account for differences in the frequency response of each microphone as well as difference in polar sensitivity of microphones. Microphones were also calibrated in the field after every recording session using a 40 kHz (84 dB SPL) signal generator (Pettersson Elektronik, Sweden) at a distance of 0.25 meter, following the recommendations of the supplier. Microphones were not calibrated before recording to avoid interfering with the microphone array system once it was setup.

Acoustic analysis

The initial classification of recorded bat echolocation pulses were assigned to different species based on the peak frequency as previously reported in the literature (e.g. Schoeman & Jacobs, 2003; Schoeman & Jacobs, 2008). However, because other bat species occur in the study area which have slightly overlapping echolocation peak frequencies with those of the two focal species (*N. capensis* and *T. aegyptiaca*), a Principal Component Analysis (PCA) followed by Discriminant Function Analysis (DFA) was done on peak frequency and several other echolocation call parameters to ensure that echolocation calls were assigned to the correct species. PCA was mainly for transforming a number of possible correlated variables (i.e. all measured echolocation call parameters) into the same number of independent uncorrelated variables so that a DFA could be done. The DFA was then performed on the principal components to correctly assign calls to the different species.

Echolocation pulse parameters were measured using the Automatic Parameter Measurements tool in Avisoft-SASLAB Pro (Version 5.2.09). Sound files with high quality echolocation pulse (i.e. high signal to noise ratio) were considered for evaluation. Sequences typically contained five or more echolocation pulses. The frequency range for *N. capensis* and *T. aegyptiaca* was between 35-45 kHz and 18-25 kHz, respectively. Long duration (> 5 ms) echolocation pulses with a peak frequency of ≥ 25 kHz were assumed to be of *Sauromys petrophilus*, a species which is suspected of occurring in the study area, and not measured. Sound recordings of *N. capensis* were filtered to remove the background noise outside the echolocation pulse range (Low-pass frequency: 65 kHz and High-pass frequency: 25 kHz, Window type: Hamming). *Tadarida aegyptiaca* recordings were also filtered to remove the background noise outside the echolocation pulse range (Low-pass frequency: 35 kHz and High-pass frequency: 11 kHz, Window type: Hamming). After filtering, all the echolocation signals were manually edited to completely remove all the background noise. Detailed measurements of time and frequency parameters were performed in Avisoft-SASLAB Pro (Version 5.2.09, Avisoft Bioacoustics, Berlin, Germany) using the Automatic Parameter Measurement tool of the spectrogram window (.Avisoft-SASLAB Pro).

All the spectral and temporal measurements were calculated to a threshold of -20 dB relative to a max of -25 dB. The echolocation pulse parameters such as pulse interval, frequency, signal duration and bandwidth are mostly related to a foraging habitat (Jones and Holderied, 2007). All the parameters were measured from spectrogram, and only from the first harmonic because the energy were more concentrated on it compared to the second harmonic. Measurements of call parameters performed on the spectrograms have limitations because spectrograms are usually a trade-off between spectral and temporal accuracy (Zollinger et al., 2012). However, for the purpose for which I used these sets of parameters the accuracy is adequate. Firstly, only frequency was used in calculation of source levels and the detection range, and a change in frequency of 10 kHz resulted in only a 0.6 dB (i.e. 123.5 dB changed to 122.9 dB) change in source levels and only a 2.1 m (i.e. 10.9 m changed to 8.8 m) change in detection range. Secondly, the frequencies obtained in this study were comparable to those reported in other studies for the same species but measured from power spectra (e.g. Schoeman & Jacobs, 2003 & Schoeman & Jacobs 2008), with differences much less than the 10 kHz we used here to test the impact error on our results.

Spectrograms for analysis of the two species were generated using the FlatTop window, Fast Fourier Transform length (FFT length) 256 points, frame size 100% and overlap 50%. A short description of acoustic parameters of the sonar sounds measured for the two bat species are shown in Table 2.1. The following frequency parameters were measured at various locations viz. start, end and point of maximum amplitude within bat echolocation pulses; peak frequency, peak amplitude, minimum frequency, maximum frequency and bandwidth. Distance from start to max also called “*DistoMax*” is the time (i.e. “distance” in ms) from the start to the maximum amplitude of an echolocation pulse. DistoMax has mainly been used in literature (e.g. Knömschild *et al*., 2010) as a means of characterizing bat echolocation pulses. Measuring many different call parameters, such as DistoMax in this study was to ensure that when performing Principal Component Analysis (PCA) and Discriminant Function Analysis (DFA) there are enough variables to allow reliable classification of echolocation pulses as belonging to one or the other bat species.

Table 2.1: Echolocation pulse parameters measured from *Neoromicia capensis* and *Tadarida aegyptiaca* using the Automatic Parameter Measurements tool of Avisoft-SASLAB Pro (Avisoft Bioacoustics, Berlin, Germany).

Call parameter	***Description***
Duration (ms)	The time from the start to the end of an echolocation pulse.
Peak-to-peak amplitude (kHz)	The distance from a negative to a positive peak (amplitude) of an echolocation pulse in a waveform.
Peak frequency (kHz)	The frequency of the maximum amplitude of the spectrum
Min frequency (kHz)	The frequency at which the amplitude first goes below the threshold (when one moves from the maximum down to low frequencies).
Max frequency (kHz)	The frequency where the amplitude first goes below the threshold (when one moves from the maximum up to high frequencies).
Pulse interval (ms)	The time between the start of one echolocation pulse to the start of the next echolocation pulse in a sequence.
Bandwidth (kHz)	The difference between maximum frequency and minimum frequency.
Distance from start to max (ms)	The distance measured from the start of an echolocation pulse to the point with maximum amplitude also called ‘Distomax’.

Determination of echolocation pulse source levels

Echolocation sound recordings analyses and reconstruction of three-dimensional (3-D) acoustic flight paths were performed using a custom-made MATLAB 8.1 (The Math Works

Inc., Natick, MA, USA) functions/script ‘CalcSourcelevel.m’ (written by Marc Holderied). Temperature, atmospheric pressure and relative humidity were measured at the same time as the field recordings. Thus for each echolocation pulse emitted by the bat there were temperature, atmospheric pressure and relative humidity measurements. These measurements, in combination with call frequency, were inserted into the Matlab script which used the formula in (Bazley, 1976) to calculate the frequency dependent atmospheric absorption. This was then used in combination with the distance to the recording microphone in the estimation of source levels.

The flight path reconstruction was used to determine the position of the bat’s signal emission using time of arrival difference (TOAD) at each of the eight microphones, taking into consideration the environmental conditions and array measurements. Knowing the position of the bat at the time echolocation pulses were emitted allowed estimation of the distance between the bat and the recording microphone thus enabling the calculation of the source levels while adjusting for atmospheric attenuation. Only the sequences where the bat approached the arrays from the front were analysed while those when a bat approached the arrays from the back were not included in the analyses. The approach of only considering echolocation call sequences when the bat is approaching the microphone arrays from the front doesn’t compensate for directionality. A bat might still emit echolocation pulses in front of the microphone arrays but off axis to the microphones. Therefore, to attempt and compensate for any directionality echolocation pulses with maximum source levels in each sequence but in all likelihood the reported source levels are lower estimates. Best trajectories with individual points supporting each other in speed and space were used for analyses, because the narrowband echolocation sound pulses of high flying bats (in particular *T. aegyptiaca*) are extremely difficult to track accurately and that is likely to cause location errors.

The 3-D acoustic tracking path was cleaned by deleting any erroneous points. Whether the bat was flying from the front or behind of the microphone was easily observed through the creation of 3-D acoustic flight path. The sensitivity of the microphones is stronger on the front than any other side thus focusing on echolocation pulses where the bat was approaching the microphones enables avoidance of differences in the source levels that might be as a result of echolocation pulses coming from other angles. The echolocation pulse source levels was firstly determined at the microphones and then from this the source levels [Sound Pressure Level (SPL)] and expressed in decibels (dB) at 10 cm in front of the bat’s position was calculated using the distance to the microphone while adjusting for atmospheric attenuation. The source levels were calculated following the methods of Holderied and von Helversen (2003). For further analysis, only echolocation pulse with the highest value of source level in a sequence of the reconstructed flight paths of the two bat species, *N. capensis* and *T. aegyptiaca* were used. Instead of using the average source levels of all echolocation pulses in a sequence I used the loudest pulse in a sequence assuming that is the maximum source level of that bat. The use of the maximum source levels in a sequence was as an attempt to minimize any directionality even though this technique doesn’t necessarily and absolutely compensate for directionality. This is true because a bat can still emit its echolocation pulse in front of the microphone array but off axis hence the source levels in this study are likely an underestimate.

Determination of maximum detection distances

The detection ranges of the two bat species were estimated using an online calculator (http://134.2.91.93/~peter/calculator/range.php), which is a computer implementation of the method developed by Stilz and Schnitzler (2012). The web calculator estimates the maximum detection distances using various variables viz. atmospheric conditions (relative humidity %, temperature ˚C and atmospheric pressure Pa) and sound properties (frequency Hz, source levels dB SPL); and has an inbuilt algorithm to calculate energy absorption constant of the target-C1 and two-way geometric spreading constant between a bat and target-C2. The calculator also provides the degree of atmospheric attenuation in decibels dB [SPL root-mean-square] over the estimated maximum detection distances calculated from the inputs same as of above. The maximum detection distances were estimated for three different prey size categories with different target strength (TS) viz. Large (TS= -40 dB), medium (TS= -50 dB) and small (TS= -65 dB) following the approach explained in Stilz and Schnitzler (2012). Since the online calculator based on this approach use intensities measured at 1 m from the bat whereas the intensities reported here are based on the standard reference distance of 10 cm, the intensities were converted to a reference distance of 1 m for use in the online calculator. Target strength is influenced by the ratio of target size to wavelength of the sound pulse. A solid sphere for an example with a diameter of 4 cm has target strength of -40 dB at 1 m which is equivalent to target strength of -20 dB at 10 cm.

The size of an insect prey or target affects the maximum detection distances at which bats can detect an echo from the particular target or insect prey; usually, the smaller the insect/targets the weaker the echo and the larger insect/target the greater the echo. The maximum range is also dependent on the specific echolocation pulse frequency used by the bat. The point-reflector function which best explain the differences in detection range of insect was used to estimate the maximum detection distances. The three prey sizes were considered because a bat foraging in an open space is likely to detect a large prey, medium and small while those that forage close to vegetation clutter are likely to detect small and medium prey as they use calls of low and high frequency respectively. Various studies have estimated different detection thresholds (DTs) ranging from 0 to 59 dB. The DT for bat species in the current study was assumed to be 0 dB in line with other studies (e.g. Coles *et al.*, 1989; Kick, 1982;

Neuweiler *et al*., 1984; Holderied & von Helversen, 2003). A signal pulse having the highest source level in a sequence of the calculated source levels and its peak echolocation pulse frequency was used for calculation of the detection range as described in Holderied and von Helversen (2003). Accordingly, the maximum detection distances of the two bat species, *N. capensis* and *T. aegyptiaca* were estimated while foraging.

Statistical analysis

All statistical analyses were conducted using the analytics software package, STATISTICA 13.0 (TIBCO Software Inc., Hillview Avenue, Palo Alto, USA). A Principal Component Analysis (PCA) on the echolocation pulse parameters was conducted to extract independent principal components. A Discriminant Function Analysis (DFA) was performed on these principal components to reliably classify the echolocation pulses into their respective species. The echolocation pulse parameters were standardized before the PCA and DFA analysis in Microsoft Excel spreadsheet. To ensure that the source levels obtained were not influenced by e.g. background noise and low quality of the recorded echolocation pulses, i used simple linear regression to test the effect of wind speed (m/s), peak frequency (Hz), distance (m) of the bat to the arrays and the quality (dZ/r %) of the echolocation pulses on source levels. The data were log transformed (base ten) because of the differences in measurement scales. A Factorial Analysis of Variance (ANOVA) in General linear model (GLMs) was applied to evaluate variation in the source levels and maximum detection distances between the two different situations type (emergence from the roost and foraging).

CHAPTER 3

Results

Structure of the echolocation pulse

In all the situations, i.e. roost emergence and foraging habitats, good quality echolocation sound pulses for both *N. capensis* and *T. aegyptiaca* (Figure 3.1 & Figure 3.2) were recorded. Figure 3.1 and 3.2 shows typical echolocation search phase pulse for the two bat species as they flew freely in the field.

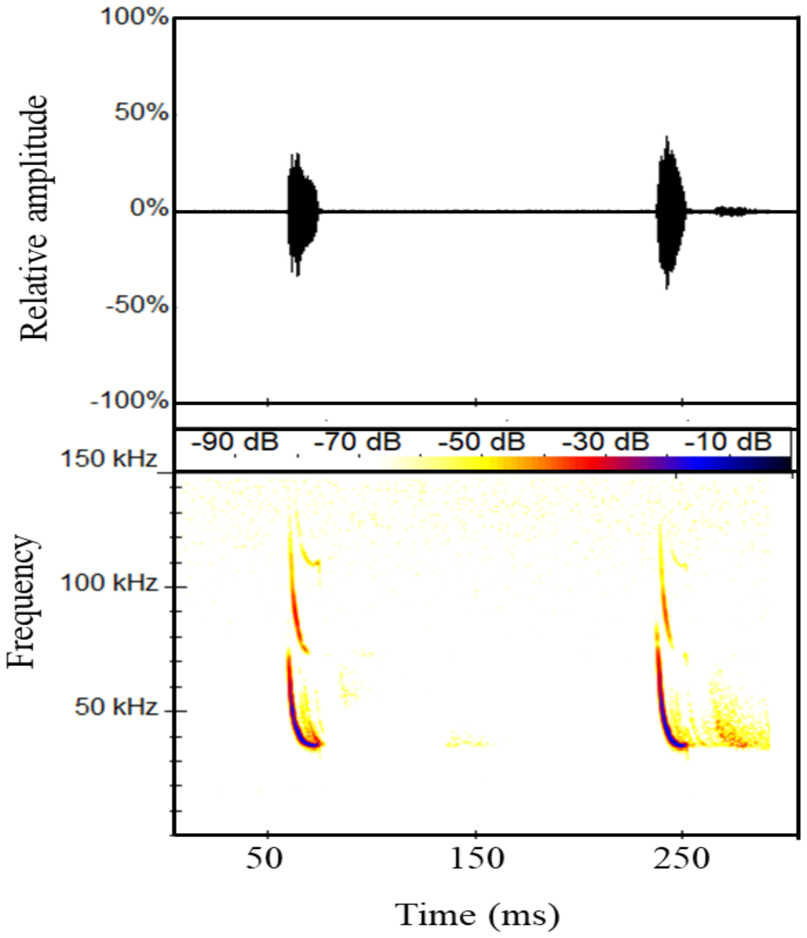

Figure 3.1: The spectrogram (bottom) and oscillogram (top) of search echolocation pulse recorded in the field from the clutter-edge aerial hawking bat, *Neoromicia capensis*.

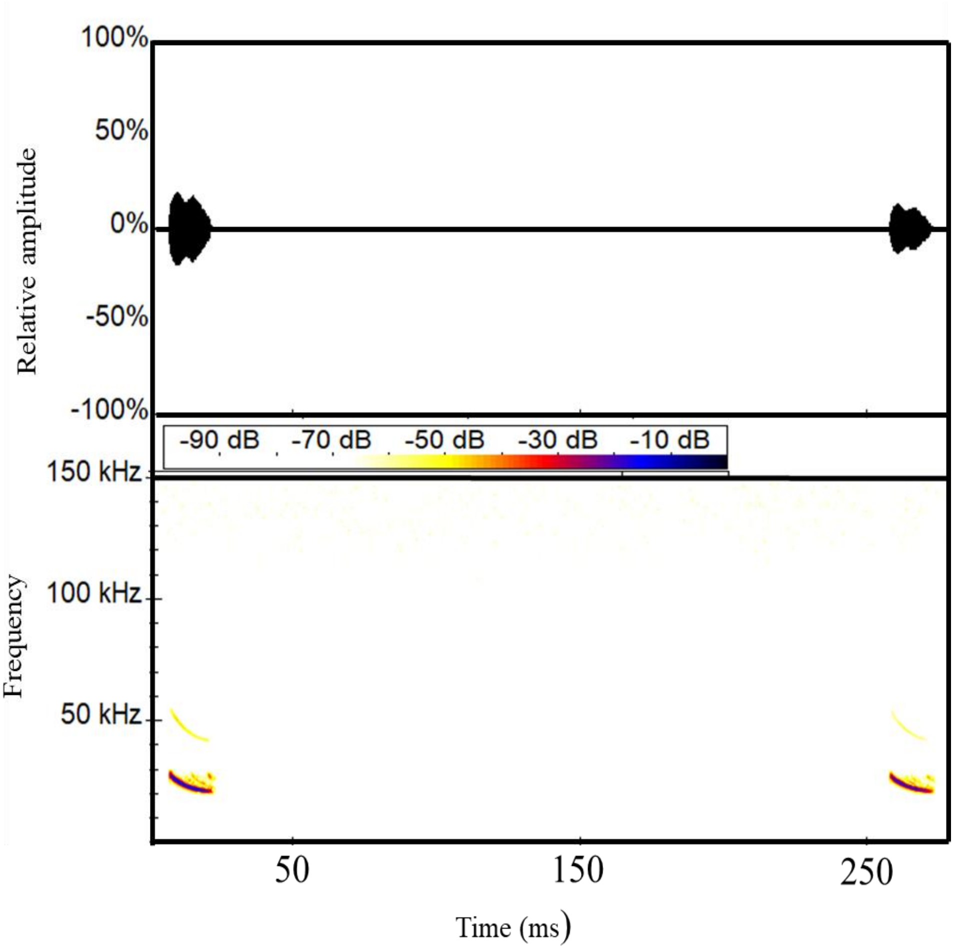

Figure 3.2: The spectrogram (bottom) and oscillogram (top) of typical search phase echolocation pulses recorded in the field from the open-air aerial hawking bat, *Tadarida aegyptiaca.*

The echolocation pulses of the two insectivorous bat species, *N. capensis* and *T. aegyptiaca* were predominantly of the frequency modulated (FM) and quasi-constant frequency (QCF) type, respectively, with both usually having the first (1st) harmonic and second (2nd) harmonic. Sometimes the echolocation sound pulses would have more than two harmonics but most energy was always concentrated in the first harmonic. The echolocation pulses of *N. capensis* were mostly shorter in duration and the peak frequency much higher than those of *T. aegyptiaca* (Figure 3.1 and Figure 3.2).

Assigning echolocation pulses to species

A Principal Component Analysis (PCA) on the echolocation pulse parameters of *N. capensis* and *T. aegyptiaca* was done to extract 19 independent and uncorrelated factors from the original set of 19 variables to meet the assumptions of a Discriminant Function Analysis (DFA). DFA was done on the factor scores (Table A1) of the three principal components which had an Eigenvalue ≥ 1 (Kaiser's criterion; Kaiser 1960; Table A2) to reliably assign pulses to species. On the basis of which variables loaded the highest on each principal component, PCA Factor 1 corresponded to the min freq. (start), max freq. (start), peak freq. (max), min freq. (max) and max freq. (max); PCA Factor 2 corresponded to peak ampl. (start), max freq. (start), peak ampl. (end) and peak ampl. (max); PCA Factor 3 corresponded to bandw. (end) and bandw. (max) (Table A1). The initial classification of the pulses into species was based on the peak frequency of the echolocation pulse. Species with a peak frequency of between 35-50 kHz were classified as *N. capensis* and those with a peak frequency ≥ 50 kHz were classified as *Miniopterus natalensis*, a species which co-occurs in the study area. Pulses with a peak frequency of between 18-25 kHz were classified as *T. aegyptiaca.* The first two roots extracted by DFA (Table 3.1 and Figure 3.3) on the three principal components extracted by PCA explained 88.8% of the variance.

Table 3.1: Discriminant functions analysis on the principal component scores extracted by principal component analysis on the 19 echolocation pulse parameters

	Root 1	**Root 2**	**Wilks'λ**	**$F_{(2,498)}$**	**P**
PCA Factor 1	1.3	-0.1	0.8	2218.356	$<$ 0.000000
PCA Factor 2	1.0	0.8	0.2	274,164	$<$ 0.000000
PCA Factor 3	0.2	0.4	0.1	14.626	$<$ 0.000001
Eigen value	10.1	0.1			
Wilks'λ	0.1	0.9			
χ^2	1225.640	28.434			
df	6	2			
p	$<$ 0.000000	$<$ 0.000000			

The classification success was 100% for *N. capensis*, and 100% for *T. aegyptiaca*. A classification success of only 5% was obtained for *M. natelensis*. Even though the DFA indicated that the incorrectly classified 5% should be classified *N. capensis* we excluded those echolocation pulses from further analysis because previous studies (Fenton and Bell, 1981; Schoeman and Jacobs, 2003) had not reported peak frequencies > 50 kHz for this species.

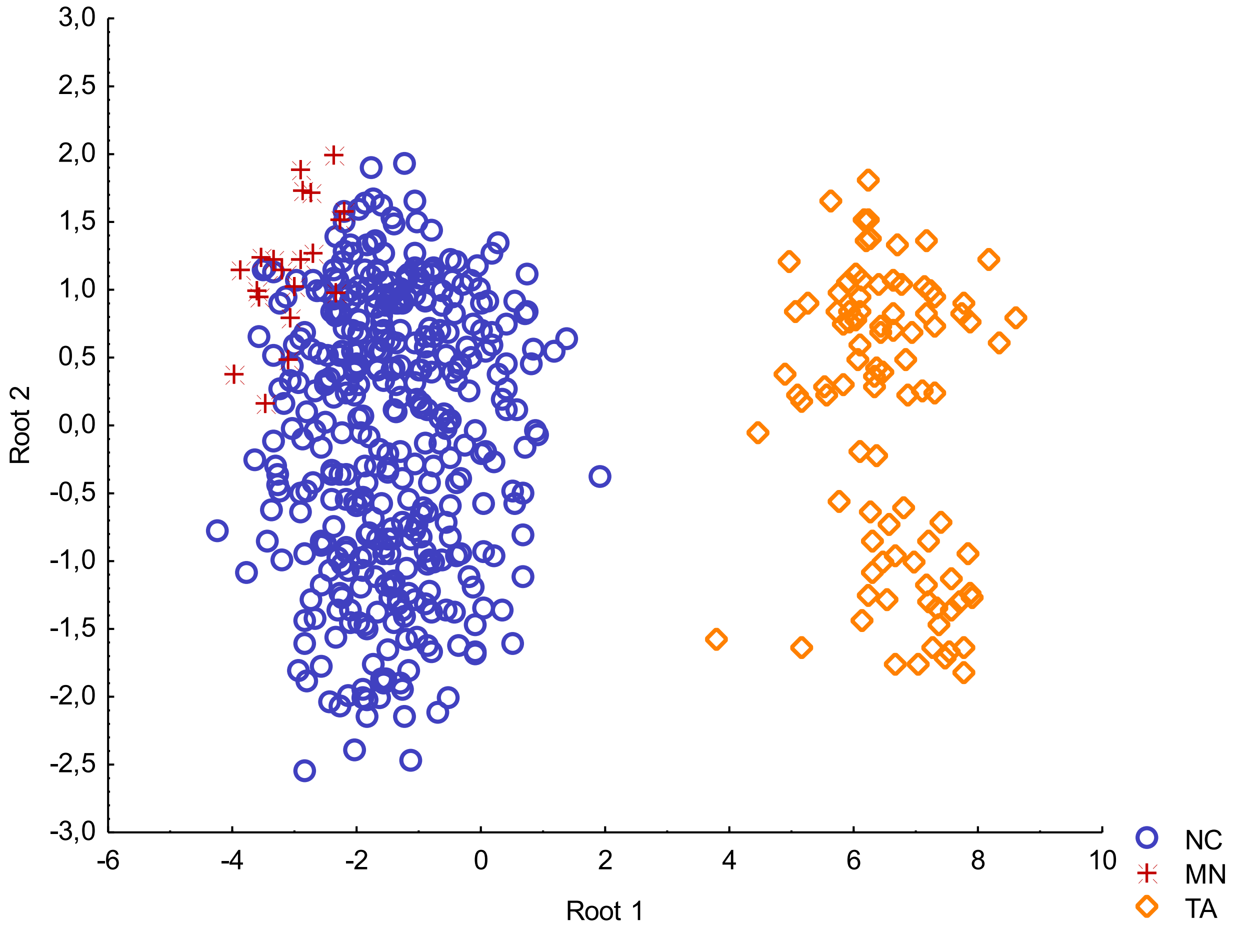

Figure 3.3: Plot of canonical scores extracted by Discriminant Function Analysis from 19 echolocation pulse parameters. Species abbreviations are, NC= *Neoromicia capensis*, MN= *Miniopterus natalensis* and TA= *Tadarida aegyptiaca*.

Reconstruction of 3-Dimensional acoustic flight path

A total of 226 3-D flight paths for *N. capensis* (Figure 3.4) relative to the arrays were successfully reconstructed and these comprised 99 and 127 flight paths for the roost and foraging situations, respectively.

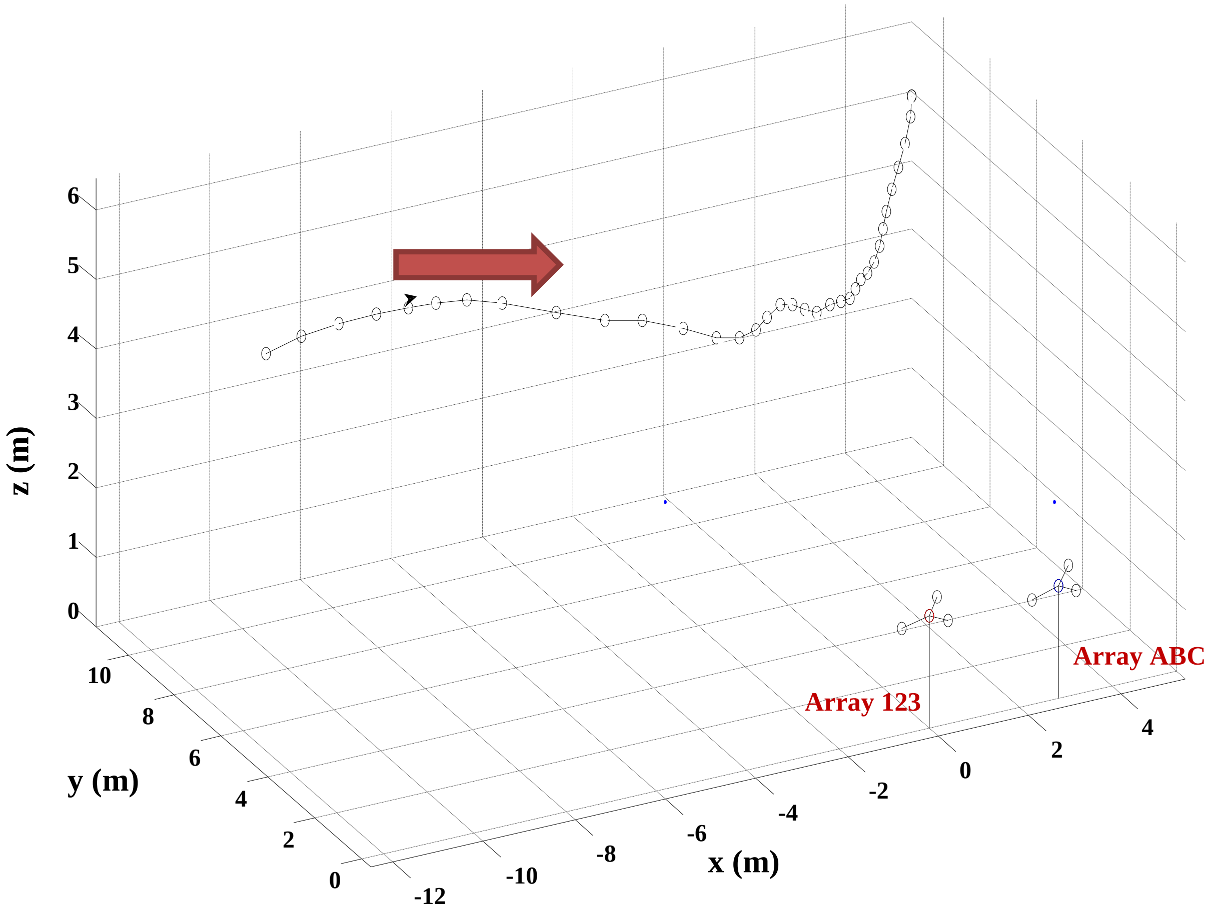

Figure 3.4: An example of a three-dimensional flight path of a free-flying *Neoromicia capensis* reconstructed from an echolocation pulse sequence recorded at a foraging site. The pulses in the sequence are indicated by circles. The direction of the bat's flight is from left to right as indicated by the arrow. The positions of the two multiple microphone arrays (Array 123 and Array ABC) are also indicated in the diagram.

A total of 28 3-D flight paths were successfully reconstructed for *T. aegyptiaca* as it flew towards the arrays and these comprised 14 flight paths for each situation type i.e. roost and foraging. It was assumed that there was more than one bat in the study area and that each flight path (Figure 3.4) represented a different bat, however, pseudo-replication is likely. The 3-D acoustic flight paths suggest that flying bats were well tracked in both situations.

Source level measurements

The source levels of the echolocation pulses (Table 3.2) for both *N. capensis* and *T. aegyptiaca* were high. *Tadarida aegyptiaca* emitted echolocation pulses at source levels > 150 dB peSPL at 10 cm in front of the bat's position during both emergence from the roost and while foraging, the highest reported to date for an open-air aerial hawking insectivorous bats. The source levels for *N. capensis* were lower (Table 3.2) and within the range reported for other species (Surlykke and Kalko, 2008).

Table 3.2: Mean±SD and ranges of echolocation pulse source levels (dB) peSPL at 10 cm for *Neoromicia capensis* and *Tadarida aegyptiaca*.

Variable	***Neoromicia capensis***			***Tadarida aegyptiaca***		
	Roost (n= 99)	Foraging (n= 127)	All situations (n= 226)	Roost (n= 14)	Foraging (n= 14)	All situations (n= 28)
Source level	129.3±4.0 (119.3-138.7)	132.8±5.0 (117.8-142.9)	130.7±4.8 (117.8-142.9)	146.9±4.6 (137.7-154.8)	143.0±4.9 (136.4-153.3)	144.9±5.1 (136.4-154.8)

The source levels for *T. aegyptiaca* were validated through visual inspection of the source levels yielded by two arrays to insure that they were not too different between the arrays. We also validated the source levels by investigating, through simple linear regression, if there were any correlations between the source levels of *T. aegyptiaca* and each of the quality (dZ/r %) of the pulses (Figure A1), the Peak frequency (Hz) of the pulses (Figure A2) and the wind speed (m/s) at the time the echolocation pulses were recorded (Figure A3). There was no correlation between the source levels of *T. aegyptiaca* and quality of the pulses (R^2= 0.00309272, F $_{(1,17)}$ = 0.05274, p > 0.82110) and between the source levels and peak frequency (R^2 = 0.13912494, F $_{(1,17)}$ = 2.7473, p > 0.11575; Table 3.3 and Figure A1).

However there was a correlation between the source levels of *T. aegyptiaca* and wind speed (R^2 = 0.24317682, F $_{(1,17)}$ = 5.4623, p < 0.03192); source levels increased with an increase in wind speed. This suggested that some of the high source levels were the result of prevailing high wind speeds when those pulses were recorded and these values were therefore excluded from the calculations of the source levels reported in Table 3.2. Nevertheless, as indicated in Table 3.2 even at low wind speed high source levels were calculated. There was no correlation between source levels and wind speed after the exclusion of the wind affected values (R^2= 0.06265927, F $_{(1,13)}$ = 0.86902, p > 0.36822). There was also no relationship between source levels and wind speed for *N. capensis* (R^2 = 0.09905886, F $_{(1,29)}$ = 3.1886, p > 0.08462; Table 3.4 and Figure A4). There was no correlation between the source levels of *Tadarida aegyptiaca* and distance to the array (R^2= 0.09243612, F $_{(1,17)}$ = 1.7315, p > 0.2, Figure A5). There was also no correlation between the source levels of *Neoromicia capensis* and distance to the array (R^2= 0.00149382, F $_{(1,17)}$ = 0.02543, p > 0.8, Figure A6).

Table 3.3: Simple regression analysis summary of the effect of wind speed (m/s), Peak Frequency (Hz) and Dz/r (%) on the source levels (dB) of *T. aegyptiaca*

Variable	**b^***	**Std.Err. of b^***	**b**	**Std.Err. of b**	**t(17)**	**p-value**
Peak frequency	-0.372995	0.225033	-1.60402	0.967727	-1.65751	0.115753
Dz/r (%)	-0.055612	0.242160	-2.29279	9.98381	-0.229650	0.821104
Wind speed	-0.250318	0.268520	-0.024002	0.025747	-0.9322	0.368217

Table 3.4: A simple regression analysis of the effect of wind speed (m/s) on the source levels (dB) of *Neoromicia capensis*

Variable	b^*	Std.Err. of b^*	b	Std.Err. of b	t(17)	p-value
Wind speed	-0.314736	0.176258	-0.013728	0.007688	-1.7857	0.084618

The Factorial ANOVA in GLM confirmed significant differences in source levels (R= 0.71, $F_{(3,250)} = 85.55$, $p < 0.01$). There were difference in the source levels between the two bat species, *N. capensis* and *T. aegyptiaca* ($F_{(1,250)} = 240.99$, $p < 0.01$) but no significant differences in the source levels between the two situation types i.e. emergence from the roost and foraging ($F_{(1,250)} = 0.68$, $p > 0.01$). Furthermore, the univariate test of significance for source levels in GLM confirmed significant difference ($F_{(1,250)} = 11.76$, $p < 0.01$) for the interaction between species and situation. Post hoc tests (Tukey HSD test) revealed significant difference ($p < 0.01$) in the source levels of *N. capensis* between roost and foraging. However, the Tukey HSD test obtained no significant different between the situation type i.e. roost and foraging in the source levels of *T. aegyptiaca.* Tests of the assumptions of ANOVA indicated homogeneity of variance of source levels for the species (The Levene's Test, $F_{(1,252)} = 0.43$, $p > 0.01$), situation type ($F_{(1,252)} = 0.98$, $p > 0.01$) and the interaction between species and situation ($F_{(3,250)} = 1.99$, $p > 0.01$). My data were normally distributed (Figure A7 and Figure A8).

Estimation of maximum detection distances

The maximum detection distances were estimated for the two bat species in their respective foraging habitats. Because no measurements were available for insect prey we used different target size categories to calculate prey detection distances for *N. capensis* and *T. aegyptiaca* i.e. small, medium and large with target strength (TS) of -65, -50 and -40 dB respectively, following the method of Stilz and Schnitzler (2012) for the point-reflector function in the online calculator (http://134.2.91.93/~peter/calculator/range.php). A Mann-Whitney U Test revealed significant differences in the maximum detection distances between *N. capensis* (N = 125) and *T. aegyptiaca* (N = 14) for small (z = 6.12, N= 125, p < 0.01), medium (z = 6.12, N = 125, p < 0.01) and (z = 6.12, N= 125, p < 0.01) prey size categories. The echolocation pulses of *T. aegyptiaca* had a longest maximum detection distances compared to *N. capensis* for the three prey size categories (Table 3.5).

Table 3.5: Mean±SD and range of the echolocation pulse maximum detection distances of three prey size categories for *Neoromicia capensis* and *Tadarida aegyptiaca*

Variable	***Neoromicia capensis*** (N = 125)		***Tadarida aegyptiaca*** (N = 14)	
	Mean±SD	range	Mean±SD	range
Small target	6.2±1.0	3.7-8.3	12.4±2.5	9.9-16.8
Medium target	9.4±1.4	6.1-12.4	18.9±3.6	15.5-25.5
Large target	11.9±1.7	8.1-15.5	24.0±4.4	19.2-32.5

CHAPTER 4

Discussion

In this study, multiple microphone arrays were used to investigate the source levels of two bat species, *N. capensis* and *T. aegyptiaca*. Specifically, the influence of body size and situation (roost emergence and foraging) on the source levels of the two bat species were assessed. The two species emitted echolocation pulses at high source levels in both situations. As predicted, *N. capensis* adjusts the source levels of its echolocation pulses in response to the situation type. Surprisingly, there was no significant difference in source levels between roost emergence and foraging for *T. aegyptiaca*. Compared to published source levels for other species (Griffin, 1958; Jensen and Miller, 1999; Surlykke *et al*., 1993; Holderied and von Helversen, 2003; Holderied *et al*., 2005; Surlykke and Kalko, 2008), *N. capensis* emitted echolocation pulses at similar source levels viz. 119.3 - 138.7 dB peSPL during emergence from the roost and 117.8 - 142.9 dB peSPL during foraging. *T. aegyptiaca* emitted echolocation pulses with relatively higher source levels of 137.7 – 154.8 dB peSPL than other species during emergence from the roosts and 136.4 – 153.3 dB peSPL during foraging. These differences in the source levels translated into differences in the detection distance of the two bat species and as predicted *T. aegyptiaca* had greater maximum detection distances (see Figure A9, Figure A10 and Figure A11) than *N. capensis* for the three different insect size categories.

Tadarida aegyptiaca thus has the highest source levels reported thus far for free-flying bats. For example Surlykke and Kalko (2008) reported bats in the families; Emballonuridae, Mormoopidae, Molossidae, Noctilionidae and Vespertilionidae emitted average maximum source levels of 121-137 dB peSPL. The single molossid in the Surlykke and Kalko (2008) study, *Molossus molossus,* is slightly smaller than *T. aegyptiaca* and this may account for its lower maximum source level of 121.7 dB peSPL at 10 cm. Similarly, *Eptesicus bottae* (Vespertilionidae; body mass of approximately 10 g) of a similar size to *T. aegyptiaca* but larger than *N. capensis* has an echolocation pulse source level of 133 dB peSPL (Holderied *et al*., 2005) also found similar to that of *T. aegyptiaca* but higher than that of *N. capensis*. These comparisons support the trend reported by Holderied and von Helversen (2003) that larger bats use echolocation pulses with higher source levels. However, even the much larger open-air forager, *Nyctalus lasiopterus* (Vespertilionidae) with a body mass of 48 g (Ibanez *et al*., 2001), emitted pulses with a maximum source level of 133 dB peSPL at 10 cm (Holderied and von Helversen, 2003), lower than that reported here for *T. aegyptiaca*.

The very high source levels reported here for *T. aegyptiaca* do not appear to be an artefact of the study. The results were validated by looking for correlations between source levels and each of wind speed, peak frequency and the quality of an echolocation pulse. Although wind speed did have an influence, the other two did not have an influence on the source levels. The presence of harmonics in the echolocation pulse can influence the source levels if the peak frequency and peak to peak voltage used for the calculations of source levels are from different harmonics. The peak frequencies of echolocation pulses and the peak to peak voltage were thoroughly checked to ensure that only those from the first harmonic were used for calculations of the source levels. There was no correlation between source levels and peak frequency. Similarly, if background noise levels are of higher source levels than the pulses, even though the pulses are good enough for localization, the voltage levels for the background noise may be used erroneously leading to artificially high source levels. However, there was no correlation between source levels and the quality of pulses. Wind speed can also influence source levels, if the echolocation pulses in the 3-D flight paths appear good. This might, for example, result in lower measurements of distance and an underestimation of atmospheric attenuation leading to artificially high source levels. Although there was a correlation between wind speed and source levels with peak frequency, only source levels calculated after high source levels associated with high wind speed were eliminated from the data are reported. I am therefore confident that the source levels reported here are not artefacts.

Due to the fact that echolocation pulses of bats are highly directional with maximum source levels of echolocation pulses only when the bat directs its pulse along axis of the microphones. I avoided utilization of echolocation pulses where the bats were not flying in the direction of the microphone arrays. Only echolocation pulses where bats were approaching the arrays were used, even though, because bats can quickly turn their heads and emit echolocation calls in an opposite direction to the arrays. This study therefore, only used the maximum source levels in an echolocation call sequence, which I assumed were emitted by bats when they faced the arrays. Assuming accurate localization of the echolocation pulses the study didn’t overestimate the source levels of *Tadarida aegyptiaca* and *Neoromicia capensis,* especially in light of the checks undertaken in Figures A1-A6.

Tadarida aegyptiaca is an open-space aerial forager which hunts insect prey mostly at high heights above the ground and far away from the obstacles such as vegetation. The emission of echolocation pulses with high source levels is probably to maximize detection range (Neuweiler and Fenton 1988; Neuweiler, 1990) because *T. aegyptiaca* has to detect insect prey at greater distances in open-space largely as a result of prey distribution being less dense. *Tadarida aegyptiaca* needs more time to manoeuvre to intercept prey while flying at high speed. Unlike *N. capensis* which forages close to the vegetation clutter where resolution is necessary, classification and detection of the insect prey for *T. aegyptiaca* is more crucial. Along with the production of echolocation pulses with higher source levels, *T. aegyptiaca* also have to emit echolocation pulses of long duration, narrow bandwidth and low frequency (see Table A3) to increase the maximum detection distances. Furthermore, to receive audible and quality echoes from the target *T. aegyptiaca* needs to emit echolocation pulses of high source levels and low frequencies (Griffin, 1971; Lawrence and Simmons, 1982; Barclay, 1983; Houston *et al*., 2004) because high frequency echolocation pulses are highly attenuated and limits the effective detection range of echolocation by bats. Experiments on atmospheric attenuation measurements (Sivian, 1947; Evans and Bass, 1972; Lawrence and Simons, 1982) reported an increase in atmospheric attenuation of echolocation sound signals as the frequency of echolocation pulse increases.

It was also expected that the two bat species would emit echolocation pulses of higher source levels in their respective foraging habitat than when they emerged from the roost. Detection distance is more important in the potentially unknown surroundings of foraging habitats than in the known surroundings of the roost. Even though, *N. capensis* did emit echolocation pulses of higher source levels during foraging than during roost emergence *T. aegyptiaca* surprisingly emitted echolocation pulses at similar source levels during emergence from the roost and when it hunted for prey in open space habitats. In Zimbabwe, a study conducted by Fenton and Griffin (1997) at Sengwa Wildlife Research Area reported *T. aegyptiaca* to be hunting and attacking insect prey as high as 600 m above the ground. At such heights it is difficult to localize pulses with microphone arrays at ground level and is the reason why our sample sizes are lower for *T. aegyptiaca* and *N. capensis*. The difficulty in localization of the echolocation pulses of *T. aegyptiaca* at such heights could lead to inaccuracies in the estimation of the source levels resulting in higher estimates of source levels (but see Figure A5 and Figure A6).

It is also at such heights that *T. aegyptiaca* is likely to use much higher source levels than those used while emerging from the roost. Hence the lack of difference in the source levels between roost emergence and foraging.

The findings of the current study show that bats emit echolocation pulses at higher source levels while flying freely in their natural habitat than under laboratory conditions. Brinklov *et al.* (2008) in a flight experiment under laboratory conditions recorded *Artibeus jamaicensis* (40-60 g) a plant-feeding bat larger than *T. aegyptiaca* and *N. capensis* (Jennings *et al*., 2004) and *Macrophylum macrophyllum* (6-9 g; an insectivore similar in size to *N. capensis*; Harrison, 1975) foraging on the wing to emit echolocation pulses of 110 dB SPL and 105 dB SPL, respectively, at a standard reference distance of 10 cm. Other results obtained (e.g. Water and Jones, 1995; Brinklov *et al*., 2008) that bats in confined man-made structures tend to emit echolocation pulses with source levels lower than free-flying bats. Furthermore, depending on the situation, bats may adjust their echolocation pulses source levels to suit their foraging mode and foraging habitat. The huge differences in the source levels reported in the current study and those reported by Griffin (1958) and others discussed above elucidate the great flexibility of the echolocation system (Jakobsen *et al*., 2013) and is probably attributable to foraging habitat, situation (natural and artificial), the frequency of the echolocation pulses and the size of the bat.

Contrary to the current study where echolocation frequency, source levels and detection distance varied between species and situation. Surlykke and Kalko (2008) reported bat species that are open-space aerial hawkers, edge-space aerial hawkers and edge-space trawling hawkers to have similar maximum detection distances despite a large variation in their echolocation frequency and maximum source levels. The similar maximum detection distances reported by Surlykke and Kalko (2008) might probably be as a result of the situation in which echolocation was recorded. Most of the recordings were done at a forest edge with only a few recordings done close to water surfaces. The bat species in their study might have faced similar situations in the sampling site and were limited to fly in a similar way, in terms of flight speed and manoeuvrability, despite difference in body sizes and echolocation pulse frequency. There may therefore have been optimum detection distance for that particular situation. The bats may have achieved this distance by compensating for differences in atmospheric attenuation, as a result of their use of different frequencies, by altering their source levels (see Surlykke and Kalko, 2008). In the current study the two species were recorded in different situations which included their different respective foraging habitats. The optimal detection distances likely varied in each situation. In the current study *N. capensis* did not compensate for its higher pulse frequency, and the consequent increased atmospheric attenuation (Lawrence and Simmons, 1982), by using higher source levels than *T. aegyptiaca*, likely because in their respective foraging habitats the optimum detection range differed.

Overall, the current study demonstrates that source levels do differ between species using different foraging habitats and, at least with respect to *N. capensis*, bats vary their source levels from one situation to the next. This study therefore makes an important contribution to our knowledge of an echolocation parameter that has heretofore been little studied but that plays an important role in the functioning of echolocation. For the first time the source levels and detection ranges of two bat species of different body size and known to forage in different habitats has been documented under different situations in their natural habitat. To be able to gather more reliable source levels on high flying bat species like *T. aegyptiaca* advanced technological equipment such as Helium filled balloons, radar and helicopters with fixed arrays may have to be employed. At 3000 m above the ground in North America, *Tadarida brasiliensis* a species belonging to the family Molossidae was sighted or tracked by radar (Davis *et al*., 1962; Williams *et al*., 1973). High flying forage high above the ground, away from the obstacles and fly at high speed. It would thus require other methods of sampling (e.g. on board recorders) that can yield more and higher quality echolocation pulses. The question of whether species in assemblages use the same or different detection distances can only be answered through a comparison of several assemblages across environmental gradients with some overlap in species composition across the compared assemblages. The latter would allow, at least in some cases, controls for phylogeny and foraging microhabitat. The acoustic signal data including amongst others, source levels and maximum detection ranges generated in this study can be used to assess how bats use various habitats. Foraging habitats play a vital role in the design of various call parameters i.e. spectral, temporal, source levels and detection ranges, and habitats are mostly affected by anthropogenic activities which result in habitat loss. It is in these foraging habitats that the survival of bats lies as they mostly hunt and attack insect prey in such habitats. Therefore, the knowledge generated in this study on how bats use different habitats can be used to facilitate conservation thus contributing to the conservation of bat species.

In conclusion, as predicted *T. aegyptiaca*, an open aerial hawker and larger of the two species emitted echolocation sound pulses of greater source levels and had a longer maximum detection distances than *N. capensis*, an aerial clutter-edge hawker and smaller bat species. Thus bats might vary their echolocation pulse source levels to suit their situations and foraging habitat.

CHAPTER 5

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APPENDIX

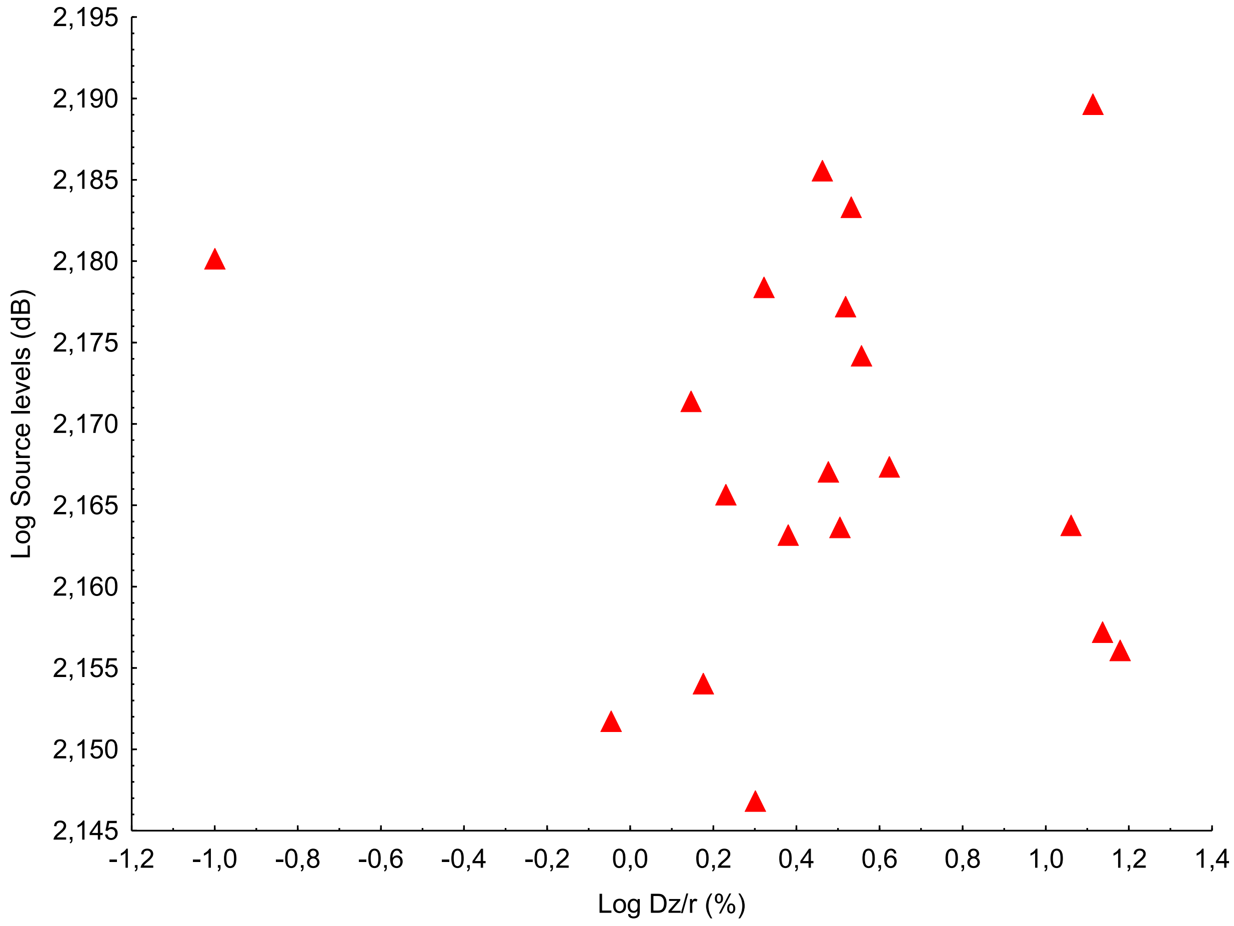

Figure A1: The regression of log source levels (dB) and the quality of the echolocation pulse Dz/r (%) of *Tadarida aegyptiaca*.

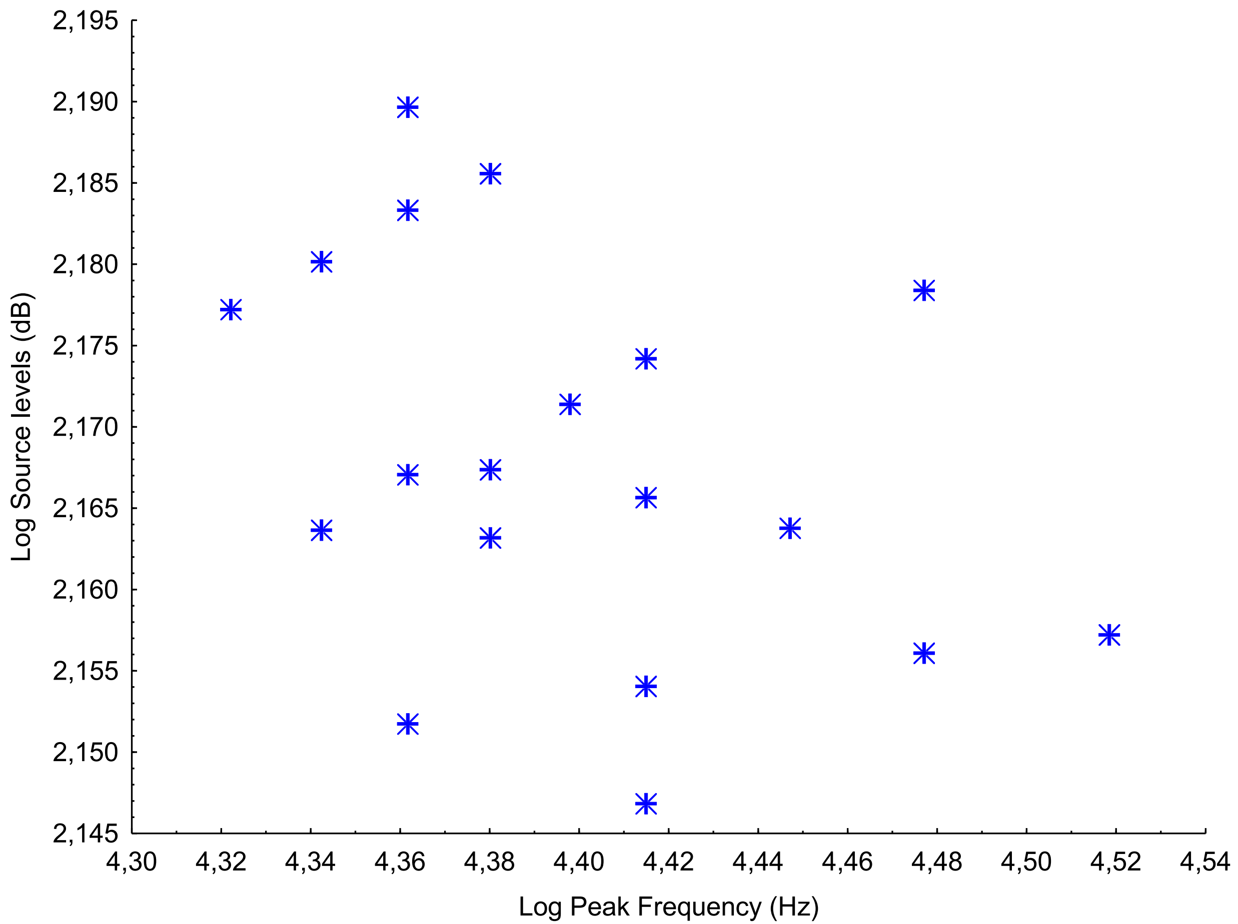

Figure A2: The regression of log source levels (dB) and peak frequency (Hz) of echolocation pulses of *Tadarida aegyptiaca*.

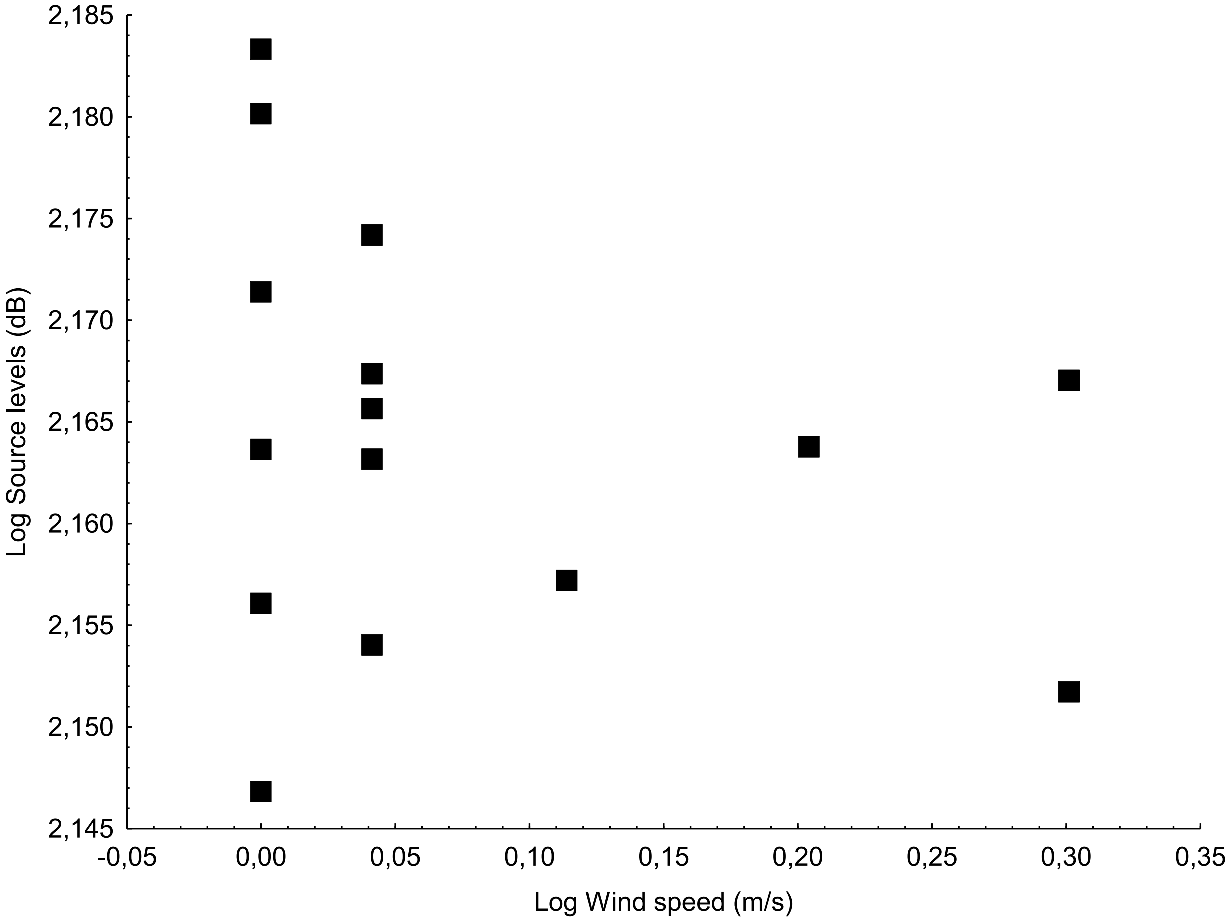

Figure A3: The regression of log source levels (dB) and wind speed (m/s) during the time of echolocation pulses recording for *Tadarida aegyptiaca*.

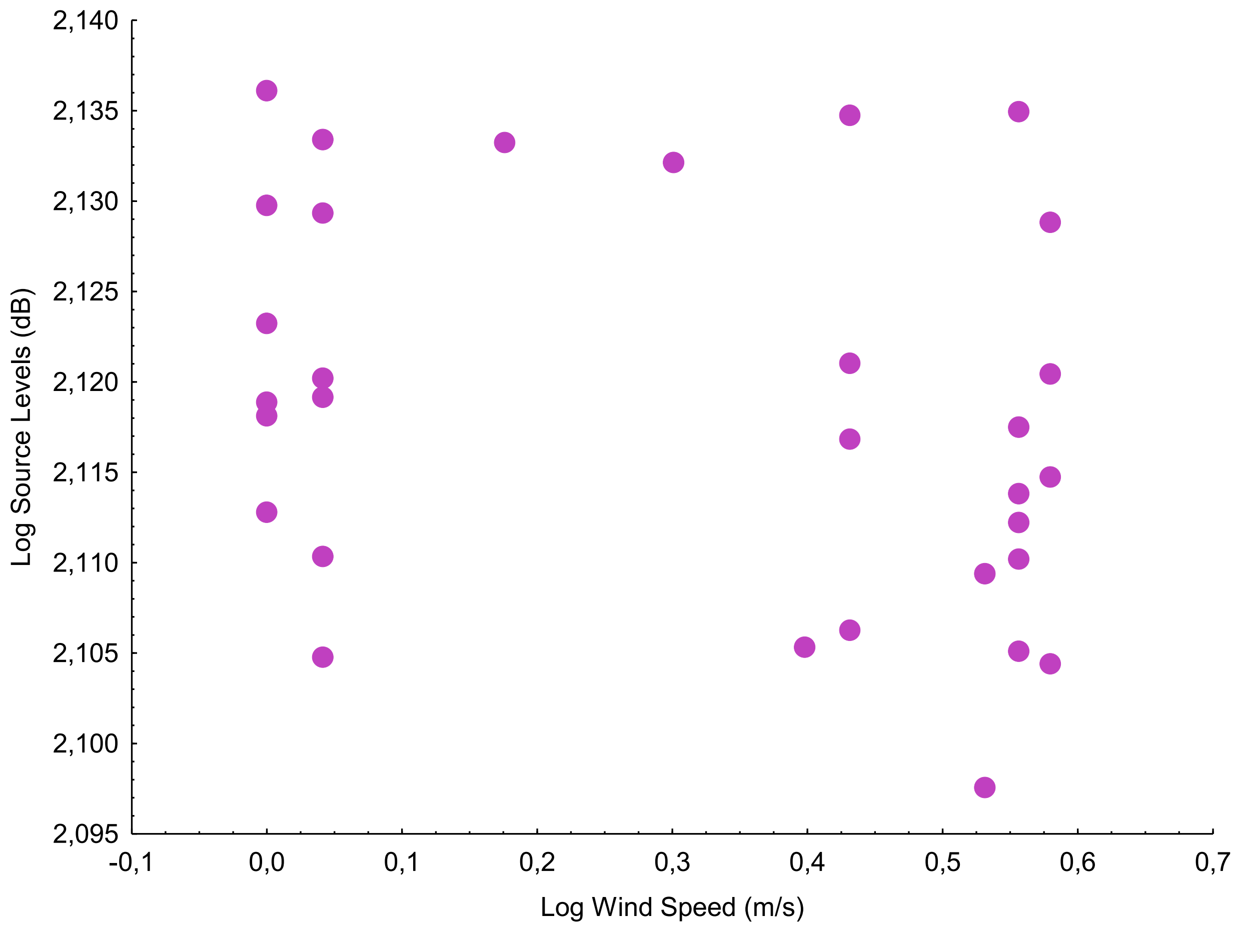

Figure A4: The regression of log source levels (dB) and wind speed (m/s) during the time of echolocation pulse recording for *Neoromicia capensis*.

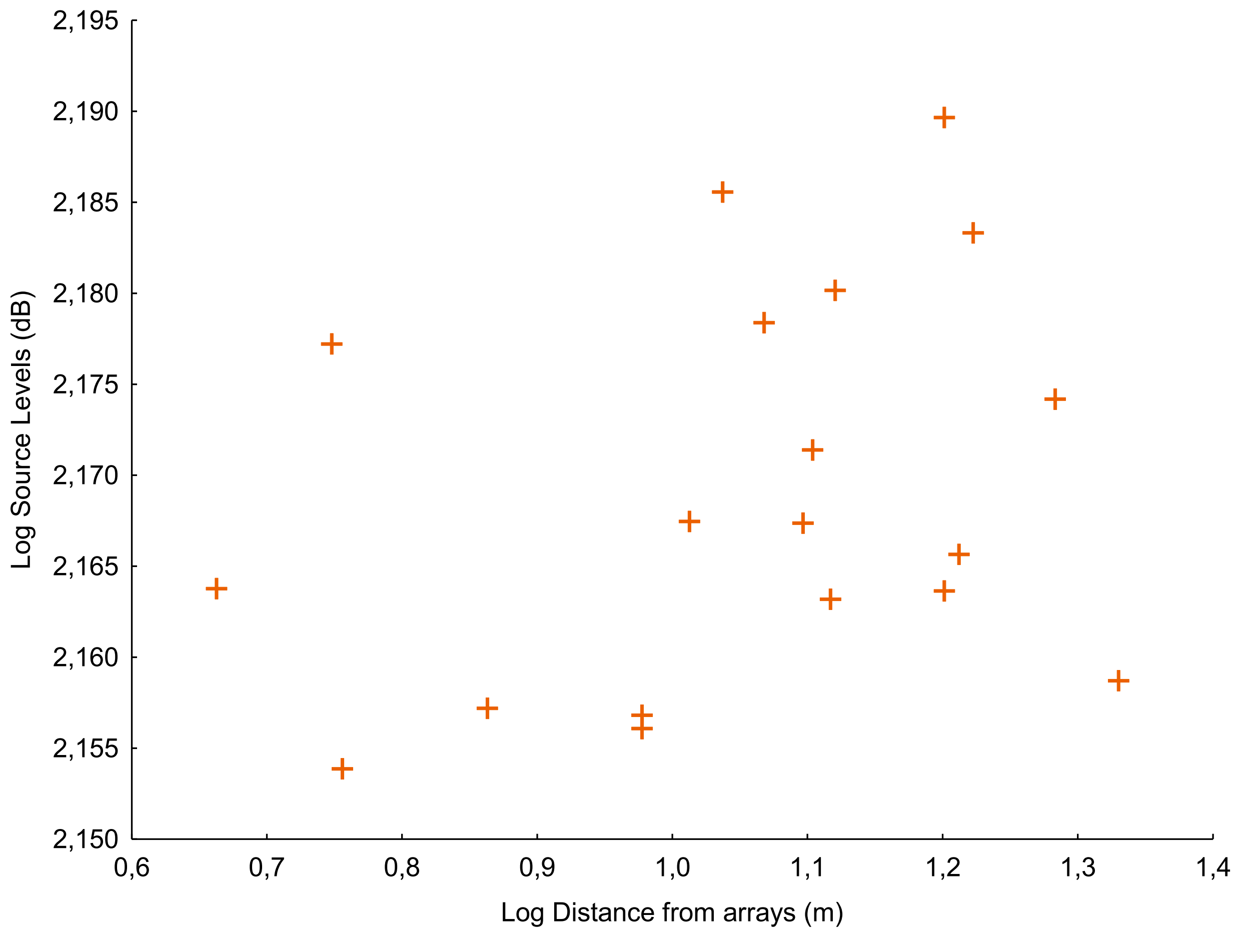

Figure A5: Relationship between the emitted source levels (dB) and the distance to the arrays (m) for *Tadarida aegyptiaca*.

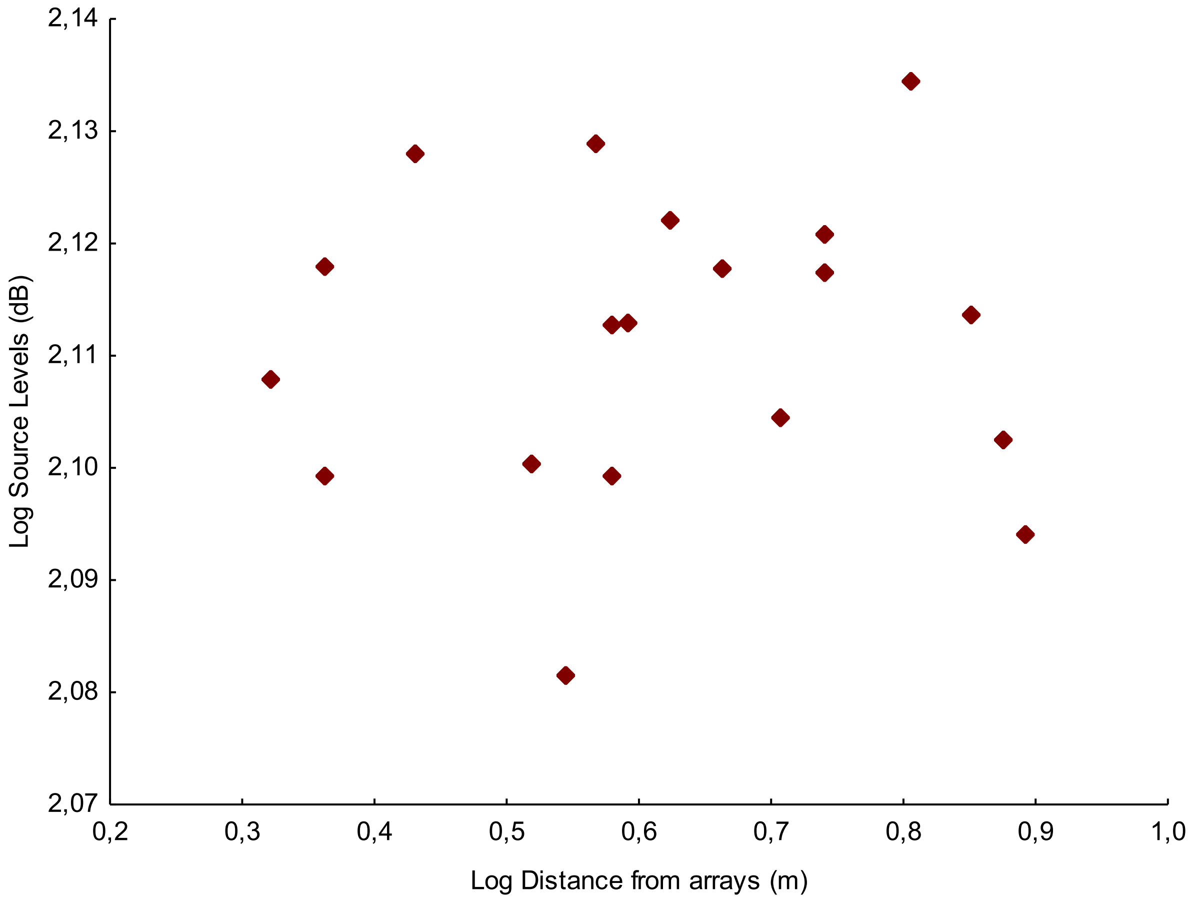

Figure A6: Relationship between the emitted source levels (dB) and the distance to the arrays (m) for *Neoromicia capensis*.

Table A1: Factor-variable correlations (factor loadings) based on correlations for *N. capensis and T. aegyptiaca.* P.F= peak frequency, P.A= Peak amplitude.

Variable	Fact. 1	Fact. 2	Fact. 3	Fact. 4	Fact. 5	Fact. 6	Fact. 7	Fact. 8	Fact. 9	Fact. 10	Fact. 11	Fact. 12	Fact. 13	Fact. 14	Fact. 15	Fact. 16	Fact. 17	Fact. 18	Fact.19
Duration	0,89	0,11	-0,12	-0,17	0,09	-0,13	0,27	0,01	-0,22	0,02	-0,03	-0,01	0,02	0,00	0,00	0,00	0,00	0,00	0,00
Interval	0,87	0,24	0,06	-0,01	-0,13	-0,17	0,06	0,32	0,14	-0,01	-0,03	0,01	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Disttomax	0,69	-0,11	-0,15	-0,56	0,40	0,06	-0,12	0,06	0,03	-0,02	0,03	0,01	-0,01	0,00	0,00	0,00	0,00	0,00	0,00
Peaktopeak	-0,51	0,69	-0,42	-0,12	-0,11	0,01	0,07	-0,07	0,04	-0,25	-0,02	0,00	0,02	0,00	0,00	0,00	0,00	0,00	0,00
P.F (start)	-0,97	-0,06	-0,01	-0,17	-0,03	-0,15	0,01	-0,07	0,05	0,06	0,00	-0,01	0,04	0,00	0,02	-0,01	0,00	0,00	0,00
P.A (start)	-0,36	0,89	-0,15	0,11	0,08	0,02	0,02	0,07	-0,03	0,05	0,17	0,02	0,05	0,00	0,00	0,00	0,00	0,00	0,00
Min freq(start)	-0,96	-0,04	-0,05	-0,14	0,02	-0,16	0,02	-0,08	0,08	0,06	0,00	0,00	0,04	0,00	-0,01	0,01	0,00	0,00	0,00
Max freq(start)	-0,96	-0,10	-0,03	-0,19	-0,09	-0,11	0,00	-0,04	0,04	0,05	0,00	0,00	0,03	0,00	-0,01	0,01	0,00	0,00	-0,01
Bandw(start)	-0,73	-0,26	0,06	-0,33	-0,48	0,12	-0,05	0,12	-0,12	0,00	0,03	0,01	-0,01	0,00	0,00	0,00	0,00	0,00	0,00
P.F (end)	-0,93	-0,28	-0,03	0,06	0,14	0,06	0,02	0,11	-0,01	-0,02	-0,01	-0,08	0,02	-0,05	0,00	0,00	0,00	0,00	0,00
P.A (end)	-0,60	0,72	-0,20	0,05	0,09	0,09	-0,13	0,07	-0,06	0,08	-0,13	0,07	0,05	0,00	0,00	0,00	0,00	0,00	0,00
Min freq(end)	-0,89	-0,37	-0,15	0,06	0,12	0,06	0,04	0,11	-0,01	-0,02	0,00	-0,05	0,04	0,03	0,00	-0,01	0,01	0,00	0,00
Max freq(end)	-0,95	-0,18	0,15	0,00	0,13	0,12	0,11	0,08	0,02	-0,01	-0,02	-0,03	0,03	0,02	0,00	0,01	-0,02	0,00	0,00
Bandw(end)	-0,28	0,46	0,78	-0,15	0,03	0,16	0,20	-0,04	0,08	0,02	-0,01	0,04	-0,01	-0,01	0,00	0,00	0,01	0,00	0,00
P.F (max)	-0,97	-0,15	0,01	0,06	0,10	-0,07	0,02	0,05	-0,03	-0,04	0,01	0,06	-0,06	-0,01	-0,02	-0,02	-0,01	0,00	0,00
P.A (max)	-0,55	0,74	-0,33	-0,09	-0,04	0,03	0,04	0,00	0,03	0,10	-0,02	-0,09	-0,12	0,01	0,00	0,00	0,00	0,00	0,00
Min freq(max)	-0,95	-0,25	-0,11	0,06	0,09	-0,04	0,06	0,04	-0,01	-0,02	0,01	0,07	-0,06	0,00	0,01	0,01	0,01	0,01	0,00
Max freq(max)	-0,97	-0,07	0,11	0,05	0,11	-0,09	0,00	0,05	-0,04	-0,05	0,01	0,04	-0,06	0,00	0,00	0,01	0,00	-0,01	0,00
Bandw(max)	-0,36	0,55	0,70	-0,02	0,08	-0,16	-0,18	0,02	-0,11	-0,07	-0,01	-0,07	0,00	0,01	0,00	0,00	0,00	0,00	0,00

Table A2: Eigenvalues of correlation matrix, and related statistics for *Neoromicia capensis* & *Tadarida aegyptiaca*.

Value number	Eigenvalue	% Total variance	Cumulative Eigenvalue	Cumulative %
1	11,97860	63,04527	11,97860	63,0453
2	3,33727	17,56460	15,31588	80,6099
3	1,55618	8,19040	16,87205	88,8003
4	0,61178	3,21988	17,48383	92,0202
5	0,54424	2,86443	18,02807	94,8846
6	0,21731	1,14374	18,24538	96,0283
7	0,20621	1,08531	18,45159	97,1136
8	0,18858	0,99254	18,64017	98,1062
9	0,12234	0,64389	18,76251	98,7501
10	0,10147	0,53408	18,86399	99,2841
11	0,05096	0,26822	18,91495	99,5524
12	0,04003	0,21069	18,95498	99,7631
13	0,03827	0,20141	18,99325	99,9645
14	0,00367	0,01929	18,99691	99,9838
15	0,00102	0,00536	18,99793	99,9891
16	0,00094	0,00492	18,99887	99,9940
17	0,00069	0,00365	18,99956	99,9977
18	0,00039	0,00206	18,99995	99,9998
19	0,00005	0,00025	19,00000	100,0000

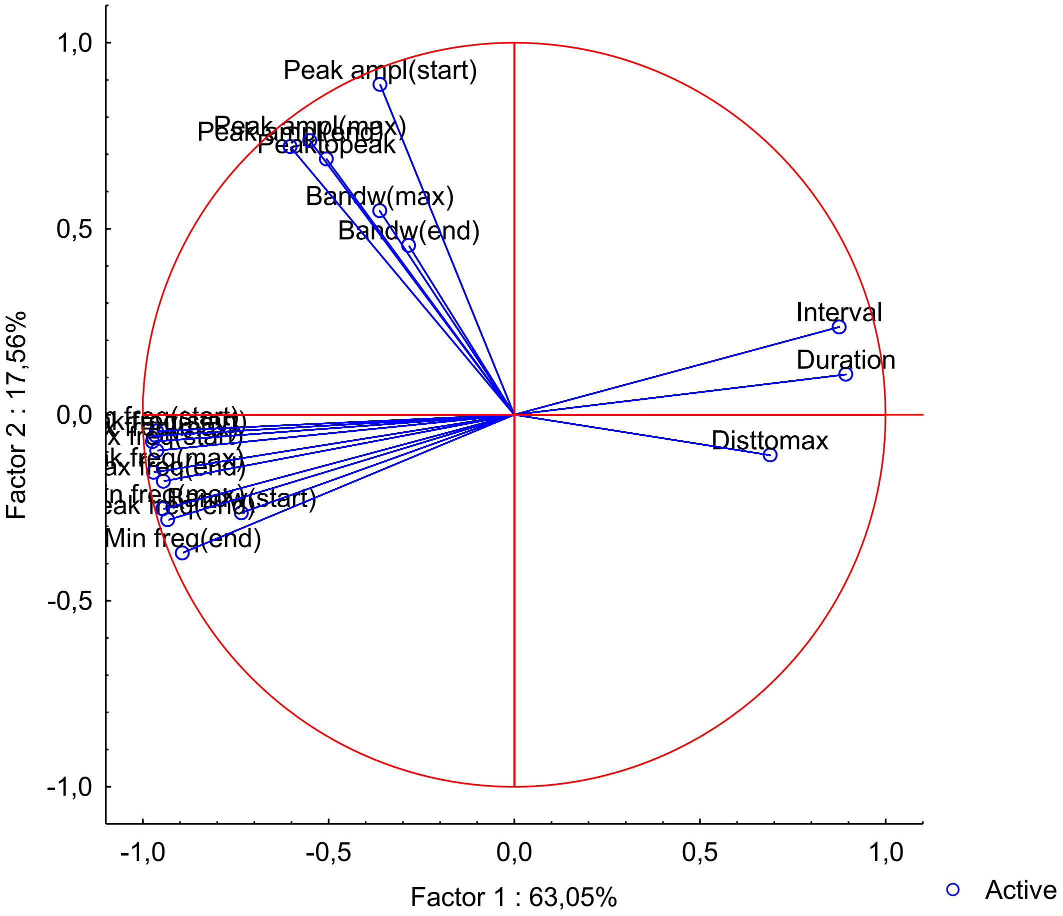

Figure A7: Projection of the echolocation pulse variables of *Neoromicia capensis* and *Tadarida aegyptiaca* on the factor-plane (1×2).

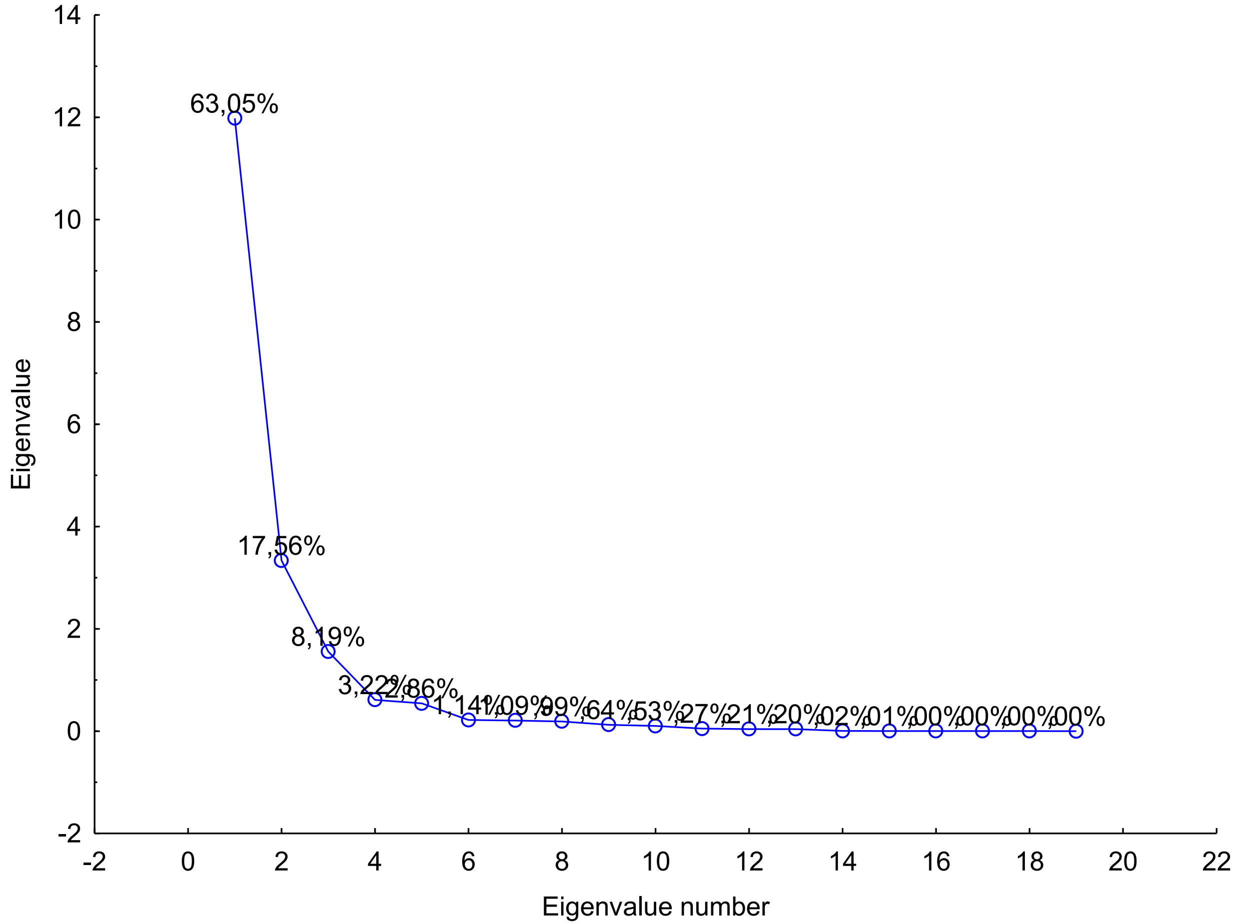

Figure A8: Eigenvalues of correlation matrix for variables of *Neoromicia capensis* and *Tadarida aegyptiaca*.

Table A3: Mean±SD and range of the echolocation pulse temporal (ms) and spectral (kHz) parameters of the two bat species, *N. capensis* and *T. aegyptiaca*.

Variable	***Neoromicia capensis*** **(N=419)**		***Tadarida aegyptiaca*** **(N=101)**	
	Mean±SD	range	Mean±SD	range
Duration	5.5±1.5	2.5-11.9	13.1±4.2	6.9-25.9
Interval	97.6±24.6	75.3-201.8	319.7±104.9	124.4-805.7
Distomax	2.8±0.8	1.3-6.5	4.3±1.8	0.8-12.0
Peaktopeak)	18.9±12.0	22.2-62.5	124.8±83.0	22.6-37.7
Peak freq (start)	61.4±10.0	40.4-94.4	27.0±5.2	18.9-41.1
Peak ampl(start)	40.4±7.3	60.9-22.8	41.4±6.4	57.4-29.2
Min freq(start)	54.6±9.0	36.2-87.5	23.3±4.8	16.3-36.6
Max freq(start)	70.6±10.8	45.9-103.1	32.7±5.7	23.1-47.4
Bandw(start)	15.5±3.2	7.8-30.8	9.0±2.0	4.7-17.8
Peak freq(end)	36.7±1.6	33.9-37.9	21.0±1.3	18.4-23.6
Peak ampl(end)	38.6±6.3	57.4-24.2	44.3±6.2	58.7-30.3
Min freq(end)	33.7±1.7	29.3-45.1	17.7±9.2	15.8-21.1
Max freq(end)	42.8±2.5	35.7-56.4	26.7±2.7	22.4-45.4
Bandw(end)	8.5±2.4	3.3-18.1	8.3±2.8	4.1-26.3
Peak freq(max)	39.8±3.2	34.2-49.4	22.6±2.0	18.8-24.9
Peak ampl(max)	27.3±6.3	45.5-14.0	31.3±6.2	45.6-19.0
Min freq(max)	37.0±2.7	31.1-49.8	19.9±1.7	16.3-23.7
Max freq(max)	45.2±4.0	37.6-64.2	27.5±2.8	22.9-33.1
Bandw(max)	7.7±2.5	4.0-13.7	7.1±2.4	4.0-10.3

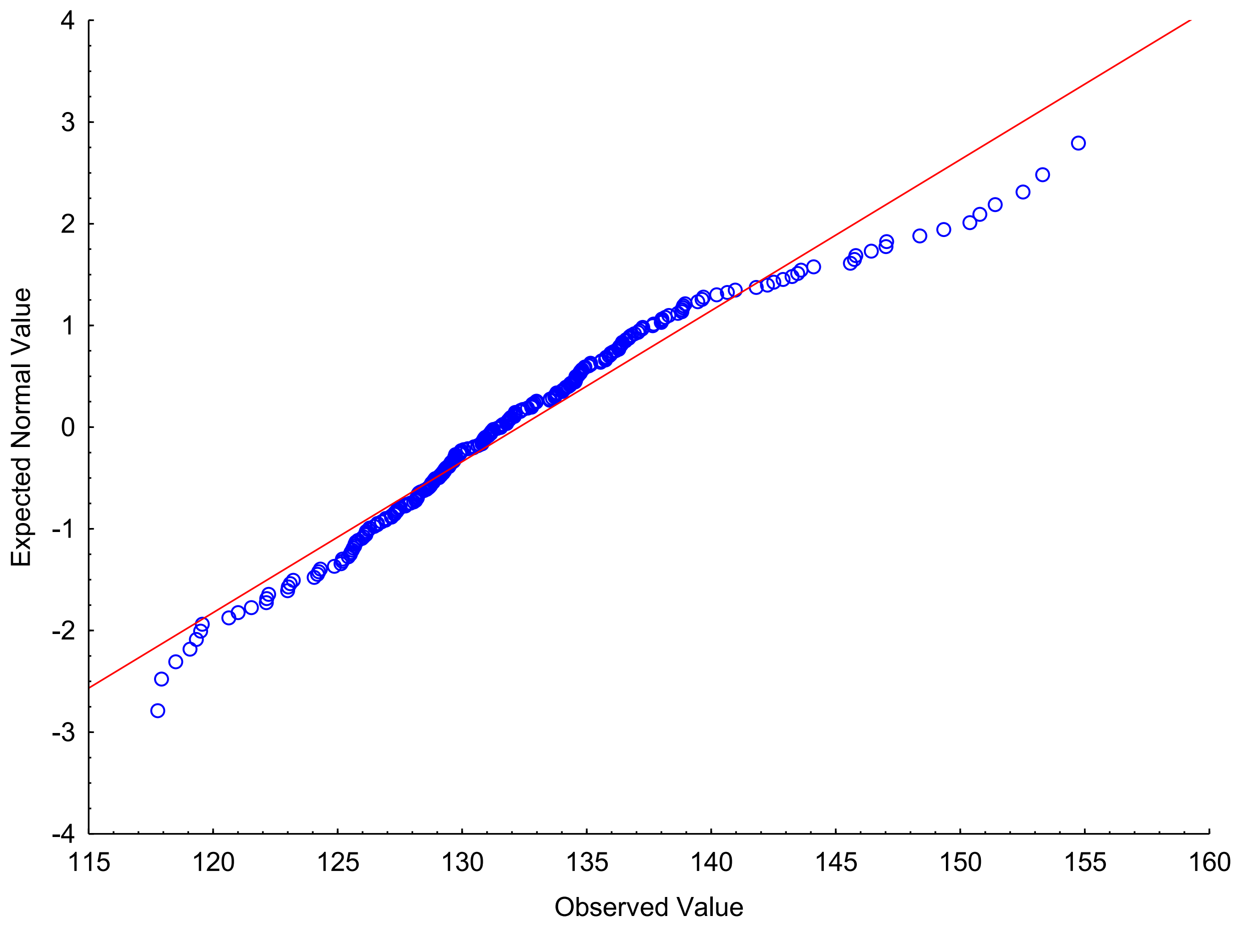

Figure A9: A linear graph showing the relationship between expected normal value and observed value for the source levels.

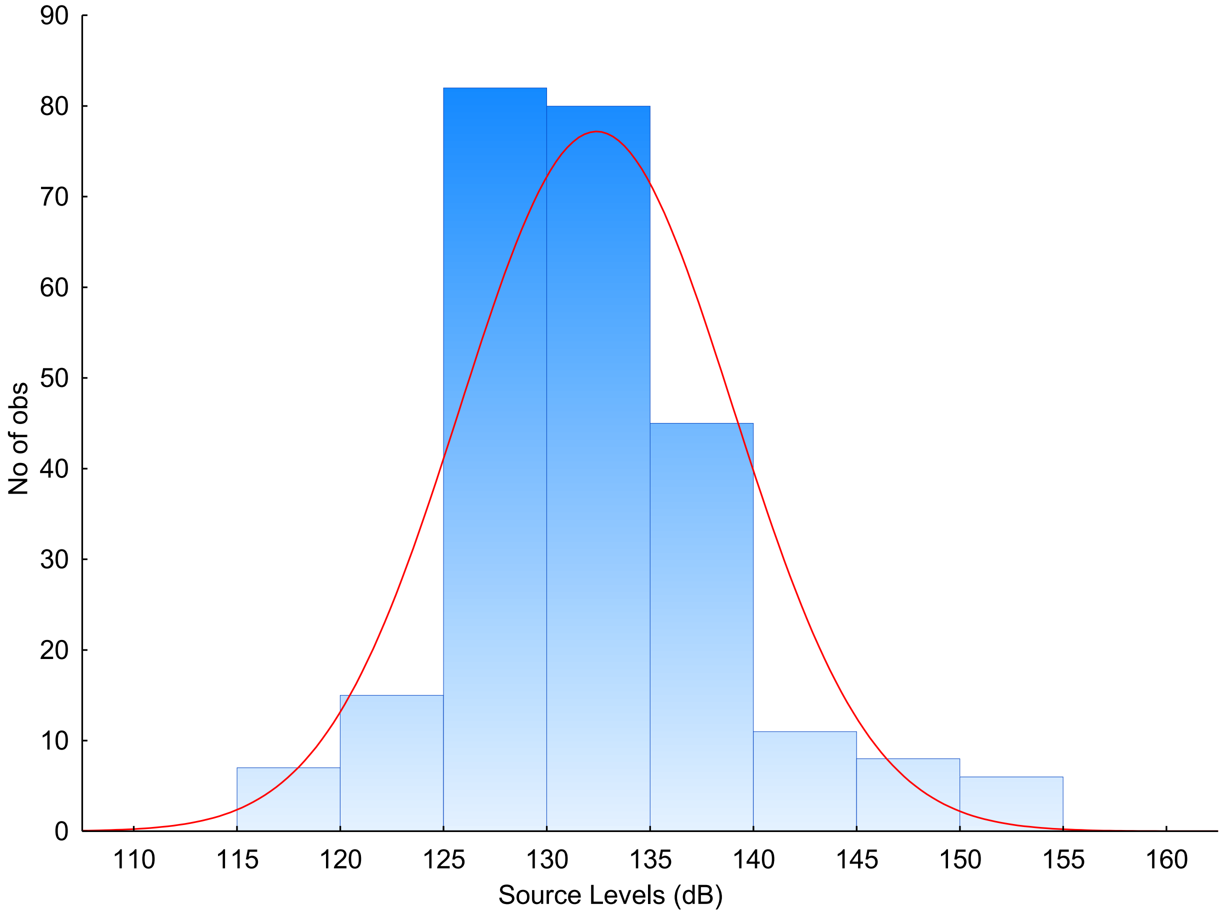

Figure A10: Histogram showing a normal distribution between the number of observation and source levels (dB).

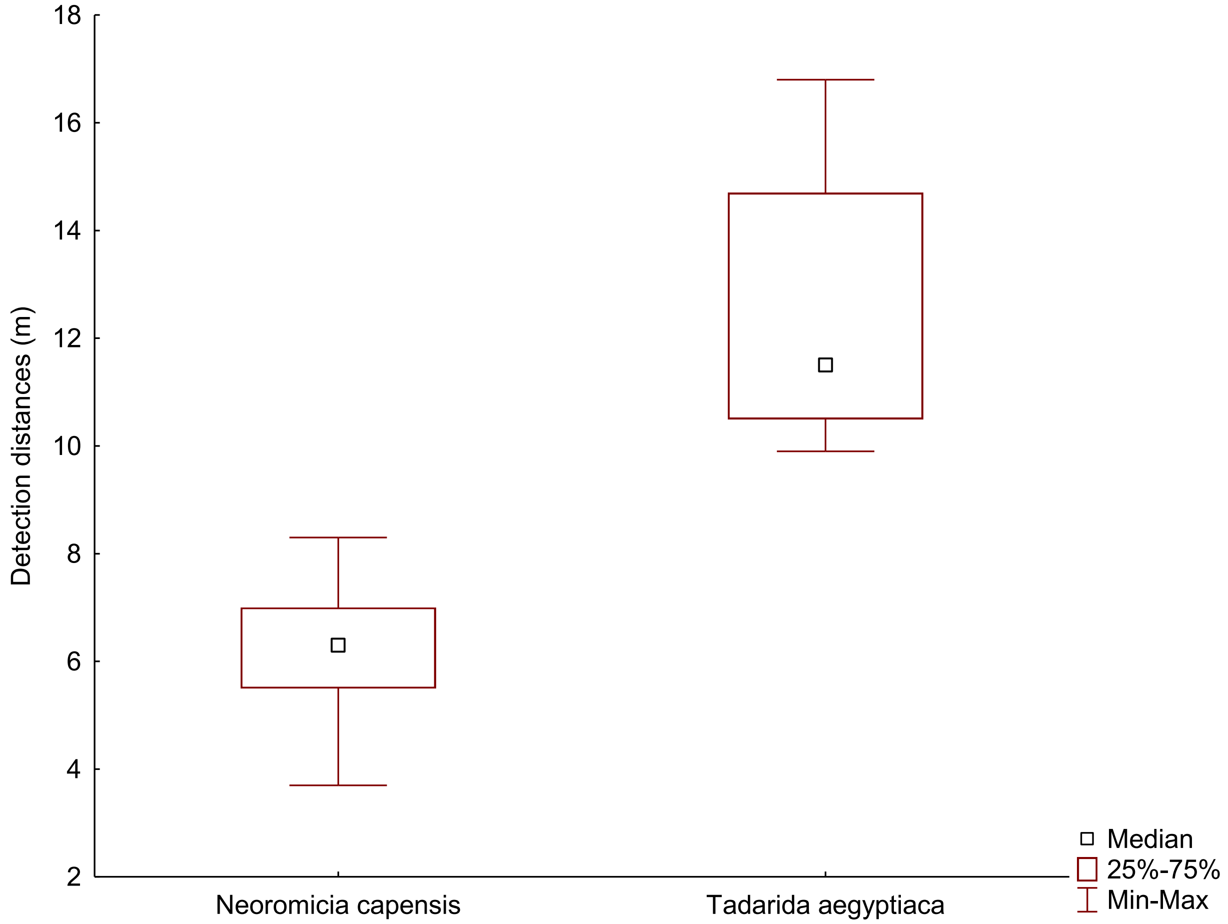

Figure A11: Box-plot showing the estimated maximum detection distance (m) for a small size insect between the two species of bats *Neoromicia capensis* and *Tadarida aegyptiaca*.

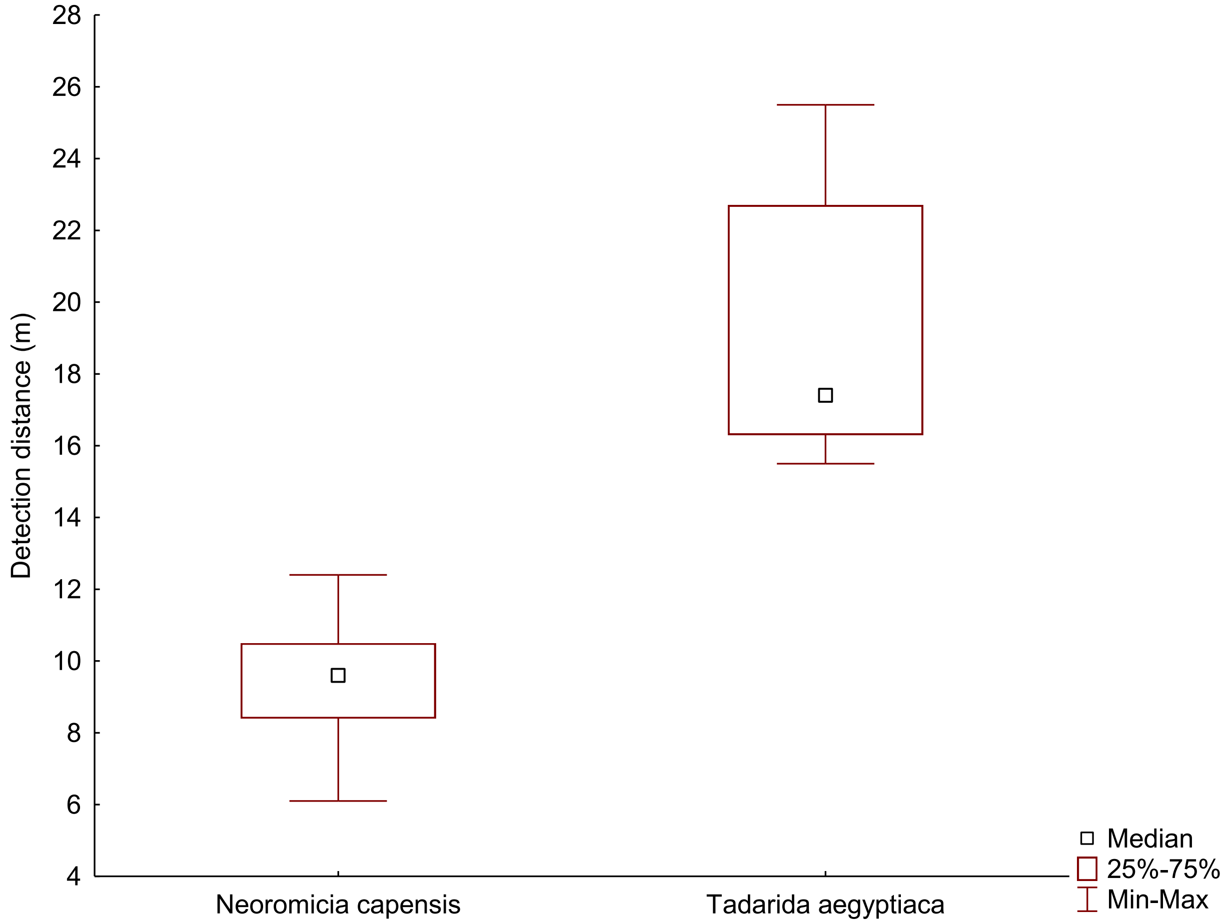

Figure A12: Box-plot showing the estimated maximum detection distance (m) for a medium size insect between the two species of bats *Neoromicia capensis* and *Tadarida aegyptiaca*.

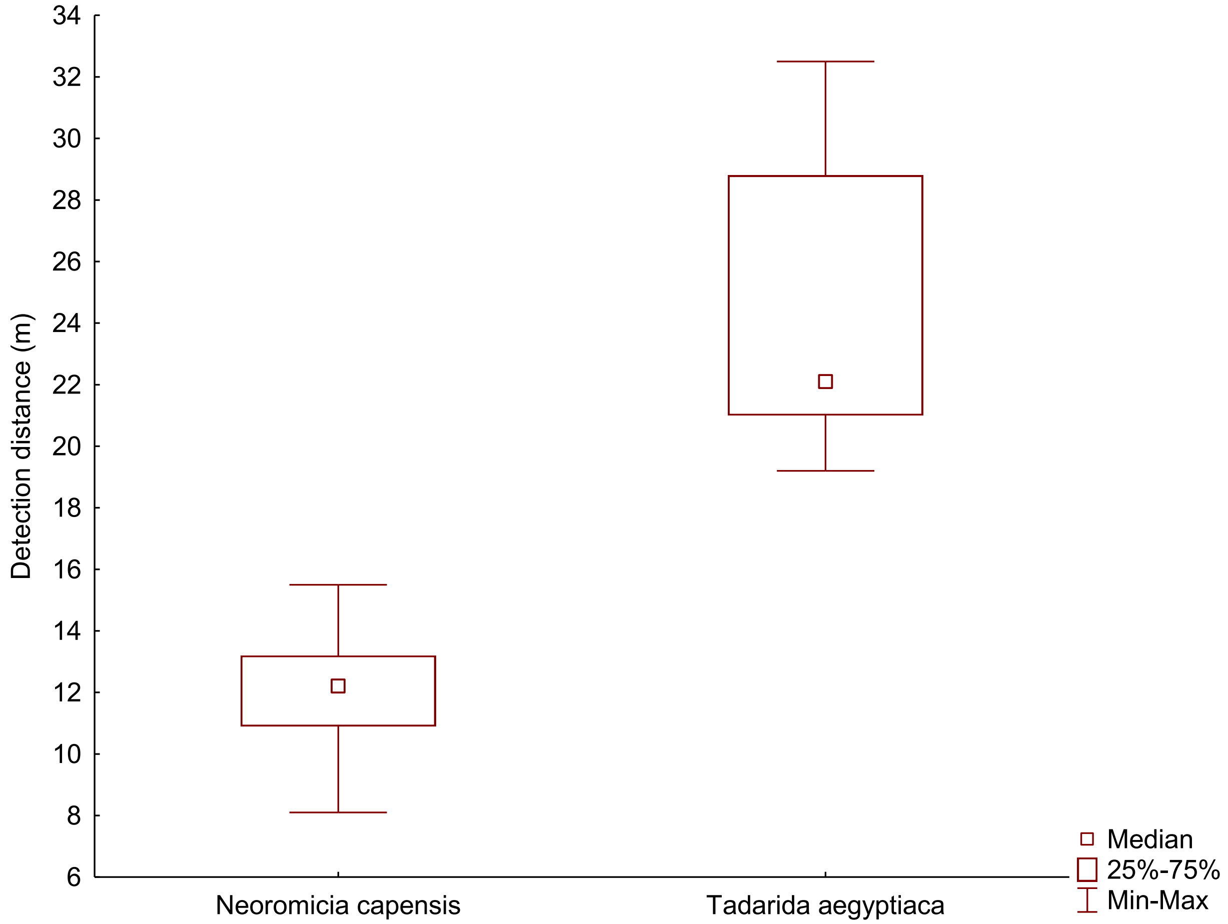

Figure A13: Box-plot showing the estimated maximum detection distance (m) for a large size insect between the two species of bats *Neoromicia capensis* and *Tadarida aegyptiaca*.