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Ecological niche partitioning and resource utilization in two sympatric lacertid lizard species (*Meroles anchietae* and *M. cuneirostris*) from the Namib Desert

By

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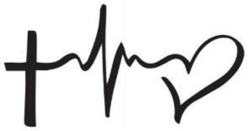
Dedication

I dedicate this work to my sister Tia Saara Ndafudha Iiyambo for believing in me.

I see in her what she sees in me.

Remember this quote: "Never let the books get to you, senses are free".



1 Corinthians 13: 13

DECLARATION

I, Novald Kandali Iiyambo, the undersigned hereby declare that the dissertation, which I hereby submit for the degree of Master of Science (Zoology) at the University of Pretoria, is my own work and has not previously been submitted by me for a degree at this or any other tertiary institution.

SIGNATURE……………………………
DATE……08 February 2019..………………

GENERAL ABSTRACT

The ability of two lizard species to co-exist within one habitat requires divergence into one or more niche dimensions (i.e., spatial, temporal and trophic) to reduce competition. Coupled with a scarcity of resources, the Namib Desert is an arid ecosystem with a high lizard diversity and presents an ideal ecosystem to investigate niche partitioning in lizards. In the Namib, fog is the main source of moisture and due to climate change, the Benguela Current which is responsible for most of the climatic patterns on the western coast of Namibia is warming, which could reduce fog production. Biodiversity response to changing climate has been of great concern in many recent studies. Species generally respond to challenges of climate change by shifting their climatic niches along space, time and organismal (i.e., physiology). The present study aimed to assess the nature and extent of genetic and morphological variation between populations of two sympatric lizard species: The shovel-snouted lizard, *Meroles anchietae* and the wedge-snouted lizard, *M. cuneirostris* of the Namib Desert in Namibia. The study also investigated the seasonal (autumn and spring) ecological niche differences between populations of the two lizard species, addressed through comparing three niche dimensions (space, time and food), focusing on the significant microhabitat separation of these populations. Seasonal influence of fog on the morphology and thermal biology of populations of the two species was also examined. Sampling in winter was not considered because of low lizard activity, while sampling in summer was not possible due to logistical constraints. Mitochondrial cytochrome *b* gene sequencing recovered two monophyletic clades within *M. cuneirostris*, Clade A (comprising of sequences from the central Namib Desert) and Clade B (comprising of sequences from the southern Namib Desert), with a 96% bootstrap support, and one monophyletic clade comprising *M. anchietae* from the central Namib Desert, Namibia, with a 99% bootstrap support. Although the genetic identity of the two lizard species was confirmed, the results of the molecular analysis suggest further investigations of genetic variation particularly in *M. cuneirostris* from the southern-most areas of its geographical range. Space niche dimension contributed significantly to the microhabitat separation of *M. anchietae* and *M. cuneirostris* (and its associated clades). All three clades indicated a bimodal pattern of activity and an omnivorous diet. The effects of fog were compared between coastal and inland populations of Clade A of *M. cuneirostris* and *M. anchietae.* Clade B *M. cuneirostris* was not considered due to the lack of fog data from the sampled area. The snout-to-vent length of the inland *M. anchietae* was shown to be negatively correlated with the amount of fog. Body temperature of the inland Clade A of *M. cuneirostris* was also negatively correlated with the amount of fog. The findings of the present study contribute to better understanding of how changes in the desert ecosystems may affect the ecology of lizard species considering consequences of future climate change.

Keywords: *Meroles*, genetic identity, niche partitioning (trophic, spatial and temporal niche), fog, climate change, Namib Desert, Namibia

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CHAPTER 1

General Introduction

1.1 Introduction

Communities are composed of organisms that co-exist and interact with one another in a particular habitat (Pianka 1973; Parejo & Aviles 2015). These interactions contribute to community properties such as energy flow, trophic structure, species diversity and relative abundance to ensure stability within a community (Pianka 1973; Ricklefs 1979; Patterson *et al.* 2003). Because of difficulties involved with studying an entire community, the focus is typically on convenient and tractable subsets of a community, usually taxonomic (Pianka 1973; Patterson *et al.* 2003). Co-existence of closely related species in a community has historically been the subject of considerable debate by ecologists (Pianka 1974; Belovsky 1986; Codron *et al.* 2007; Uno *et al.* 2011; Kartzinel 2015). A species' niche is influenced by biotic and abiotic factors, resource use and competition (Elton 1946; Hutchinson 1957), and a competitive interaction among species reflects niche partitioning (Parejo & Aviles 2015), which can be determined by analysis of ecological niches in sympatric species (Pianka 1973; 1986; Ricklefs 2008; Kartzinel 2015).

A summary of the structure of lizard communities and niche relationships among sympatric lizard species was given by Pianka (1973) who gave four different explanations on how the number of species co-existing in a particular community differ, namely: (1) diverse communities have a great variety of available resources (Finke & Snyder 2008), thus hosting only a few co-existing species and *vice-versa*; (2) species of a particular community, on average, may use smaller diversity of available resources; (3) communities with similar ranges of resources may differ in the density of species depending on the degree of overlap in resource use; therefore, greater overlap may result in more species using every resource available; and (4) communities may not contain the full diversity of species they could feasibly support and the density of species may differ depending on the degree of exploitation of resources available by many different species (Pianka 1973). MacArthur (1972) summarized the above-mentioned factors by the following equation:

$$N = \frac{R}{\bar{U}}\left(1 + C\frac{\bar{O}}{\bar{\bar{H}}}\right)$$

where N is the total number of species in a community, R is the total range of available resources utilized by all species, $\bar{U}$ is the variety of resources used by a species (average niche breadth), C is the measure of the potential number of neighbours in niche space, which increases with total niche dimensions utilized, and $\bar{O}/\bar{H}$ is the degree of overlap in niche dimensions between average sympatric species (MacArthur 1972; Pianka 1973; Magurran 2004; Ferreira & Patrere 2007).

Several studies have indicated the lack of understanding of how time influences ecological interactions and community structures (Jaksic 1982; Schoener 1986; Wiens *et al*. 1986; Albrecht & Gotelli 2001; Kronfeld-Schor & Dayan 2003). Temporal partitioning of a niche may encourage co-existence between predators and prey and among competitors (e.g., Schoener 1974; Wiens *et al*. 1986; Albrecht & Gotelli 2001). Due to difficulties in studying entire communities, the interest is usually on convenient subsets of communities such as plant, fish or bird communities (Pianka 1973). The focus of the present study is on reptile communities. In an ecosystem, reptiles play important roles as grazers, seed dispersers, prey, predators, and symbiotic species (Paine 1980). They serve as biological indicators of health conditions and provide ideal study organisms to indicate differences in biological and evolutionary processes (Read 1998; Raxworthy *et al*. 2008). Compared to other vertebrates, reptiles have narrower distributional ranges (Anderson 1984; Anderson & Marcus 1992), making them more vulnerable to anthropogenic threats such as habitat fragmentation, environmental pollution and over-harvesting (Anderson 1984; Anderson & Marcus 1992; Ettling & Schmidt 2015), and they are therefore, a taxonomic group of conservation concern (Bohm *et al*. 2013; Ettling & Schmidt 2015). Studying niche partitioning is therefore important to understand how similar species divide their habitats to avoid or reduce competition for resources (i.e., food and shelter). Interest in lizard ecology has increased in the last 20 years partially because lizards are viewed as "model organisms" (Huey & Pianka 1983; Luiselli 2007, 2008), and play important roles in ecosystems.

Two kinds of studies have dominated attempts to understand patterns within lizard assemblages. Firstly, comparative studies of entire lizard assemblages (for reviews, see Pianka 1986; Schoener 1974; Vitt 1991) and secondly, experimental manipulations performed on portions of lizard assemblages (Schoener & Spiller 1987a). Previous studies indicated niche partitioning in sympatric species to occur in three fundamental dimensions, namely, spatial (space), temporal (time) and trophic (food) (Schoener 1968; Pianka 1973; Vitt *et al*. 1981; Vitt & Carvalho 1995; Kronfeld-Schor & Dayan 2003; Luiselli 2008). In other words, species differ in times at which they are active, the spaces they use, and/or the food they eat (Pianka 1973; Luiselli 2008), although the causes underlying this apparent partitioning are complex. Such differences in activities result in niche separations, reduced competition, and most likely allow co-existence of a variety of species (Hutchinson 1957; MacArthur 1972). Although dealing with subsets of lizard assemblages, experimental studies have provided insights into mechanisms causing differences in relative abundances as well as differences in habitat utilization (e.g., Schoener & Spiller 1987b; Spiller & Schoener 1988).

1.1.1 Niche dimensions

Among lizards, the three fundamental niche dimensions of time, space and food are independent of each other but may interact (Pianka 1973). Pianka (1973) gave an example of this interrelation where the mode of foraging (active and ambush foragers) influences the three niche dimensions. To reduce inter-specific competition and facilitate co-existence, lizards may partition one or more niches (Pianka 1986; Luiselli 2008), and evidence showed that most lizards partition the spatial niche dimension (Pianka 1973, 1986; Toft 1985; Luiselli 2008). This is different from other ectotherms (e.g., snakes that partition mostly the food niche dimension; Luiselli 2006, 2008) that generally use a range of niche dimensions. Desert lizards, however, are an exception because they partition more of the temporal niche dimension (Huey *et al*. 1974; Luiselli 2006, 2007, 2008), but most experimental studies on lizards in independent habitats support more of the spatial niche dimension (Pianka 1986; Luiselli 2008).

The three fundamental niche dimensions of time, space and food are detailed below based on a study on lizard community structure by Pianka (1973):

(a) *Temporal niche*: Temporal division of activities reduces competition between lizard species because of different activity times during the day, thus leading to exploitation of different resources (Pianka 1973; Kronfeld-Schor & Dayan 2003). The most noticeable temporal separation of activities is the division into two, diurnal and nocturnal lizards, which are completely non-overlapping in time (Pianka 1973; Kronfeld-Schor & Dayan 2003). Among lizards, the temporal differences in daily and seasonal activity patterns are widespread within and between species (Pianka 1973).

(b) *Spatial niche*: The use of space differs between lizard species. Use of space in lizards range from those that are entirely fossorial or terrestrial, to those that are exclusively arboreal with various degrees of semi-fossorial and semi-arboreal activity also occurring (Pianka 1973). Species microhabitat preferences are different based on these groups. Thus, some terrestrial species forage primarily in open spaces between plants, whereas others forage mainly under or between plants (Pianka 1973). Lizards have evolved different morphological adaptations to use space in different ways (Pianka 1969; Pianka & Parker 1972; Sage 1973). Fossorial species therefore, typically have reduced appendages or have none at all. Diurnal arboreal lizards are usually long-tailed and slender, while the nocturnal arboreal lizards are usually short-tailed and fat (Pianka 1969). Terrestrial species that forage in the open between shrubs or grass clumps generally have long hind legs relative to their body size, while those that forage closer to cover or within dense clumps of grass usually have proportionately short hind legs (Pianka 1969; Pianka & Parker 1972).

(c) *Trophic niche*: The majority of lizards are insect specialist and opportunists (Arnold 1987; Perez-Mellado & Corti 1993; Cascio & Capula 2011), taking any arthropod (Capula *et al.* 1993; Corti & Cascio 2002; Corti *et al.* 2011) they encounter with little restriction on size and preferences (Pianka 1973). Larger lizard species however, tend to eat larger prey compared to smaller lizard species (Hotton 1955; Pianka 1969; Schoener 1967, 1968; Schoener & Gorman 1968). Different ranges of prey species are utilised because of differences in foraging techniques, and space and time niches (Pianka 1973). Some lizards are specialists and focus on specific prey items (Pianka & Pianka 1970; Huey *et al.* 1974; Rugiero 1994; Bonacci *et al.* 2008), whereas various herbivorous lizards are secondary carnivores that prey on eggs and young vertebrates, and adults of smaller prey species (Pianka 1966, 1969). Other factors such as length of the jaw, head proportions and dentition provide useful indicators for food niche (Hotton 1955; MacArthur & Pianka 1966; Schoener 1967), especially the body size and type of prey eaten. Another factor that influences the food niche of lizards is the way in which lizards hunt for prey (Pianka 1973). Two types of foraging behaviours have been documented (Pianka 1966, 1973; Schoener 1969, 1971; Arnold 1987), namely: (a) actively searching for prey (i.e., "widely foraging strategy"), or (b) ambush-inactively waiting for prey (i.e., "sit-and-wait strategy"). In general, the success of a sit-and-wait lizard depends on the density, mobility and energy of prey (Schoener 1969, 1971; Pianka 1973). The effectiveness of the widely foraging tactic depends on the same factors, but in this case, the distribution of prey in space and a predator's ability to search for prey is more important (Schoener 1969, 1971).

Pianka (1973) explained the interaction between the three fundamental niche dimensions of time, space and food, as detailed below:

The interaction between time, space and food niche dimensions: A lizard's space and food niches change with time, both during the day and between seasons (Pianka 1973). When air and substrate temperatures are low, lizards position themselves in warmer microhabitats, such as depressions, side of a rock, slope or tree with direct sunlight (Pianka 1973; Hertz & Huey 1981; Carrascal *et al.* 1992; Bauwens *et al.* 1996; Webb & Shine 1998). Often an animal orients its body at angles of direct sunrays, maximizing heat gained from the sun (Pianka 1973; Heatwole & Johnson 1979; Martins *et al.* 1995; Kearney & Predavec 2000). Later during the day when temperatures rise, the same lizard spends most of its time in the cooler microhabitats such as shady spots underneath shrubs or trees (Schoener 1969; Pianka 1971b; Huey *et al.* 1989; Kearney & Predavec 2000; Kearney 2002). Finally, when surfaces get very hot, lizards move into cool burrows and, some species climb off the ground into spaces with cooler air (Heatwole 1970; Pianka 1971a, 1973). Thus, the time at which an individual is active strongly affects the lizard's space niche and its habitat and microhabitat requirements may dictate the time when the animal can be active (Pianka 1973).

The mode of foraging or the way in which a lizard uses space can influence both its space and food niches; thus, widely foraging species typically have broader space niches than sit-and-wait species, while the latter types of foragers often tend to have broader food niches than the former (Pianka 1973). Furthermore, the food and time niche interact when a lizard's diet composition changes as the relative abundance of prey fluctuates with season (Pianka 1973). Consequently, nocturnal lizards encounter a different range of prey items than diurnal lizards, and those that forage in different spaces usually encounter different prey (Pianka 1973). Therefore, lizard species that overlap highly along one niche dimension may overlap lowly along another niche dimension (Pianka 1973).

Arid regions commonly have higher lizard biomass and species diversity than those in wetter areas, and as such, most ecological studies on saurofaunas are on desert species (Pianka 1967). Desert lizard community studies have, therefore, been used to improve the understanding of ecological and bio-geographical principles on niche partitioning (Schoener 1971; Pianka 1986; Murray *et al*. 2015). The Namib Desert in Namibia is one of the hyper arid deserts in Africa and is known to support high levels of lizard endemism (Herrmann & Branch 2013; Murray *et al*. 2015).

1.1.2 The Namib Desert

Namibia is a dry country with higher rainfall in the northeast compared to the southwestern parts of the country (Seely & Henschel 1998). To the west coast of Namibia is the Namib Desert (Figure 1.1), a hyper arid desert, about 140 km wide, and expanding along the west of the Atlantic Ocean coastline (Kimura 2005). The Namib Desert is about 2000 km long from the mouth of the Orange River in the extreme northwest of South Africa to Mossamedes in southern Angola (Bakker 1975) and receives less than 50 mm of rainfall per year and between 0 and 12 mm in the western half (Henschel & Seely 2008). The Namib Desert lies along the cold, upwelling Benguela Current that is responsible for most of the fog produced (Schulze 1969; Seely & Stuart 1976; Lancaster *et al.* 1984; Seely & Henschel 1998). Although the Namib Desert is considered to be hyper arid, with low rainfall, several other sources of atmospheric moisture are present, such as dew, humidity and fog, that makes it possible for organisms to survive (Henschel & Seely 2008). Organisms in the desert use these moisture sources in different ways including drinking from wet surfaces, locating moist micro-climates, collecting water on their bodies (such as the well-known Namib Desert fog basking beetle – *Onymacris unguicularis*; Seely & Henschel 1998), consuming moist food, and absorbing water vapour (Seely & Henschel 1998; Henschel & Seely 2008).

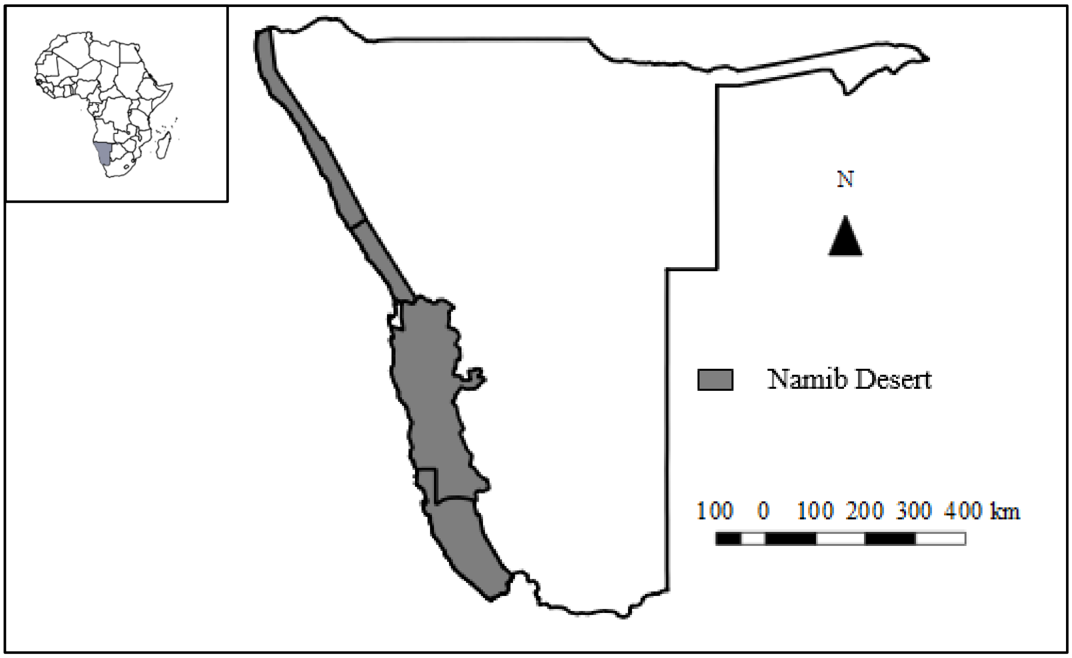


Figure 1. 1: A map of Namibia showing the Namib Desert.

1.1.3 Fog

Among the several sources of atmospheric moisture, fog is the most important source of water in the Namib Desert and its density and distribution is influenced by the climatic pattern of the western part of the desert because of the Benguela Current (Schulze 1969; Seely & Stuart 1976; Lancaster *et al.* 1984). There is an increase in fog and decrease in rainfall towards the west of the Namib Desert (Hachfeld 2000; Soderberg 2010) (Figure 1.2). The distance from the coast has impacts on the density and distribution of fog along the Namib Desert, however, other factors such as geographic location and elevation may affect the density and distribution of fog (Lancaster *et al*. 1984). Fog is more predictable and is responsible for five times more water than rain (Pietruszka & Seely 1985). Hence, fog serves as a major source of water for most desert life such as lichens, plants and animals (Seely 1979; Seely & Henschel 1998) and influences the geological processes within the Namib Desert (Martin 1963; Eckardt 1996; Goudie 1972). Availability of fog as a source of water may have implications on desert biota, including lizards, when changes in fog patterns are experienced (Seely 1979).

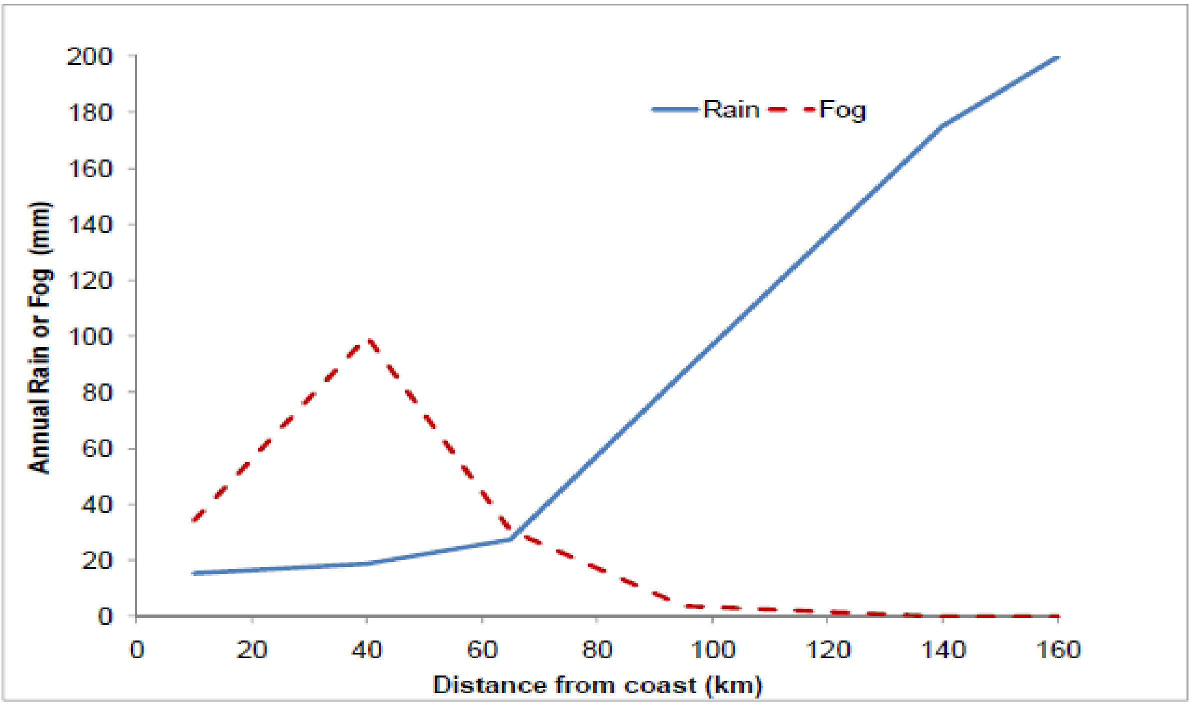


Figure 1. 2: The occurrence of fog and rainfall in relation to the distance from the Namib Desert coast, Namibia (Adopted from Soderberg 2010; after Lancaster *et al.* 1984).

Unlike rain, fog is a more frequent and reliable source of moisture (Louw 1971; Shanyengana *et al*. 2002; Henschel & Seely 2008) and occurs between 60 and 200 days per year along the coast but also extends some distance inland (Shanyengana *et al*. 2002). In the Namib Desert, fog is created by temperature inversion of hot air from the interior that passes over the cold waters of the Benguela upwelling regions and cooled until it reaches saturation (Haensler *et al*. 2011a). Based on climate predictions, however, the Benguela Current may be warming, which may result in less fog (Belkin 2009; Haensler *et al.* 2011a, b). Climate change influences populations of ectotherms because they rely on their external environment to raise their body temperature (Lourdais *et al.* 2004; Chamaille-Jammes *et al.* 2006). In Europe, the bioclimatic reptile models predict a decline in species range because of decreased suitable habitats, however, positive influence of warming have been documented for some species, expanding their range

(Lourdais *et al.* 2004; Araujo *et al.* 2006; Chamaille-Jammes *et al.* 2006). Consequences of climate change on reptiles highly depend on their balancing need for heat and water (Araujo *et al.* 2006). Precipitation (i.e., rainfall and fog) is related to humidity as it may influence lizard activity patterns, consequently influencing their growth (Lorenzon *et al.* 1999; Sears & Angilletta 2003). Precipitation may also influence food webs (i.e., prey abundance and composition) and habitat (i.e., soil moisture) (Tinkle *et al.* 1993). Apart from the direct influence of precipitation on activity patterns, it may therefore, potentially have cascading consequences on lizards' demography through environmental and trophic effects (Marquis 2008).

Despite the warming Beguela Current, evidence indicate significant increases in surface temperatures in Africa (Boko *et al*. 2007; Niang *et al*. 2014; Engelbrecht *et al*. 2015). Because lizards depend on the environmental temperature to maintain their body temperature (Porter & Tracy 1983), their body temperature is higher with higher environmental temperatures (Huey 1982). In ectotherms, body temperature affects behavioural and physiological processes such as immune function, growth rate, locomotion, foraging ability and sensory input (Greenwald 1974; Dutton *et al.* 1975; Bennett 1980; Stevenson *et al.* 1985; Ayers & Shine 1997; Weinstein 1998; Kingsolver & Woods 1997; Ojanguren & Brana 2000; Mondal & Rai 2001; Angilletta *et al.* 2002). Ectotherms respond to changes in the thermal environment through shifting their behaviour and physiology to regulate their body temperatures (Casey 1981; Hutchinson & Dupre 1992; Angilletta 2002). The performance function in ectotherms however, can be improved through adaptation to environmental temperature (Angilletta *et al.* 2002). Thermal physiological adaptations involve modification of cell membranes, expression of allozymes and alteration to the intracellular environment that may not be reversible (Somero & Dahlhoff 2008). Thermoregulation can also be improved by phenotypic changes through adaptation (i.e., change in the structure of the epidermis and increased vascularization) (Angilletta *et al.* 2002).

1.1.4 Species distribution

The Namib Desert is considered as one of the driest and oldest deserts in the world (Ward *et al*. 1983; Hartley *et al*. 2005; Herman & Branch 2013) with diverse reptile species (Griffin 2000, 2003; Herrmann & Branch 2013). To this end, the present study focused on two sympatric lacertid species endemic to the Namib Desert; the shovel-snouted lizard (*Meroles anchietae*), which ranges from the Klinghardt mountains to southern Angola, and the wedge-snouted lizard (*M. cuneirostris*), which is restricted to southern Namib Desert from Richtersveld – the border of the extreme northwest of South Africa to Walvis Bay (Figure 1.3) (Branch 1998). These diurnal, terrestrial lizards are well-adapted for desert life with the ability to cope with desert extremes of low water availability, through conserving water by decreasing their output or obtaining more water each day by increasing their water input (Nagy 2004), and high surface temperatures through behavioural, physiological and morphological adaptations (Herrmann & Branch 2013; Murray *et al*. 2015).

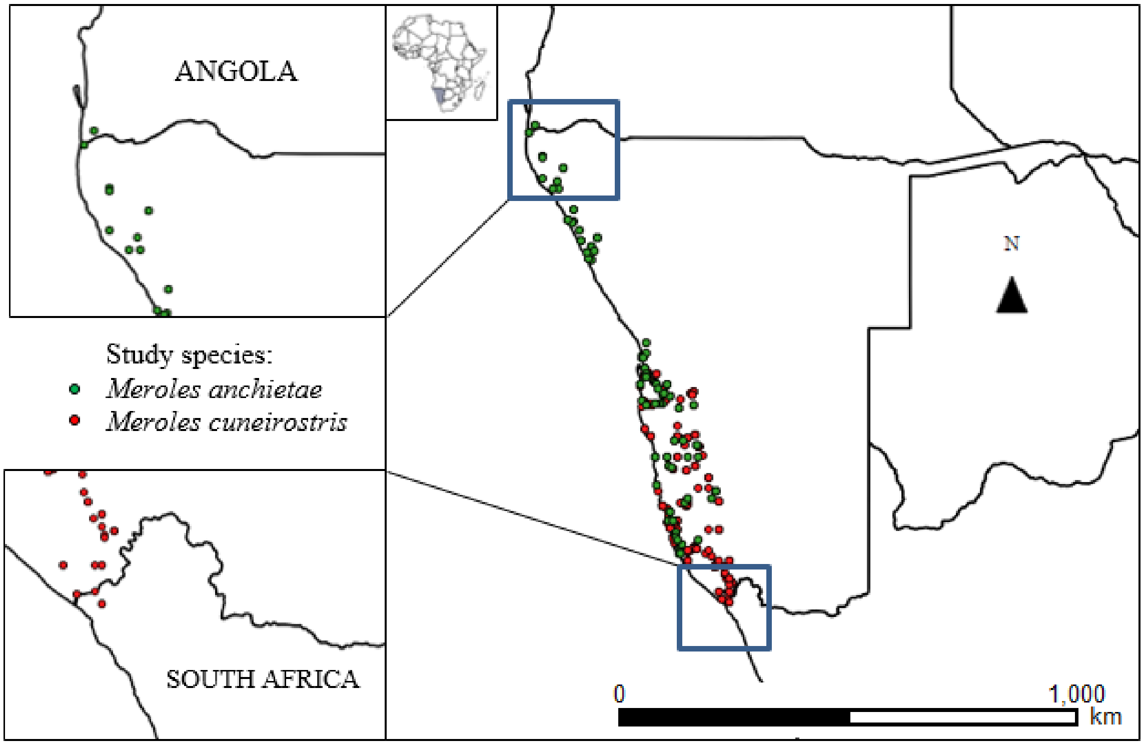


Figure 1. 3: The distributional range of the shovel-snouted lizard (*Meroles anchietae*) and the wedge-snouted lizard (*M. cuneirostris*) in the Namib Desert, Namibia.

To study niche separation, there is a critical need to compare the morphological differences, characteristics of preferred microhabitat, behavioural activity patterns, feeding ecology and thermal biology of species that share the same niche (Murray *et al*. 2016). The present study will allow insights into the understanding of species seasonality (spring and autumn) and the effects of fog on lizard ecology. Another way morphologically similar species may co-exist is through a non-overlap pattern of resources used (Murray *et al*. 2016).

Consequently, the observed movement behaviour of the two lacertid lizard species have indicated activities that encroach into each other's territories and therefore, expected to result in competition for resources.

Study species

The shovel-snouted lizard, *M. anchietae* (Bocage, 1867) (Figure 1.4A), is a small (3-6 g) lacertid lizard endemic to the Namib Desert (Robinson & Barrows 2013). Robinson and Burrows (2013) described the distribution of *M. anchietae* to coincide with two large dune fields that are approximately 300 km apart. The north dunes extend from the south of the Curoca River in Angola to the Unjab River in Namibia (Robinson & Barrows 2013). The dunes in the south field extend from the south of the Kuiseb River towards Chamais Bay near the Orange River (Robinson & Barrows 2013). Based on Griffin (2003), the northern and southern populations of *M. anchietae* are different morphologically and genetically. Goldberg and Robinson (1979) reported on the reproductive activity of *M. anchietae* that declined in March 1977, and increased in April (reproduction completed by June, and continued again in December). The causes of declined reproduction in March 1977 were not clear, but it appeared to be associated with the decreased rainfall and low production of insects as prey (Goldberg & Robinson 1979). Eighty-five female clutches were averaged to 1.3 eggs (range 1-2) per clutch, and between two and four clutches were produced yearly (Goldberg & Robinson 1979).

Figure 1.4: *Meroles anchietae* (A) and a male *M. cuneirostris* (B) endemic to the Namib Desert, Namibia.

Meroles anchietae prefers habitats with loose deep sand on the inclined dune steep slipface, but may on rare occasions venture onto the nearby dune bases (Louw & Holm 1972; Robinson & Seely 1980; Robinson & Barrows 2013). Older males appear more intensely coloured than the yellowish beige females (Branch 1998; Robinson & Barrows 2013). Several other species of *Meroles* (*M. ctenodactylus*, *M. micropholidotus* and *M. cuneirostris*) sand-dive and inhabit flatter shallow areas away from the slipface (Arnold 1995; Robinson & Barrows 2013). Observations indicated the lizards taking advantage of condensed water from fog (Louw 1972; Louw & Holm 1972; Louw & Seely 1982). *Meroles anchietae*, also known as the sand-diving lizards, is well known on television documentaries for the dance they perform when on hot sand as they regulate their body temperature and for the speed, they can run on the dunes, even up the steepest slipface.

The wedge-snouted lizard, *M. cuneirostris* (Strauch, 1867) (Figure 1.4B), is a small (5-9 g) (Murray & Schramm 1987; Childers & Eifler 2015) lacertid lizard also endemic to the Namib Desert (Branch 1998; Childers & Eifler 2015). Coloration matches sand colour, and the back may be greyish, sand-coloured or reddish-brown with pale spots and dark flecks (Branch 1998). This species sprints between tufts of vegetation on sand hummocks but has also been observed sun basking on the dune slipface during cold sunny periods (Robinson & Cunningham 1978; Murray & Schramm 1987; Branch 1998; Childers & Eifler 2015). In addition, a dietary study by Murray & Schramm (1987) described *M. cuneirostris* using both active and ambush (sit-and-wait) foraging tactics. Their diet varies seasonally, depending on the availability of food. During summer, they eat adult beetles, but feed on termites and other small insects during winter (Branch 1998). The species have also been observed foraging in the cool morning and evening, and often sits next to ant paths and termite mounts as they wait for the ants and termites to emerge (Murray & Schramm 1987). The reproductive cycle of *M. cuneirostris* is like that of a temperate zone species, with spermatogenesis occurring between August and February (spring-summer) (Goldberg & Robinson 1979). Goldberg & Robinson (1979) described 29 females with a clutch size averaging 2.9 eggs (range 1–4), and that in each year, females may produce two clutches. Branch (1998) reported that females lay between 2 to 4 eggs and bury them up to approximately 600 mm below the surface (Branch 1998). Both *M. anchietae* and *M. cuneirostris* have seasonal cycles of fat bodies extending to autumn and the fats are used up by spring, however, the amount of fat stored depends on the species (Goldberg and Robinson 1979).

To understand the causes of genetic variation among and within individual populations of the same species requires studies on phenotypic variation (Jetz *et al.* 2009; Garcia-Rosales *et al.* 2017). Factors influencing genetic variation, such as the ecology of the species and the geology of the environment, provide the necessary description for differentiating populations (Meiri & Dayan 2003; Pincheira-Donoso *et al.* 2008; Garcia-Rosales *et al.* 2017). Genetic variation within populations has a potential to contribute to speciation, thus providing a basis for ecological and geographic trends such as differences in an organism’s body size across latitudinal and altitudinal gradients (Meiri & Dayan 2003; Pincheira-Donoso *et al.* 2008; Garcia-Rosales *et al.* 2017). Environmental differences across populations of the same species lead to adaptive divergence in ecological characters (Edwards & Kot 1995). Morphological differences among population of the same species may be related to differences in climate, the availability and quality of the resources, size-specific predation, sexual selection, competition and population density (Berven & Gill 1983; Massot *et al.* 1992; Sandland & Minchell 2004; Hileman *et al.* 2017; Wei *et al.* 2018). Food availability across climatic gradients due to seasonal differences also affects body size patterns (Murphy 1985; Meiri *et al.* 2005). For example, most ectotherms grow larger in relations to lower temperatures (Atkinson 1994; Angilletta & Dunham 2003; Horvathova *et al.* 2013), whereas some grow smaller in relation to lower temperature (Ashton & Feldman 2003; Cvetkovic *et al.* 2009). Although the Namib Desert support high levels of lizard endemism (Hermann & Branch 2013; Murray *et al.* 2015), the genetic and morphological variation of populations is not well-documented. The present study therefore, attempts to address this knowledge gap in order to gain insights into the causes of variation in lizard populations.

Study area

The study was conducted on the dunes of the Namib Desert in Namibia (24°45′4.19S, 15°16′21.00E). Although the Namib Desert generally appears to support no life, at night, there is an array of activities from various organisms, such as insects, snakes and geckos (Van Damme 1991). Part of the Namib Desert, the ‘Namib Sand Sea’ (24°53′7S, 15°24′28E), has been proclaimed as a world heritage site since 2013 because of its natural beauty, ability to host natural phenomena, record of ancient life, on-going geological, ecological and biological processes as well as its ability for *in-situ* conservation of threatened species and for the outstanding contribution to the universal value of science (UNESCO World Heritage Centre 1992-2017).

Study site

Sand dunes with little vegetation cover are characteristic of the Namib Desert. Vegetation cover consisting mainly of grasses and shrubs are sparsely located at the base of the dunes (Childers & Eifler, 2015). The dune habitat appears most hostile, consisting of bare dune sand, with steep slipface on the side of the barchans formation (Holm & Edney 1973). The dunes consist mainly of the tall, spiky clusters of dune Bushman's grass (*Stipagrostis sabulicola*), that usually forms hummocks at the dune base (Holm & Edney 1973; Childers & Eifler 2015). Species of love-grass (*Eragrostis sp*.) are also more commonly distributed on gravel plains of the inter dune systems (Holm & Edney 1973; Childers & Eifler 2015), and to a lesser extent, the endemic !nara plant, *Acanthosicyos horridus* (Hughes *et al*. 1994), that occurs in individual clusters of sandy hummocks. The spiky grass, *Stipagrostis sabulicola* may grow up to 2 m high with seeds produced during summer after when sufficient rainfall (Hughes *et al*. 1994). The sharp thorny leaves of the !nara plant grows up to 1.5 m high in dense bushes (Robinson 1976; Hughes *et al*. 1994) and spreads over a few meters wide (Craven & Marais, 1986; Hughes *et al.* 1994). The melons produced by the female plants only ripen during summer (October to February) and animals such as jackals, ostriches, rodents as well as humans commonly feed on them (Robinson 1976; Hughes *et al*. 1994). Based on an intra-specific behavioural study by Childers & Eifler (2015), *M. cuneirostris* has been observed using the *S. sabulicola* grass and the *Acanthosicyos horridus* plant for cover from over-heating when the sand is hot and as an escape tactic from predators.

The lizard species investigated in the present study occupy the dune habitat with *M. anchietae* preferring the loose sand on the slipface and *M. cuneirostris* inhabiting the base of the dune (Figure 1.5). Observations (*pers. obs.*) however, show the two species running in and around both habitats from one side of the dune to the other. The slipface has little or no vegetation, whereas the bottom has plenty of vegetation cover.

Figure 1. 5: Habitat preferences of *Meroles anchietae* and *M. cuneirostris* showing the dune slipface and dune base as part of the study area in the Namib Desert, Namibia.

1.2 Aims of study

Given the above background, the aims of the present study were to investigate the seasonal (autumn and spring) ecological niche differences between populations of *M. anchietae* and *M. cuneirostris* endemic to the Namib Desert by comparing three niche dimensions of food, space and time, and assessing their contributions to the microhabitat separation of the populations of the two lacertid lizard species. Sampling in winter was not considered because of low lizard activity, while sampling in summer was not possible due to logistical constraints. The study also investigated the seasonal influence of fog on lizard morphology and thermal biology to assess the potential influence of climate change on the behavioural ecology of the populations of the two lacertid lizard species. To understand the ecological niche and fog effects, the genetic and morphological differences between populations of the two lacertid lizard species were first investigated.

1.3 Research questions

The present study therefore attempted to address the following key research questions:

1. What are the important genetic and morphological differences between populations of the two species?
2. What is the nature and extent of the seasonal contribution of the three niche dimensions of time, space and food to the microhabitat separation of the populations of the two lacertid lizard species?
3. Does the seasonal variation in fog density influence the morphology and thermal biology of the populations of the two lacertid lizard species?
4. Is there a resource use overlap between the populations of the two lacertid lizard species?

1.4 Research hypotheses

The present study tested the following research hypotheses:

Hypothesis 1:

H_0: There are no genetic and morphological differences between the populations of the two lacertid species.

H_a: There are genetic and morphological differences between the populations of the two lacertid lizard species.

Hypothesis 2:

H_0: Time, space and/ or food niche dimensions seasonally contribute to the separation of the microhabitat of the populations of the two lacertid lizard species.

H_a: Time, space and/or food niche dimensions do not seasonally contribute to the separation of the microhabitat of the populations of the two lacertid lizard species.

Hypothesis 3:

H_0: Seasonal fog density does not influence the morphology and thermal biology of the populations of the two lacertid lizard species.

H_a: Seasonal fog density influences the morphology and thermal biology of the populations of the two lacertid species.

Hypothesis 4:

H_0: There is no resource use overlap between populations of the two lacertid lizard species.

H_a: There is resource use overlap between populations of the two lacertid lizard species.

1.5 Relevance of study

The increase in human activities, contributing to global climate change, influences the increase in atmospheric temperatures (Pachauri *et al.* 2014). Consequently, the increasing surface temperatures contributes to the reduction of fog production on the coastal Namib Desert with future predictions indicating a decrease in the number of days of fog events per year (Haensler *et al.* 2011a). Life in the coastal zone of the Namib relies heavily on fog as a source of moisture and a coolant of the desert surface (Louw 1972; Seely 1979; Seely & Henschel. 1998; Henschel & Seely 2008; Murray *et al.* 2014). Lizards rely on their external environment to allow for daily their activities such as feeding, finding mating partners, and to regulate their body temperature (Porter & Tracey 1983; Lourdais *et al.* 2004; Chamaille-Jammes *et al.* 2006). With increasing surface temperature, lizard species may reduce their distributional range because of decreased suitable habitats; however, some species may expand their ranges because of the positive influence of climate change (Lourdais *et al.* 2004; Araujo *et al.* 2006; Chamaille-Jammes *et al.* 2006). The present study may allow insights into how geographically separated lizard populations of the same species behave in response to variation in fog density, for predicting how they may survive the influence of changing climate. Species that depend on fog and lower surface temperatures may retract in distribution through migration or become extinct, while other species that are less reliant on fog, or which prefer higher temperatures, may expand their distributional range, leading to potential shifts in behaviour. Putting pressure on fog as a water source may eventually have effects on the resources used by the two lacertid lizard species such as food and water. Species in an ecosystem depend on each other for trophic relationships involving role players such prey, predators, commensal organisms and seed dispersers, therefore, alteration in their availability may cause changes in food chains and webs (Paine 1980), and as a result, the dominant species may take over the least dominant species.

1.6 Study approach

The study focused on five sites on the dunes of the Namib Desert, Namibia. Four sites (Kuiseb Delta, Rooibank, Near Gobabeb and Far Gobabeb) were located in the central Namib Desert (west to east; coast to inland) for niche overlap studies and the other (Oranjemund) located further south of the Namib Desert to account for genetic differences in the population and control sites for non-overlapping niches (Figure 1.6). The sites Near Gobabeb (10 km) and Far Gobabeb (20 km) were named according to the distance away from Gobabeb Research and Training Centre, located in the central Namib Desert in the Namib Naukluft Park. Specimens were sampled and maintained under the Research and Collection permit number 2171/2016 issued by the Ministry of Environment and Tourism, Namibia, the Non-invasive Research permit number GRP 2016-04.3 issued by the Gobabeb Research and Training Centre, Namibia, and the Animal Ethics permit number EC036-16 issued by the Animal Ethics Committee of the University of Pretoria, South Africa. All samples were transported to the laboratory at the University of Pretoria, South Africa for analysis with export permit number MET 69515 issued by the Ministry of Environment and Tourism, Namibia and the import permit P0080298 issued by the Department of Agriculture, Forestry & Fisheries, South Africa. All permits and approvals are included in Appendices 1 to six.

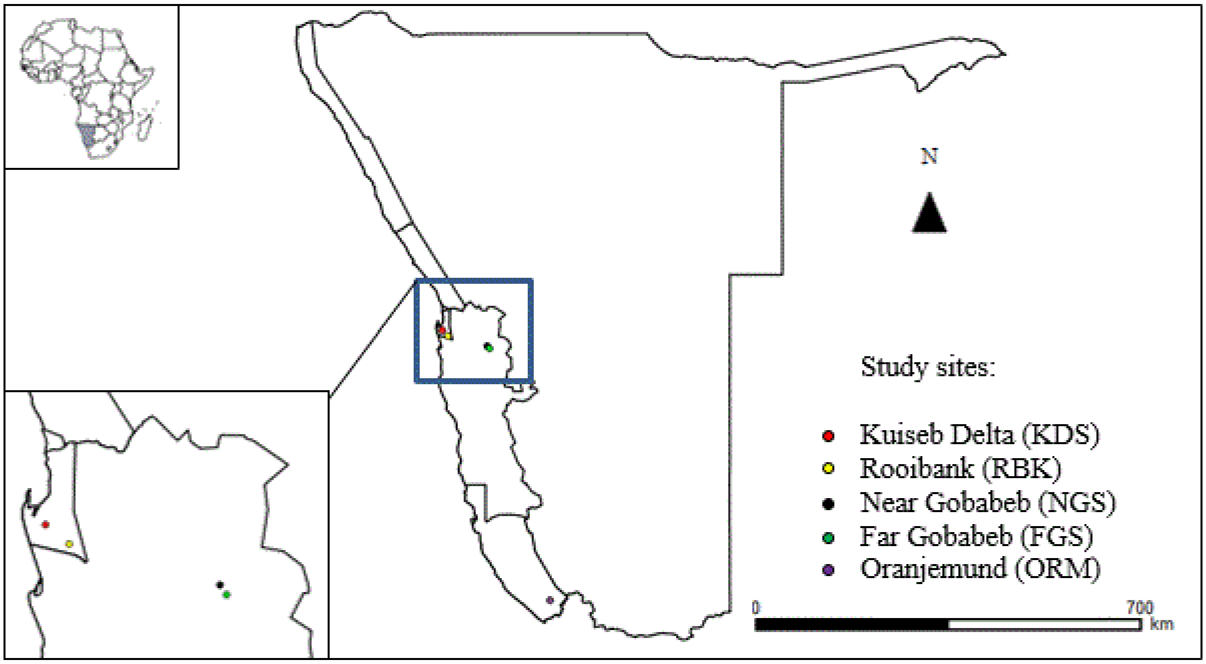


Figure 1. 6: A map showing the sampling sites of species of the genus *Meroles* in the Namib Desert, Namibia sampled between September 2016 and April 2017.

The lizards sampled were used to assess genetic and morphological variation between the populations of the two species. Faecal pellet and stable isotope analyses were used to quantify the dietary variation between populations of the two species. Data on lizard morphology and thermal biology were linked with the opportunistically available data on fog (depending on the location of a fog station) to assess the seasonal (autumn and spring) influence of fog density on the behavioural ecology of the populations of the two species. Although the hypotheses included multiple factors affecting multiple responses, each hypothesis was accepted or rejected based on individual effects of each predictor variable on each response variable for the populations of the two species.

1.7 Study outline

The first part of this study (Chapter 2) investigated the genetic variation among populations of *M. anchietae* and *M. cuneirostris* from the Namib Desert, Namibia. In this chapter, the study also assessed the seasonal differences in morphology, microhabitat preferences, thermal biology and behavioural activity of the populations of the two species. Chapter 3 assessed the diet of the populations of *M. anchietae* and *M. cuneirostris* by evaluating the possibility of trophic niche partitioning by measuring dietary niche breath (the range of food types each species feeds on) and dietary niche overlap (the overlap in food type between populations of the two sympatric species). Chapter 4 focused on the assessment of the influence of fog on the morphology and thermal biology of the populations of *M. anchietae* and *M. cuneirostris*. Lastly, Chapter 5 provides a general discussion and conclusions on the findings in this study and highlights its limitations, and with recommendations for future studies.

CHAPTER 2

Genetic and morphological differences, microhabitat preferences, thermal biology, and daily activity patterns of populations of two sympatric lacertid lizard species (*Meroles anchietae* and *M. cuneirostris*) from the Namib Desert, Namibia

Abstract

Sequenced data from mitochondrial cytochrome *b* gene region were used to investigate the genetic variation among sympatric populations of two lacertid lizard species, the shovel-snouted lizard, *Meroles anchietae* and the wedge-snouted lizard, *M. cuneirostris* from the Namib Desert, Namibia. The study also assessed the differences in morphology and seasonal (autumn and spring) variation in microhabitat preferences, thermal biology and behavioural activity patterns of the two species. Because of low lizard activity during winter, sampling was not considered, while sampling in summer was not possible due to logistical constraints. DNA extracted from tail, tissue using PCR, recovered two monophyletic clades within *M. cuneirostris*, Clade A (comprising of sequences from central Namib Desert, clustered with the *M. cuneirostris* reference sequences) and Clade B (comprising of sequences from southern Namib Desert), with a 96% bootstrap support, and one monophyletic clade comprising *M. anchietae* from the central Namib Desert, Namibia, that clustered with the *M. anchietae* reference sequences with a 99% bootstrap support. The phylogenetic results suggest further investigation on the taxonomic status of *M. cuneirostris*. Individuals of Clade A of *M. cuneirostris* showed heavier body masses and longer body lengths than individuals of Clade B of *M. cuneirostris* and *M. anchietae*. During both autumn and spring, both Clade A and B of *M. cuneirostris* were observed on vegetated dune base as dominant substrate type while *M. anchietae* was observed on slipface. Clade B of *M. cuneirostris* showed lower body and air temperatures at sampling locations compared to those of Clade A of *M. cuneirostris* and *M. anchietae*. All three clades indicated a bimodal activity pattern. The results in the present study contribute to our better understanding of desert ecosystems and have highlighted the critical need to further investigate the systematics and taxonomy of lacertid lizards in the Namib Desert in Namibia.

Keywords: *Meroles*, cytochrome *b* gene, morphology, systematics, taxonomy, behavioural activity patterns, thermal biology, microhabitat, Namib Desert, Namibia

2.1 Introduction

Genetic differences within species serve as driving factors of evolutionary change (Wiens 1999). Ecological and evolutionary biologists have shown great interest in studies of phenotypic variation among and within individual populations of the same species with the aim of understanding the causes of genetic variation (Jetz *et al.* 2009; Garcia-Rosales *et al.* 2017). Ecological and geological factors leading to genetic variation provide the necessary information for differentiating populations, with potential contribution to speciation, thus providing a basis for ecological and geographic trends such as differences in an organism's body size across latitudinal and altitudinal gradients (Meiri & Dayan 2003; Pincheira-Donoso *et al.* 2008; Garcia-Rosales *et al.* 2017). Adaptive divergence in ecological characters such as morphology, physiology and behaviour is a result of environmental differences across populations of the same species (Edwards & Kot 1995). Genetic and morphological analyses have been widely used in understanding variation among populations (Hillis & Wiens 2000). To date, phylogenetic analyses based on DNA sequences are increasingly used to describe and classify species (Hillis & Wiens 2000; Marshall *et al.* 2006; Garcia-Rosales *et al.* 2017).

Although the Namib Desert is known to support high levels of lizard endemism (Hermann & Branch 2013; Murray *et al*. 2015), and there has been taxonomic studies on reptiles in Namibia (Conradie *et al.* 2012), , there has been very little documentation on variation between populations of the same species across latitudinal and altitudinal gradients. The present study therefore attempts to address this critical knowledge gap in Namibian lizards prior to addressing morphological, behavioural and physiological components of the present study.

Griffin (2003) and Lamb & Bauer (2003) reported that *M. anchietae* differs in its genetic and morphological profiles between its northern and southern populations. These differences may be related to ecological and geological factors that interact to influence phylogeographic patterns within the species (Wares & Turner 2003; Byrne 2008; Zhao *et al*. 2011). Given these *M. anchietae* profiles, the genetic and morphological profiles of *M. cuneirostris* populations may also differ. Several studies on phylogeography reveal evidence of sympatric species exhibiting diverse genetic patterns (Hewitt 2004; Gomez & Lunt 2007; Byrne 2008; Zhao *et al*. 2011), thus contributing to genetic differences between populations.

The genus *Meroles* consist of *M. ctenodactylus, M. micropholidotus, M. suborbitalis, M. reticulatus* and *M. knoxii* that inhabit a variety of environments ranging from highly to less compacted sandy habitats (Robinson & Barrows 2013) varying in substrate inclination and openness (Vanhooydonck & Van Damme, 1999). Morphological adaptations vary between *M. knoxii*, a generalist that is adapted mainly to dense substrates, to a highly derived *M. anchietae* that prefers dune slipface with loose sand (Arnold 1990, 1995; Robinson & Barrows 2013). Ward *et al.* (1983) reported that sand-diving morphological adaptations occurred with an increase in aridity and sand accumulation such that variation in morphological adaptations leads to differences in behavioural patterns such as feeding. Behavioural variation may be expressed in the form of sexual dimorphism (Childers & Eifler 2015) and age-related differences where males and females, as well as adults and juveniles, tend to differ in their use of microhabitats (Amat *et al*. 2003; Martín & López 2003), ability to move from one place to another (Xu & Ji 2006; Brecko *et al*. 2008), and activity patterns (Amat *et al*. 2003).

Desert species are usually faced with extreme climatic conditions and limited resources, and are thus of considerable interest in ecology, because species are usually forced to compete for shared resources, or partition resources by making use of different niche dimensions (Ward 2008; Childers & Eifler 2015). Within and between desert-dwelling lacertid species, niche partitioning has been documented with seasonal activity or timing of the day and microhabitat use as the most commonly observed (Pérez-Mellado 1992; Adamopoulou & Valakos 2005; Rouag *et al*. 2007; Du Plessis & Mouton 2011).

The aim of the present study is to assess the genetic variation between populations of two sympatric lacertid lizards, the shovel-snouted lizard, *Meroles anchietae* and the wedge-snouted lizard, *M. cuneirostris* from the Namib Desert, Namibia. Consequently, for this study, the genetic variation is defined to ensure correct use of the species names before analyses of morphological and seasonal (autumn and spring) behavioural comparisons between the species. Thereafter, the study investigates whether the seasonal partitioning of time (activity) and space (microhabitat) differed between the populations of the genetically defined taxa. Due to low lizard activity in winter, sampling was not considered, while in summer sampling was not possible due to logistical constraints. Environmental differences across populations of the same species often result in adaptive divergence in morphology, physiology and behaviour (Edwards & Kot 1995).

Thus, we hypothesize that the populations of *M. anchietae* and *M. cuneirostris* would differ genetically and morphologically, due to ecological and geographic variation (latitude and altitude). Furthermore, we hypothesize that there would be seasonal variation in the partitioning of time and space between populations of *M. anchietae* and *M. cuneirostris* because of the variation in the preferred microhabitat. We address these hypotheses by comparing the genetics and morphology, the seasonal partitioning of time and space niche dimensions between populations of the two species to evaluate the degree of overlap in resource use between them.

2.2 Materials and Methods

2.2.1 Molecular analyses

Sampling of the populations of the two sympatric lacertid lizards, *M. anchietae* and *M. cuneirostris* targeted five sites, namely, Rooibank (RBK), Near Gobabeb site (NGS), Far Gobabeb site (FGS), Kuiseb Delta site (KDS) and Oranjemund (ORM) along the Namib Desert, Namibia (Chapter 1). Due to differences in the distributional range of the two sympatric lizard species across the Namib Desert, *M. anchietae* was sampled from three sites (RBK, NGS and FGS) and *M. cuneirostris* sampled from all five sites. *Meroles anchietae* and *M. cuneirostris* populations were sampled using cotton mesh bags (D. A. Eifler, unpublished) and noose poles (Murray *et al.* 2016), respectively. The difference in sampling method is because of differences in lizard anti-predatory behaviour. *Meroles anchietae* buries entirely in open sand (Robinson & Barrows 2013) and mesh bags are used to sieve the sand, leaving the lizard in the bag. On the other hand, *M. cuneirostris* buries entirely in sand beneath vegetation and noose poles are used to sample them quietly to avoid burying (*pers. obs*.). The sampled lizards were later bagged in individual cotton mesh bags and transported to the nearest workstation. For each sampled individual, a tail tissue sample (approximately 5 mm) was obtained from the tail tip and stored in micro tubes at -5° C.

Genomic DNA was extracted from tail tissue (stored at -5° C) of populations of *M. anchietae* (*n* = 28) and *M. cuneirostris* (*n* = 50) using a High Pure PCR template preparation kit (Roche Diagnostics) involving a Proteinase-K digestion according to the manufacturer's protocol. Standard PCR procedures were utilized to amplify the mitochondrial cytochrome *b* (cyt *b*) gene region using the primers LGL765 5'-GAAAAACCACTCGTTGTTAATTCAACT-3' and H15149 5'-AAACTGCAGCCCCTCAGAATGATATTTGTCCTCA-3' (Meyer *et al.* 1990; Bickham *et al*. 1995; Lamb & Bauer 2003). Polymerase Chain Reaction (PCR) amplification was performed in 28 µl reaction volume containing 1U *Taq* Polymerase (Fermentas), double-distilled water (ddH$_2$O), 0.2 µM of each primer, and 100-200 ng DNA template. The thermal cycling profile consisted of initial denaturation at 96° C for 20 s, followed by two cycles of denaturation at 96° C for 12 s, annealing at 49° C for 25 s and extension at 72° C for 60 s, three cycles of denaturation at 96° C for 12 s, annealing at 47° C for 20 s and extension at 72° C for 55 s and finally 35 cycles of denaturation at 96° C for 12 s, annealing at 45° C for 15 s and extension at 72° C for 50 s with a final extension at 72° C for 1 minute. All positive DNA-extracted samples were viewed by agarose gel electrophoresis and purified using Roche PCR Product Purification Kit (Roche Diagnostics) according to the manufacturer's protocol. BigDye^{TM} Terminator v3.1 cycle sequencing kit (Perkim-Elmer, Foster City, U.S.A.) was used to sequence the purified products with forward and reverse primers in separate reactions. Samples were run on ABI 3130 sequencer. DNA sequences were viewed and edited in MEGA7 (Tamura *et al.* 2011) and a BLAST nucleotide database search (http://www.ncbi.nlm.nih.gov/blast) was used to identify *Meroles* reference species with the highest nucleotide sequence identical (≥ 98%). The species identified by the BLAST search were *M. anchietae* - AY184401.1 and *M. cuneirostris* - AY184403.1 and JX962929.1.

2.2.2 Phylogenetic analyses

Phylogenetic analysis was based on 78 individuals from the populations of *M. anchietae* (*n* = 28; 3 localities) and *M. cuneirostris* (*n* = 50; 5 localities) across their geographic range in the Namib Desert, Namibia. Only one sequence for *M. anchietae* and two sequences for *M. cuneirostris* were available on GenBank (http://www.ncbi.nlm.nih.gov). A best-fit model of nucleotide sequence evolution was identified in jModeltest (version 2.1; Posada 2008). Maximum Likelihood (ML) and Neighbour-Joining (NJ) (Saitou & Nei 1987) analyses were performed using MEGA7 (Tamura *et al.* 2011). Nodal support was assessed through 10,000 non-parametric bootstrap replications. Bayesian Inference (BI) with Mr Bayes (version 3.1.2; Huelsenbeck & Ronquist 2001; Ronquist & Huelsenbeck 2003) was performed using 4 parallel chains, 100 frequencies, default heat setting and run for 20 million MCMC generations. Out-group taxa included *M. micropholidotus, M. ctenodactylus, M, reticulatus, M. suborbitalis* and *M. knoxii* (Table 2.3).

For *M. anchietae*, 28 sequences of *Meroles* cyt *b* gene region database were generated containing specimens from RBK, NGS and FGS. The database was reduced to 22 sequences retaining diversity per site. For *M. cuneirostris*, 50 sequences of *Meroles* cyt *b* gene region database were generated containing specimens from KDS, RBK, NGS, FGS and ORM. The database was reduced to 46 sequences also retaining diversity per site. The two databases were combined and complemented with 9 cyt *b* gene region sequences containing 3 reference sequence (one for *M. anchietae* and two for *M. cuneirostris*) and six out-group sequences of sister species of *Meroles* also available on GenBank database (Table 2.1; 2.2), resulting in a final database of 77 sequences. The final dataset of populations of the two sympatric lacertid species was 308 nucleotides in length. The *M. anchietae* reference, AY AY184401.1 was sampled from the south bank of Kuiseb River near Rooibank Road, Walvis Bay District, Erongo Region, Namibia (Lamb & Bauer 2003), whereas the *M. cuneirostris*, AY184403.1 sampled from the North Bank of Kuiseb River at Rooibank Road, Walvis Bay District, Erongo Region, Namibia and *M. cuneirostris*, JX962929.1 sampled from Grasplatz, Luderitz, Karas Region, Namibia.

Table 2. 1: A summary of the cytochrome *b* gene sequence generated for populations of two sympatric lacertid lizard species, *Meroles anchietae* and *M. cuneirostris* from the Namib Desert, Namibia and GenBank reference sequences used for genetic analyses. *n* = sample size.

Sampling locality	Species	*n*	GenBank accession number	Reference
Kuiseb Delta (KDS)	*M. cuneirostris*	6	JX962929.1; AY184403.1	Engleder *et al.* (2013) Lamb & Bauer (2003)
Rooibank (RBK)	*M. anchietae*	7	AY184401.1	Lamb & Bauer (2003)
Rooibank	*M. cuneirostris*	9	JX962929.1; AY184403.1	Engleder *et al.* (2013) Lamb & Bauer (2003)
Near Gobabeb (NGS)	*M. anchietae*	7	AY184401.1	Lamb & Bauer (2003)
Near Gobabeb	*M. cuneirostris*	10	JX962929.1; AY184403.1	Engleder *et al.* (2013) Lamb & Bauer (2003)
Far Gobabeb (FGS)	*M. anchietae*	8	AY184401.1	Lamb & Bauer (2003)
Far Gobabeb	*M. cuneirostris*	10	JX962929.1; AY184403.1	Engleder *et al.* (2013) Lamb & Bauer (2003)

Oranjemund (ORM)	*M. cuneirostris*	11	JX962929.1; AY184403.1	Engleder *et al.* (2013) Lamb & Bauer (2003)

Table 2. 2: A list of specimens (cyt *b* gene region) used as reference sequences and out-groups in the phylogenetic analysis of populations of two sympatric lacertid lizard species, *Meroles anchietae* and *M. cuneirostris* from the Namib Desert, Namibia. Specimens are indicated with their GenBank accession numbers, reference studies and reference type use.

Genus	Species	GenBank accession number	Reference	Sequence type use
Meroles	*anchietae*	AY184401.1	Lamb & Bauer (2003)	reference
Meroles	*cuneirostris*	AY184403.1	Lamb & Bauer (2003)	reference
Meroles	*cuneirostris*	JX962929.1	Engleder *et al.* (2013)	reference
Meroles	*ctenodactylus*	AY184402.1	Lamb & Bauer (2003)	out-group
Meroles	*micropholidotus*	AY184404.1	Lamb & Bauer (2003)	out-group
Meroles	*knoxii*	AY184407.1	Lamb & Bauer (2003)	out-group
Meroles	*knoxii*	JX962928.1	Engleder *et al.* (2013)	out-group
Meroles	*suborbitalis*	JX962927.1	Engleder *et al.* (2013)	out-group
Meroles	*reticulatus*	AY184405.1	Lamb & Bauer (2003)	out-group

2.2.3 Morphological analyses

Sampling of populations of the two sympatric lacertid lizards, *M. anchietae* and *M. cuneirostris* targeted the same five sites (Chapter 1) and data were collected over two seasons, spring (September 2016) and autumn (March-April 2017). Spring and autumn were characterized by the differences in daily average air temperature; spring daily average air temperature was 16.2 ± 3.0° C (daily average minimum air temperature was 9.5 ± 2.6° C and daily average maximum air temperature was 24.2 ± 4.5° C), whereas autumn daily average air temperature was 24.1 ± 3.7° C (daily average minimum air temperature was 17.4 ± 3.4° C and daily average maximum air temperature was 31.9 ± 4.1° C) (http://www.sasscalweathernet.org).

For every sampled individual, following Murray *et al.* (2016), the snout-vent length (SVL; to the nearest mm) and tail length (mm) of the lizards were measured using a standard millimetre ruler. Body mass (to the nearest g) was recorded using a spring scale (Pesola®, PESOLA AG, Feusisberg, Switzerland). Sexing of *M. anchietae* was determined by squeezing the cloaca gently for the presence or absence of the hemipenis in males and females, respectively (D.A. Eifler, unpublished), or using a probe inserted into the cloaca of young individuals because of the absence of a hemipenis due to individuals not having reached sexual maturity. The male cloaca is usually deep and allows for the smooth entry of the probe to approximately 5 mm depending on the age of an individual whereas female cloaca is shallow. This sex differentiation method was used because female and male *M. anchietae* are not easy to distinguish morphologically (*pers. obs*.). In *M. cuneirostris*, however, the females and males differ in colouration and pattern with the females possessing a distinct dark pink-orange lateral stripe that extends from the eye to the tail while the males lack this stripe and possess a more reticulated pattern (Branch 1998; Childers & Eifler 2015). Relative age of either juveniles or adults was based on body size and general external appearance following Goldberg & Robinson (1979) who noted that individual's ≤ 36 mm SVL for populations of *M. anchietae* and ≤ 42 mm SVL for populations of *M. cuneirostris* were regarded as juveniles. Goldberg & Robinson (1979) reported that the smallest sexually matured female and male *M. anchietae* measured 37 mm and 40 mm SVL, whereas the *M. cuneirostris* measured 43 mm and 45 mm SVL for females and males, respectively.

A requirement for many behavioural ecological studies is to re-sight an individual. Most lizard species however, lack natural marks to enable identification by means of visual cues, and it is thus necessary to mark individuals (Galdino *et al.* 2014). Several methods have been used to mark lizards such as toe-clipping (Waichman 1992), implanting integrated transponders (Smyth & Nebel 2013), implant of visible elastomers (Schmidt & Schawarzkopf 2010; Waudy & Petite 2011) and marking dots with non-toxic ink (Van Sluys 1997). Nace & Manders (1982) developed a technique for marking amphibians with coloured beads, and Fisher & Muth (1989) adopted the same technique to mark lizards. In their study, no lizards were observed missing their beads, having necrosis, tail loss or juveniles showing abnormal growth (Fisher & Muth 1989). Iiyambo *et al*. (2016) also indicated the use of beads for marking lizards as safe and convenient for long-term studies when they observed a marked male *M. anchietae* in the wild for over three years.

Fisher & Muth (1989) did not observe indications of beads interfering with lizard's behaviour. Moreover, there is no documentation on the effects of bead marking on lizard mortality, because the hypothesis that coloured beads compromise the cryptic colouration of lizards increasing predation would require a controlled population of unmarked individuals of the same species that could be recognized during re-sighting (Fisher & Muth 1989). Indirect observations by Jones & Ferguson (1980) and Simon & Bissinger (1983) of paint marking however, indicate no effect on survivorship of lizards because of predation.

In the present study, individual lizards were marked with different coloured plastic jewellery beads (Paramount Novelties, Los Angeles, California) (Figure 2.1) when first sampled for identification (Fisher & Muth 1989). Four beads (2 mm thick x 2.5 mm in diameter) were stitched through the tail skin with surgical steel monofilament (Clinisut (Pty) Ltd, Port Elizabeth, South Africa). The resulting identification mark is about 2.5 mm long by 7 mm wide lying perpendicular to the long axis of the tail (Fisher & Muth 1989; D. A. Eifler, unpublished). Before stitching, the individuals were exposed to a cold iced gel on the tail skin to ensure little or no pain during stitching (D. A. Eifler, unpublished). Strands of approximately 15 cm long monofilament were threaded through a 22-gauge hypodermic needle (Sunray Medical Co., Ltd., Shanghai, People's Republic of China) that was then pushed through the skin of the lizard's tail just below the surface at a point distal to the cloaca and laterally to avoid the caudal vertebrae (Nace & Manders 1982; Fisher & Muth 1989). The hypodermic needle was removed leaving the monofilament (Fisher & Muth 1989). Random choices of four bead colours were selected and two beads were inserted on the one end of the monofilament and a flame was used to burn the end of the monofilament to form a loop knot (Fisher & Muth 1989). The same procedure was applied on the other end of the monofilament by inserting the remaining two beads and burning the end with a flame to form a loop knot (Fisher & Muth 1989). The bead colours were read from left to right (Figure 2.1; Table 2.3) (when holding the lizard on its belly in an upright position) (D. A. Eifler, unpublished). The marking technique ensures minimal physical handling of the lizards therefore allowing the identification of individual lizards by re-sighting rather than re-capturing (Fisher & Muth 1989).

Figure 2.1: A male *Meroles cuneirostris* from the Namib Desert, Namibia with ‘yellow yellow green yellow’ beads (code: ‘YYGY’) attached to its tail base for field identification without having to re-sample the individual. The black cross on the back is marked with a non-toxic temporary marker for quick and easy recognition from a distance.

Table 2. 3: The colour coding of beads used to mark sampled populations of two sympatric lacertid lizard species, *Meroles anchietae* and *M. cuneirostris* from the Namib Desert, Namibia for minimal physical handling during field re-sighting.

Colour	Code
Yellow	Y
Green	G
Black	K
Red	R
Dark blue	D
Light blue	L

2.2.4 Habitat characterisation

Lizard activity, including microhabitat preferences, may differ with season (Huey *et al*. 1977; Adolph & Porter, 1993), thus microhabitat data were collected seasonally. Habitat characterization was based on published data (Robinson & Cunningham 1978; Murray & Schramm 1987; Childers & Eifler 2015) and personal observations. To minimize the influence of sampling effort on microhabitat data, the potential types of microhabitat available to the two species were characterized at the beginning of fieldwork that included vegetation, soil type and gravel at sites located at 10 m interval along the length of dune study sites. The habitat was divided into two main types, namely slipface and dune base, based on general characteristics of desert dune structure associated with populations of each species. A slipface is a distinct structure of a linear barchans dune defined by steep inclines (avalanche face) on the leeward slope (Robinson & Barrows 2013) whereas the dune base is the bottom of the dune defined by long gentle windward slope (Robinson & Seely 1980). The slipface and dune base were further sub-divided into microhabitats characterised by gravel, open sand, and vegetation such as bare dune base (open sand at the bottom of the dune), gravel dune base (bottom of the dune with gravel or rocks and tufts), vegetated dune base (sparsely vegetated bottom of the dune with hummocks), vegetated dune peak (sparsely vegetated dune crest), slipface (open sand on the steep inclines), vegetated slipface (sparsely vegetated steep inclines), and slipface base (open sand at the bottom of the steep inclines). The substrate and vegetation type at the time of sampling was recorded. The sampling site for each individual was recorded using a handheld Geographical Positioning System (GPS) (GARMIN GPSMAP® 62s, Olathe, Kansas, U.S.A). General behavioural observations were noted.

2.2.5 Thermal biology

In the field, the lizard body temperature was recorded seasonally within 5 seconds after sampling (Murray *et al*. 2016) using a thermocouple digital thermometer (± 0.2° C Omega HH202A Stamford, CT, U.S.A.) that was inserted approximately 5 mm into the cloaca (Murray *et al*. 2014). The body temperature of lizards that attempted to escape during capture was not recorded to minimize the influence of behavioural movement on the readings. Microhabitat air and substrate temperatures at sampling localities were recorded 10 mm above and below ground at all sampling and observation stations using a thermocouple digital thermometer (Murray *et al*. 2016). The inability to measure thermal data from different sites at the same time may present limitations to the results and conclusions discussed in this study.

2.2.6 Activity pattern

The field site was surveyed for lizard activity between sunrise and sunset. The time at which lizards where observed and sampled was compared seasonally between the populations of *M. anchietae* and *M. cuneirostris* to assess the timing of activity, and activities, including running, sitting, feeding, and burying, observed at the time of sampling were recorded. Average sunrise, solar noon and sunset times for spring (September) 2016 were 06h10, 11h59 and 17h49, respectively. In order to minimize the influence of sampling on activity measurements, the individuals were observed from a distance (approximately 3 m) to allow for normal lizard behaviour. Average sunrise, solar noon and sunset times for autumn (March-April) 2017 were 06h50, 13h12 and 19h28, respectively. The time of day was indicated as Namibia Standard time (GMT + 2). The time in April was one hour earlier because of winter daylight saving shift thus time was converted to GMT +2 for autumn season.

2.2.7 Statistical analyses

The body length (SVL) and body mass was compared between and among populations of *M. anchietae* and *M. cuneirostris* using a two-way analysis of variance (ANOVA; Murray *et al.* 2015) with sex and taxon as factors. Chi-square (χ^2) test (Murray *et al.* 2015) was used to evaluate differences in proportional use of substrate types and behavioural activity types between the populations of *M. anchietae* and *M. cuneirostris*. Age, taxon and season as factors in a three-way ANOVA were used to compare body temperature and air temperature for populations of both species across seasons. A two-sample *t*-test (Murray *et al.* 2014) was used to assess the differences in mean samples of populations of *M. anchietae* and *M. cuneirostris* to examine the relationship between age, body and air temperature. One-way ANOVA (Murray *et al.* 2015) was used to assess for interaction between air temperature and age and taxon. Pearson's correlation (Murray *et al.* 2014) was used to assess the linear relationship between air and substrate temperature at lizard sampling localities within and among populations of *M. anchietae* and *M.*

cuneirostris. Analysis of partial correlation (Murray *et al.* 2015) was used to compare the individual effects of air and substrate temperature on body temperature on the populations of *M. anchietae* and *M. cuneirostris*. Analysis of covariance (ANCOVA; Murray *et al.* 2014, 2015) was used to test for differences between season, body temperature, with air and substrate temperatures as covariates. Values were reported as mean ± one standard deviation (±1SD) with a statistical significance level offset at alpha (α) = 0.05. All statistical analyses were based on algorithms in R statistical software (R version 3.4.1 © The R Foundation for Statistical Computing, Bell Laboratories, Murray Hill, New Jersey, U.S.A.) and Microsoft Excel 2016 (Microsoft Corp., Redmond, Washington, U.S.A.).

2.3 Results

2.3.1 Molecular assessment

The best-fit model of nucleotide sequence evolution identified in jModeltest (version 2.1; Posada 2008) under the Aikake Information Criterion (AIC) was the Kimura-2 (Kimura 1980) with six substitutions and Gamma distributed rates. The cyt *b* gene region tree (Figure 2.2) recovered two monophyletic clades within *M. cuneirostris*, Clade A from central Namib Desert and Clade B from southern Namib Desert, Namibia, and another monophyletic clade comprising *M. anchietae* from the central Namib Desert, Namibia (Figure 2.3). Within *M. cuneirostris*, all the sequences from the central Namib Desert clustered with the *M. cuneirostris* reference sequence, ID number (JX962929.1 and AY184403.1) forming a monophyletic clade (Clade A) that differed from Clade B of sequences from the southern Namib Desert with a 96% and 100% bootstrap support in ML and N-J, and 93% for BI (Figures 2.4 and 2.5). All *M. anchietae* sequences clustered with the *M. anchietae* reference sequence, ID number (AY184401.1) with a 99% and 100% bootstrap support in ML and N-J trees, respectively, 100% for BI (Figures 2.2 and 2.4).

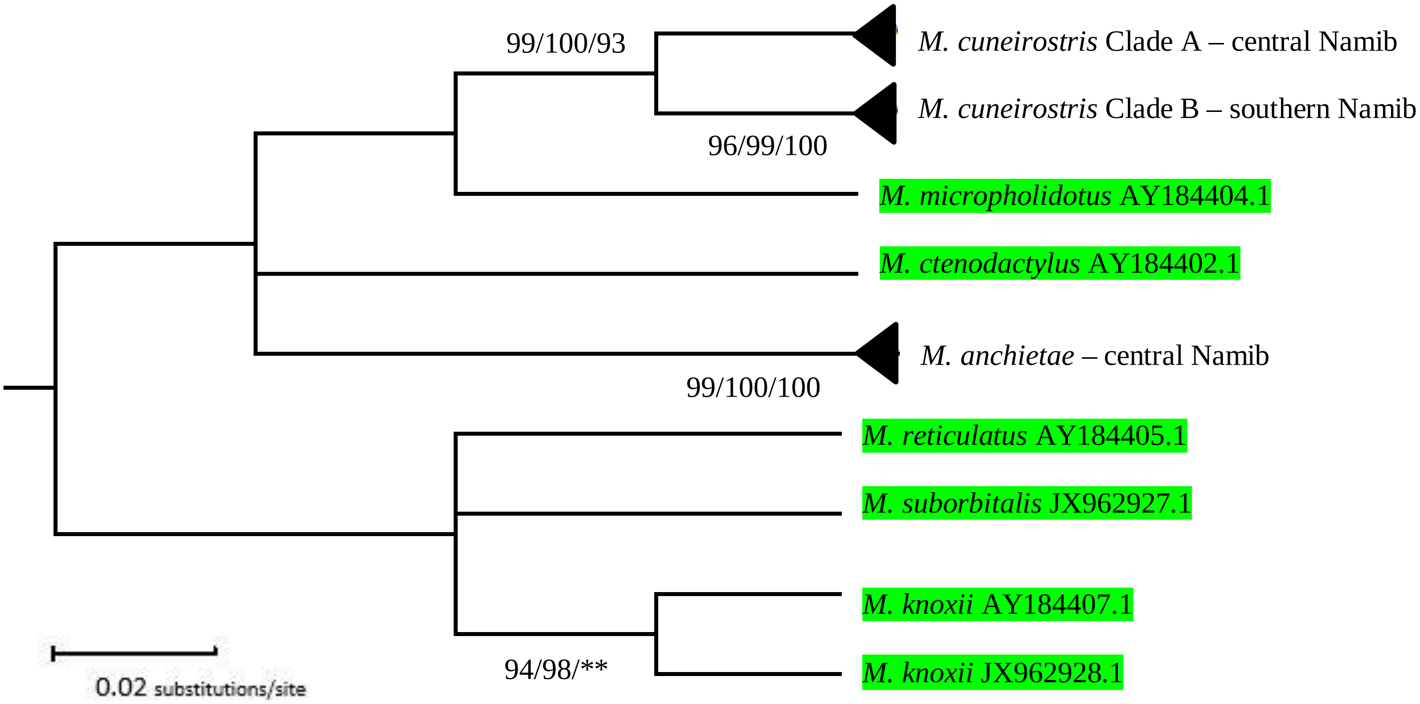


Figure 2.2: A Maximum Likelihood (ML) tree inferred using mitochondrial cytochrome *b* gene sequenced from populations of *Meroles anchietae* and *M. cuneirostris* from the Namib Desert, Namibia. Taxon names consists of recovered clades and out-group species preceded by the corresponding GenBank accession numbers. Nodal support values (≥ 75%) for ML and Neighbour-Joining (N-J) trees were based on 10,000 non-parametric bootstrap replications and are presented together with posterior probabilities from Bayesian Inference (BI) expressed as a percentage in the order of ML/N-J/BI, respectively. Out-group taxa included *M. micropholidotus*, *M. ctenodactylus*, *M. reticulatus*, *M. suborbitalis* and *M. knoxii* (colour-coded in bright green) (Table 2.2).

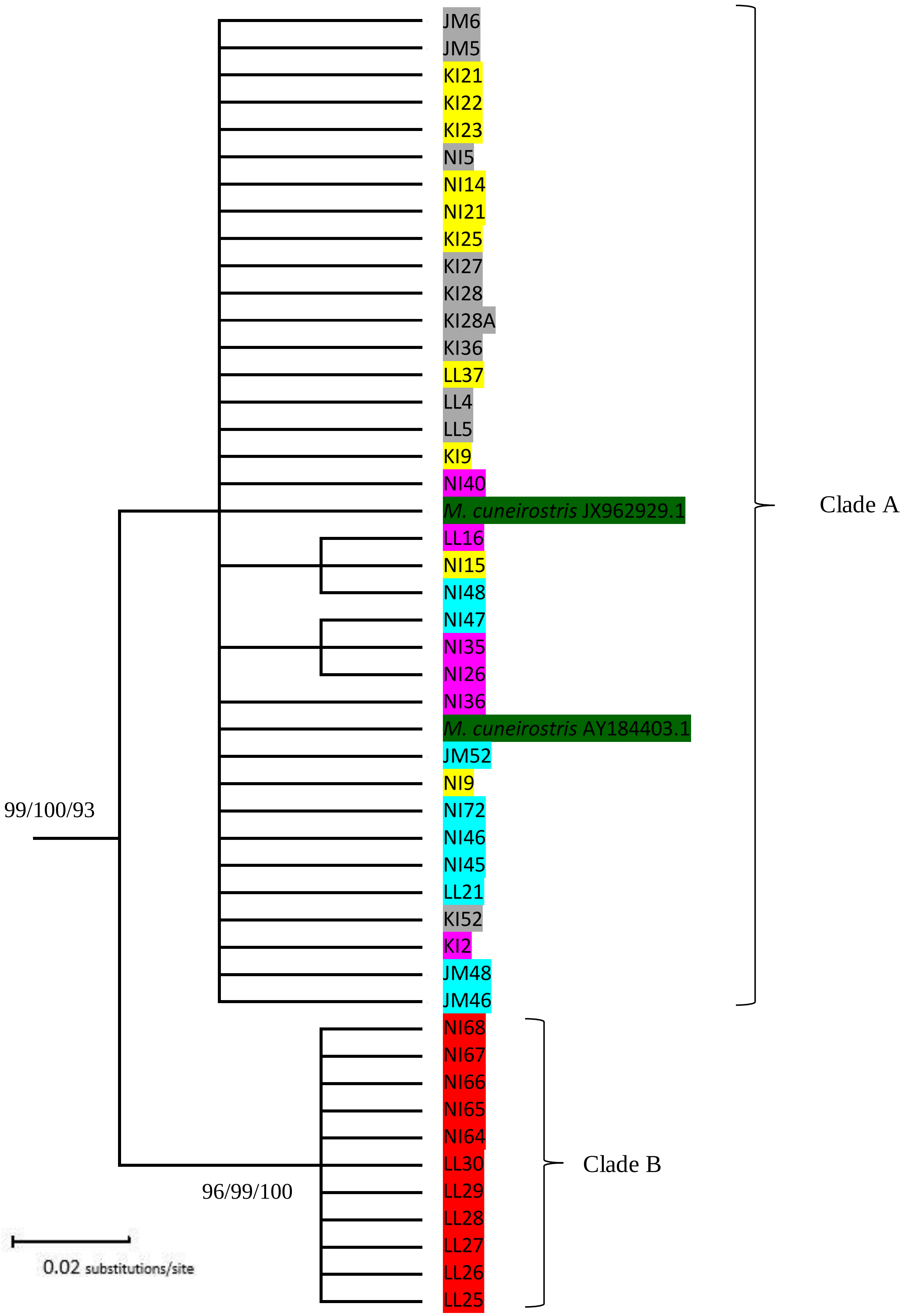

JM6
JM5
KI21
KI22
KI23
NI5
NI14
NI21
KI25
KI27
KI28
KI28A
KI36
LL37
LL4
LL5
KI9
NI40
M. cuneirostris JX962929.1
LL16
NI15
NI48
NI47
NI35
NI26
NI36
M. cuneirostris AY184403.1
JM52
NI9
NI72
NI46
NI45
LL21
KI52
KI2
JM48
JM46
NI68
NI67
NI66
NI65
NI64
LL30
LL29
LL28
LL27
LL26
LL25
Clade A
Clade B
99/100/93
96/99/100
0.02 substitutions/site

Figure 2.3: Section of the Maximum Likelihood (ML) tree inferred using mitochondrial cytochrome *b* gene sequenced from populations of *Meroles cuneirostris* from the Namib Desert, Namibia. Taxon names consists of reference species preceded by the corresponding GenBank accession numbers and field collection codes for samples collected in this study. Nodal support values (≥ 75%) for ML and Neighbour-Joining (N-J) trees were based on 10,000 non-parametric bootstrap replications and are presented together with posterior probabilities from Bayesian Inference (BI) expressed as a percentage in the order of ML/N-J/BI, respectively. The sequenced individuals are colour-coded as follows indicating region and source of data: Yellow = Far Gobabeb, Turquoise = Rooibank, Grey = Near Gobabeb, Pink = Kuiseb Delta, Red = Oranjemund and Dark Green = Reference species.

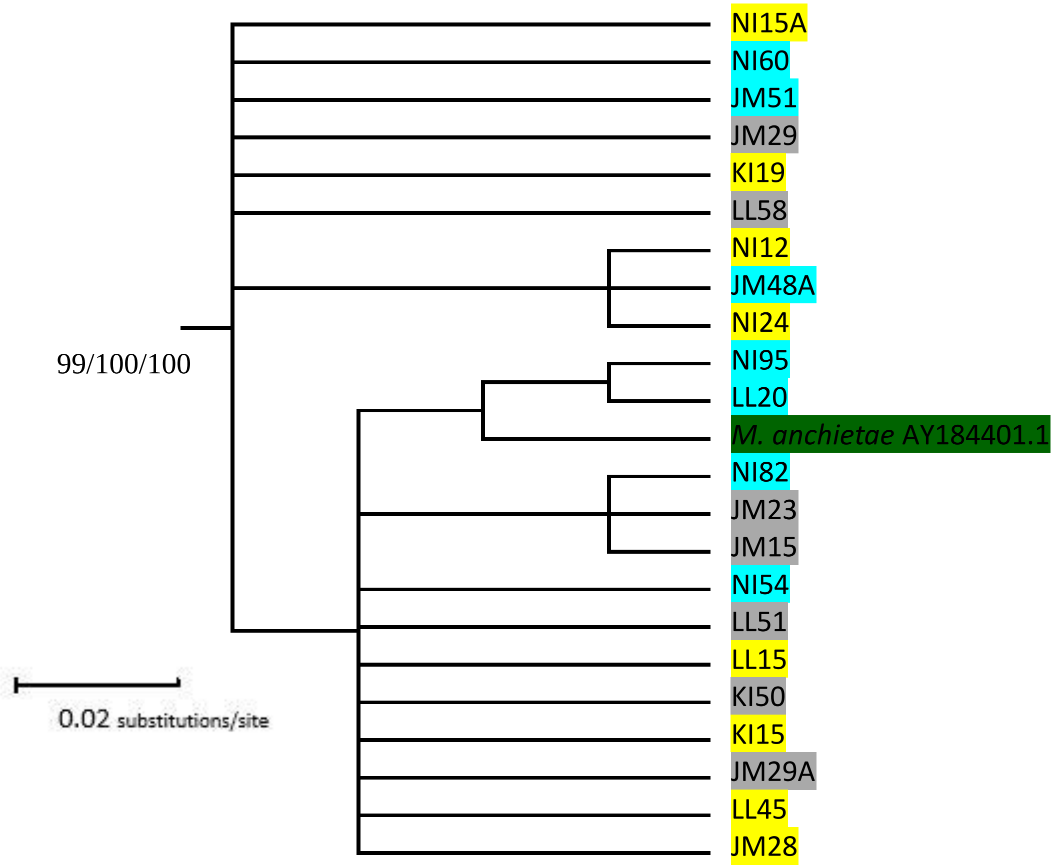


Figure 2. 4: Section of the Maximum Likelihood (ML) tree inferred using mitochondrial cytochrome *b* gene sequenced from populations of *Meroles anchietae* from the Namib Desert, Namibia. Taxon names consist of reference species preceded by the corresponding GenBank accession numbers and field collection codes for samples collected in this study. Nodal support values (≥ 75%) for ML and Neighbour-Joining (N-J) trees were based on 10,000 non-parametric bootstrap replications and are presented together with posterior probabilities from Bayesian Inference (BI) expressed as a percentage in

the order of ML/N-J/BI, respectively. The sequenced individuals are colour-coded as follows indicating region and source of data: Yellow = Far Gobabeb, Turquoise = Rooibank, Grey = Near Gobabeb and Dark Green = Reference species.

2.3.2 Morphological assessment

Because there was no difference in the genetic structure within the individuals of *M. anchietae* and the individuals of *M. cuneirostris* (Clade A) from the central Namib, the morphology, microhabitat preferences, thermal biology and activity pattern were compared between the three taxa genetically-defined in the previous section. The seasonal variation in body mass and length was not analysed because season cannot be used to compare morphological differences between species. Six males and one female of *M. anchietae*, and four males and two females of Clade A of *M. cuneirostris* captured during spring were recaptures during autumn, and these individuals were not included in the analyses for body mass and length, to reduce the influence of autumn sampling measures on the spring morphology recordings. The lizards' SVL (Table 2.4) differed significantly between sexes (two-way ANOVA; sex: $F_1 = 17.19$; $n = 378$; $P < 0.01$), with males being longer than females, and between taxa (two-way ANOVA; taxa: $F_2 = 39.19$; $n = 378$ $P < 0.01$), with Clade A of *M. cuneirostris* being longer than both *M. anchietae* and Clade B of *M. cuneirostris*. The interaction between sex and taxon was statistically significant (two-way ANOVA: sex*taxa: $F_2 = 3.66$; $n = 378$; $P = 0.03$). The lengths of male and female *M. anchietae* (two-sample *t*-test; sex: $t_{47} = -0.36$; $n = 111$; $P = 0.72$) and Clade B of *M. cuneirostris* (two-sample *t*-test; sex: $t_4 = -0.33$; $n = 12$; $P = 0.76$) were not statistically different, whereas it was significant in Clade A of *M. cuneirostris* (two-sample *t*-test; sex: $t_{142} = -4.96$; $n = 155$; $P < 0.01$) with males longer than females.

Body mass differed significantly between sexes (two-way ANOVA; sex: $F_1 = 21.08$; $n = 378$; $P < 0.01$), with males being significantly heavier than females and between taxa (two-way ANOVA; taxa: $F_2 = 34.71$; $n = 378$; $P < 0.01$), with Clade A of *M. cuneirostris* being significantly heavier than both *M. anchietae* and Clade B of *M. cuneirostris*. The interaction between sex and taxon was statistically significant (two-way ANOVA: sex*taxa - $F_2 = 23.15$; $n = 378$; $P < 0.01$). Likewise, the masses of male and female *M. anchietae* (two-sample *t*-test; sex: $t_{43} = -0.60$; $n = 111$; $P = 0.55$) and Clade B of *M. cuneirostris* (two-sample *t*-test; sex: $t_3 = -1.11$; *n*

= 12; $P = 0.33$) were not significantly different, whereas males were significantly heavier than females in Clade A of *M. cuneirostris* (two-sample *t*-test; sex: $t_{151} = -4.78$; $n = 155$; $P < 0.01$).

Table 2. 4: Comparison of mean standard deviation (± SD) of snout-vent length (SVL; mm) and body mass (g) for *Meroles anchietae* and Clade A of *M. cuneirostris* from the Namib Desert, Namibia during September (spring-2016) and March-April (autumn-2017), and Clade B of *M. cuneirostris* during March-April (autumn-2017). *n* = sample size.

Trait	*Meroles anchietae*	*Meroles cuneirostris*	
		Clade A	Clade B
SVL – female (mm)	41.64 ± 6.0 (*n* = 28)	46.07 ± 6.2 (*n* = 61)	42.50 ± 8.1 (*n* = 8)
SVL – male (mm)	42.12 ± 6.2 (*n* = 83)	51.56 ± 7.4 (*n* = 94)	45.00 ± 12.2 (*n* = 4)
Body mass – female (g)	2.36 ± 1.4 (*n* = 28)	2.94 ± 1.7 (*n* = 61)	1.29 ± 1.1 (*n* = 8)
Body mass – male (g)	2.54 ± 1.3 (*n* = 83)	4.44 ± 2.2 (*n* = 94)	2.73 ± 2.1 (*n* = 4)

An assessment of external morphology showed that Clade B of *M. cuneirostris* has a more solid reddish colour pattern compared to the lighter colour pattern of Clade A of *M. cuneirostris*, corresponding to their preferred dune colouration. Clade A of *M. cuneirostris* occurs on light coloured dunes of well-defined slipface within the Walvis Bay Town District (Rooibank through to Gobabeb), whereas Clade B of *M. cuneirostris* occurs across the dark red coloured dunes of less-defined or without slipface within the Oranjemund Town District (around dunes of the Dabaras Namdeb Mining area). Despite these differences, individuals associated with the two clades share similar vegetation type such as !nara plant (*Acanthosicyos horridus*) and the spiny love grass/ Ostrich grass (*Cladoraphis spinosa*).

2.3.3 Assessment of microhabitat preference

Due to logistical constraints, data from the Oranjemund site could only be collected during autumn. As such, comparison of microhabitat during spring was based on populations of the two species from only four sites (KDS, RBK, NGS and FGS); meaning samples of Clade B of *M. cuneirostris* were excluded from the spring data analyses. Both Clades A and B of *M.*

cuneirostris were observed on similar microhabitats (substrate type) that was different from that of *M. anchietae*. *Meroles anchietae* was observed on different substrate types with the slipface as the highly dominant substrate type utilized (80% observations during both spring and autumn), whereas Clades A and B of *M. cuneirostris* were also observed on various substrate types with vegetated dune base as the dominant substrate type used (50% and 49% observations of Clade A of *M. cuneirostris* during spring and autumn, respectively, and 98% observations of Clade B of *M. cuneirostris* during autumn only) (Table 2.5). *Meroles anchietae* and Clade A of *M. cuneirostris* showed a statistically significant difference in the proportional use of the substrate during both seasons (likelihood ratio: *M. anchietae* - χ^2 test = 28.46; d.f. = 9; n = 205; Clade A of *M. cuneirostris* - χ^2 test = 48.69; d.f. = 10; n = 433; $P < 0.01$). Due to lack of spring data for Clade B of *M. cuneirostris*, the proportional use of the substrate could not be discerned, however, apart from vegetated dune base, Clade B of *M. cuneirostris* was also observed on vegetated dune peak (Table 2.6). Apart from *M. anchietae* being mostly observed on the slipface, they were also observed on bare dune base (7%) and on vegetated slipface (2%) during spring whereas during autumn it was also observed on vegetated slipface (4%) and on slipface base (5%). During both spring and autumn, approximately 3% of *M. anchietae* individuals were observed on vegetated dune base. Clade A of *M. cuneirostris* was also observed on bare dune base (15%), vegetated dune peak (4%), vegetated slipface (1.5%) and slipface base (0.4%) during spring and during autumn observations were made on bare dune base (0.4%), vegetated dune peak (9%), vegetated slipface (3%), and on slipface base (2%). On average, about 3% of observations were made on Clade A of *M. cuneirostris* using the gravel dune base during both spring and autumn and about 0.7% of observations on slipface during both spring and autumn. Interestingly, both *M. anchietae* and Clade A of *M. cuneirostris* became more active on bare dune base substrate type during spring than autumn (Table 2.5).

Table 2. 5: Substrate types for active *Meroles anchietae* (autumn: *n* = 95; spring: *n* = 110), Clade A of *M. cuneirostris* (autumn: *n* = 247; spring: *n* = 271), and Clade B of *M. cuneirostris* (autumn: *n* = 43) from the Namib Desert, Namibia expressed as a percentage of total observations during September (spring) and March-April (autumn).

	Spring		Autumn		
Substrate type	*M. anchietae*	*M. cuneirostris* Clade A	*M. anchietae*	*M. cuneirostris* Clade A	*M. cuneirostris* Clade B
Bare dune base (%)	7.27	14.76	0	0.41	0
Gravel dune base (%)	0	2.95	0	4.47	0
Vegetated dune base (%)	3.64	49.82	3.16	49.19	97.67
Vegetated dune peak (%)	0	3.69	0	8.94	2.32
Slipface (%)	80.0	0.74	80.0	0.81	0
Vegetated slipface (%)	1.82	1.48	4.21	3.25	0
Slipface base (%)	0	0.37	5.26	2.03	0

2.3.4 Assessment of thermal biology

Due to logistical constraints, similar to microhabitat data, it was only possible to collect thermal data from the Oranjemund site during autumn. Consequently, samples of Clade B of *M. cuneirostris* were excluded from the spring data analyses. Within each species, there was no statistically significant difference in body temperature between males and females (two-sample *t*-test; sex: t_{172} = -0.83 *n* = 274; *P* = 0.41), thus male and female data were pooled in subsequent analyses. Body temperature differed significantly between ages (three-way ANOVA; age: F_1 = 4.58; *n* = 274; *P* = 0.03), with adults having higher body temperatures than juveniles, between taxa (three-way ANOVA; taxa: F_2 = 3.08; *n* = 274; *P* = 0.05), with Clade A of *M. cuneirostris* having higher body temperatures than *M. anchietae* and Clade B of *M. cuneirostris*, and across seasons (three-way ANOVA; season: F_1 = 36.67; *n* = 274; $P < 0.01$), with body temperatures higher during autumn compared to spring (Figure 2.5). The interactions between age, taxon and season were all not statistically significant (three-way ANOVA; age*taxa: F_2 = 2.17; *n* = 274; *P* = 0.12; age*season: F_1 = 0.08; *n* = 274; *P* = 0.77; taxa*season: F_1 = 1.70; *n* = 274; *P* = 0.19; age*taxa*season: F_1 = 0.40; *n* = 274; *P* = 0.67).

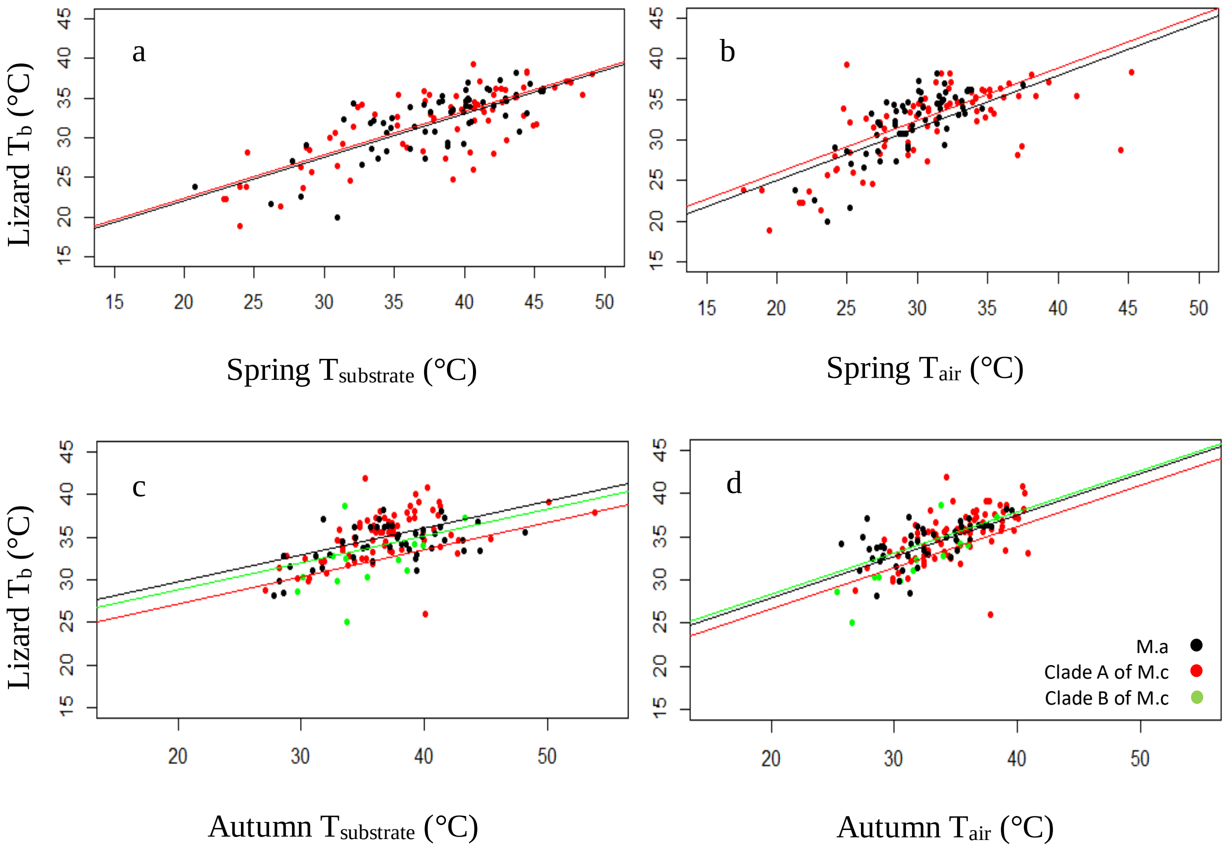


Figure 2. 5: The seasonal relationship between body temperatures (T_b) of *Meroles anchietae* (M.a - black circles), Clade B of *M. cuneirostris* (Clade A of M.c - red circles) and Clade B of *M. cuneirostris* (Clade B of M.c - green circles) and substrate (10 mm below ground) and air temperatures (10 mm above ground) at lizard sampling localities in the Namib Desert, Namibia during spring (September) = a and b, and in autumn (March-April) = c and d. Regression relationship is shown relative to line of identity ($T_{body} = T_{substrate}$ or T_{air}).

During spring, the relationship between body and substrate temperatures at sampling localities for *M. anchietae* ($T_b = 0.35\ (T_{sub}) + 18.90$; $r^2 = 0.37$; d.f. = 1; $n = 59$; $P < 0.01$; ANCOVA; $F_1 = 34.41$; $n = 59$; $P < 0.01$) had similar slopes and a greater intercept compared to the equivalent relationship in Clade A of *M. cuneirostris* ($T_b = 0.39\ (T_{sub}) + 17.42$; $r^2 = 0.39$; d.f. = 1; $n = 75$; $P < 0.01$; ANCOVA; $F_1 = 49.38$; $n = 75$; $P < 0.01$) (Figure 2.7). During autumn, the relationship between body and substrate temperature at sampling locations of *M. anchietae* ($T_b = 0.32\ (T_{sub}) + 21.15$; $r^2 = 0.30$; d.f. = 1; $n = 109$; $P < 0.01$; ANCOVA; $F_1 = 47.43$; $n = 109$; $P < 0.01$) and Clade A of *M. cuneirostris* ($T_b = 0.35\ (T_{sub}) + 22.1$; $r^2 = 0.26$; d.f. = 1; $n = 77$; $P < 0.01$; ANCOVA; $F_1 = 26.3$; $n = 77$; $P < 0.01$), had lower slopes and greater intercepts compared to the equivalent relationship in Clade B of *M. cuneirostris* ($T_b = 0.44 (T_{sub}) + 16.6$; $r^2 = 0.25$; d.f. = 1; $n = 11$; $P = 0.07$; ANCOVA; $F_1 = 3.56$; $n = 11$; $P = 0.09$).

The air temperature differed significantly between sampling localities (three-way ANOVA; taxa: $F_2 = 7.76$; $n = 274$; $P < 0.01$), with Clade A of *M. cuneirostris* localities having higher air temperatures compared to those of *M. anchietae* and Clade B of *M. cuneirostris*, and across season (three-way ANOVA; season: $F_1 = 53.07$; $n = 274$; $P < 0.01$), with autumn having higher air temperatures than spring. The air temperature at sampling localities did however, not differ between age (three-way ANOVA; age: $F_1 = 0.61$; $n = 274$; $P = 0.43$) (Figure 2.7). The interaction between age, taxa and season were not statistically significant for age*season (three-way ANOVA; age*season: $F_1 = 2.86$; $n = 274$; $P = 0.09$; taxa*season: $F_1 = 3.31$; $n = 274$; $P = 0.07$; and age*taxa*season: $F_1 = 0.39$; $n = 274$; $P = 0.53$). The interaction between age and taxa was however, statistically significant (three-way ANOVA; age*taxa: $F_2 = 3.11$; $n = 274$; $P = 0.05$). Adults of Clade A of *M. cuneirostris* had significantly higher air temperatures at sampling localities compared to those of *M. anchietae* and Clade B of *M. cuneirostris* (one-way ANOVA; Adults of Clade A of *M. cuneirostris*: $F_2 = 11.51$; $n = 224$; $P < 0.01$). The air temperature at sampling localities for juveniles was not significantly different (one-way ANOVA; juvenile: $F_2 = 0.58$; $n = 50$; $P = 0.57$).

During spring, the relationship between *M. anchietae* body temperature and air temperature at sampling localities had a significantly higher slope and a significantly lower intercept ($T_b = 0.96 (T_{air}) + 3.57$; $r^2 = 0.58$; d.f. = 1; $n = 59$; $P = 0.26$; ANCOVA; $F_1 = 83.04$; $n = 59$ $P < 0.01$) than that of Clade A of *M. cuneirostris* ($T_b = 0.57 (T_{air}) + 14.45$; $r^2 = 0.46$; d.f. = 1; $n = 75$; $P < 0.01$; ANCOVA; $F_1 = 65.23$; $n = 75$; $P < 0.01$) (Figure 2.7). During autumn, the slope was significantly greater for Clade B of *M. cuneirostris* ($T_b = 0.73 (T_{air}) + 8.98$; $r^2 = 0.65$; d.f. = 1; $n = 11$; $P = 0.11$; ANCOVA; $F_1 = 20.51$; $n = 11$; $P < 0.01$) and the intercept significantly lower compared to that of Clade A of *M. cuneirostris* ($T_b = 0.53 (T_{air}) + 16.60$; $r^2 = 0.33$; d.f. = 1; $n = 77$; $P < 0.01$; ANCOVA; $F_1 = 37.99$; $n = 77$; $P < 0.01$), and *M. anchietae* ($T_b = 0.36 (T_{air}) + 22.46$; $r^2 = 0.28$; d.f. = 1; $n = 48$; $P < 0.01$; ANCOVA; $F_1 = 20.32$; $n = 48$; $P < 0.01$.

Air and substrate temperatures at sampling localities were significantly correlated for *M. anchietae* ($T_{substrate} = 0.26 (T_{air}) + 21.52$; Pearson correlation: $r_{109} = 0.42$; $n = 111$; $P < 0.01$), Clade A of *M. cuneirostris* ($T_{substrate} = 0.40 (T_{air}) + 20.10$; Pearson correlation: $r_{77} = 0.53$; $n = 79$;

$P < 0.01$), and Clade B of *M. cuneirostris* ($T_{substrate} = 0.73 (T_{air}) + 5.46$; Pearson correlation: $r_{11} = 0.76$; $n = 13$; $P < 0.01$). Clade B of *M. cuneirostris* indicated a stronger relationship between air and substrate temperature in predicting body temperature compared to the similar relationship in Clade A of *M. cuneirostris* and *M. anchietae*. The body temperatures in both *M. anchietae* and Clade A of *M. cuneirostris* showed a statistically significant correlation with substrate temperatures compared to the similar correlation in Clade B of *M. cuneirostris* (Partial correlation: body temperature-substrate temperature of *M. anchietae* = 0.45; d.f. = 1; $n = 11$; $P < 0.01$; Clade A of *M. cuneirostris* = 0.29; d.f. = 1; $n = 79$; $P = 0.01$; and Clade B of *M. cuneirostris* = -0.30; d.f. = 1; $n = 13$; $P = 0.34$). In addition, the body temperature in *M. anchietae*, and Clades A and B of *M. cuneirostris* was significantly correlated with air temperature at sampling localities (Partial correlation: body temperature-air temperature of *M. anchietae* = 0.59; d.f. = 1; $n = 111$; $P < 0.01$; Clade A of *M. cuneirostris* = 0.42; d.f. = 1; $n = 79$; $P < 0.01$, and Clade B of *M. cuneirostris* = 0.76; d.f. = 1; $n = 13$; $P < 0.01$).

2.3.5 Assessment of activity pattern

Activity pattern data for Clade B of *M. cuneirostris* were only collected during autumn due to logistical constraints. During the morning, all species emerged from the sand with the rising sun to take advantage of the early morning heat. *Meroles anchietae* spent most of its time on the slipface hunting for prey, whereas individuals of Clades A and B of *M. cuneirostris* spent most of their time in open spaces between vegetation searching for prey. For the activity type ‘sitting’, it only applied to Clade A individuals when they were observed seated under vegetation for cover (in most cases when the sand was very hot), *M. anchietae* individuals rarely use vegetation for cover. When temperatures increased by mid-morning, the lizards moved closer to vegetation for shade (Clades A and B of *M. cuneirostris*) or buried in deep sand of the slipface (*M. anchietae*).

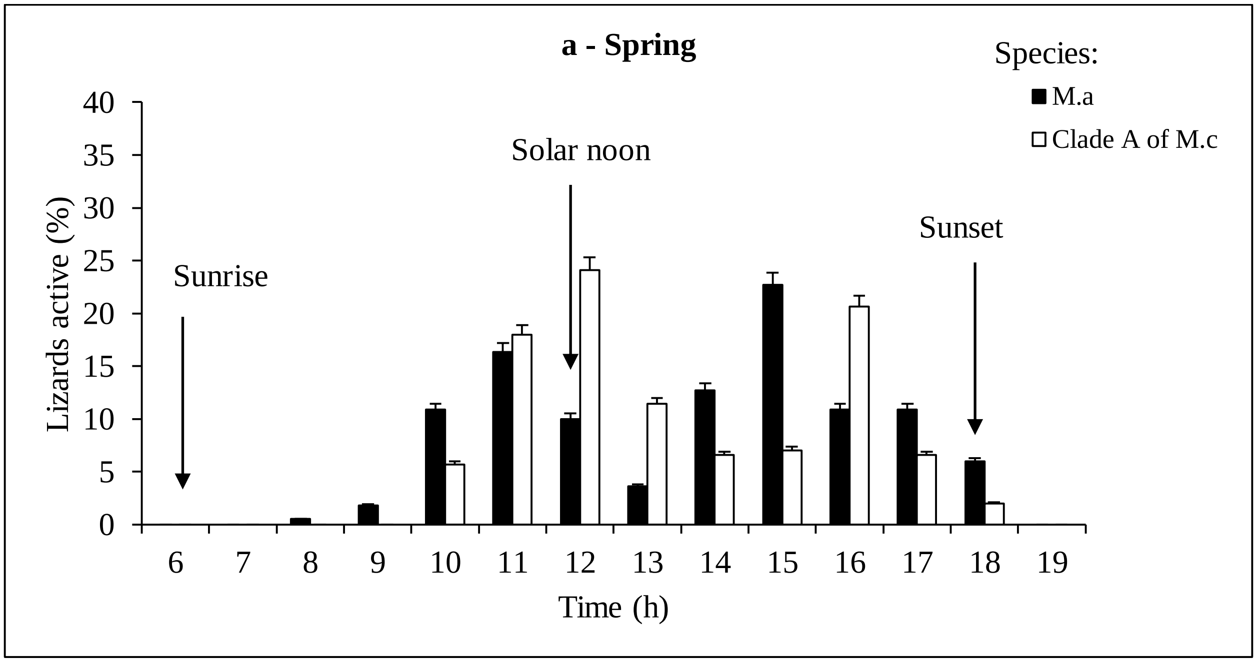
Meroles anchietae and Clade A of *M. cuneirostris* showed a statistically significant difference in the proportional behavioural activity types during both seasons (likelihood ratio: *M. anchietae* - χ^2 test = 27.87; d.f. = 6; $n = 205$; Clade A of *M. cuneirostris* - χ^2 test = 1269.02; d.f. = 7; $n = 475$; $P < 0.01$). Due to lack of spring data for Clade B of *M. cuneirostris*, the proportional behavioural activity types could not be discerned. Of their activity, 58% of *M. anchietae* individuals spent most of the time sun basking on the slipface during autumn compared to 79% individuals during spring, whereas about 56% of Clade A of *M. cuneirostris* individuals were sun basking during autumn and only 13% individuals during spring, and about 42% of Clade B of *M. cuneirostris* individuals sun basking during autumn (Table 2.6). Apart from sun basking, some lizards were observed running in and around the microhabitat and some seated in both open and hidden places. Activities such as chasing (example, >1% of *M. anchietae* individuals during spring), feeding (i.e., >1% of Clade A of *M. cuneirostris* individuals during spring), half buried with head out (i.e., 13% of *M. anchietae* individuals during autumn) and fully buried (i.e., 6% *M. anchietae* individuals during autumn) were also observed. Only one individual of Clade A of *M. cuneirostris* was observed with activity related to burrowing when it was observed sitting in a burrow (vegetated dune base as a substrate type) with its head out (Table 2.6).

Table 2. 6: Lizard activities of *Meroles anchietae* (autumn: *n* = 95; spring: *n* = 110), Clade A of *M. cuneirostris* (autumn: *n* = 247; spring: *n* = 288), and Clade B of *M. cuneirostris* (autumn: *n* = 43) from the Namib Desert, Namibia expressed as a percentage of total observations during September (spring) 2016 and March-April (autumn) 2017. The dash (-) indicates no recorded activity for *M. anchietae* as it rarely uses vegetation for cover.

	Spring		Autumn		
Activity	*M. anchietae*	*M. cuneirostris*	*M. anchietae*	*M. cuneirostris*	
		Clade A		Clade A	Clade B
Chasing (%)	0.91	0	0	0.81	0
Feeding (%)	0.91	0.88	0	0	0
Fully buried (%)	0.91	0.44	6.32	0	0
Half-buried (%)	1.82	0.44	12.63	0.41	0
Running (%)	16.36	43.42	13.68	4.86	23.26
Sitting (under vegetation) (%)	-	41.67	-	37.25	34.88
Sitting in burrow (%)	0	0	0	0.35	0
Sun basking (%)	79.09	13.16	57.89	56.28	41.86

Meroles anchietae activity followed a bimodal pattern during both seasons with peak activity between 09h00 and 11h00 and between 13h00 and 15h00 during spring and between 07h00 and 08h00 and between 13h00 and 15h00 during autumn (Figure 2.6). The activity of *M.*

anchietae declined between 09h00 and 12h00 during autumn as compared to between 12h00 and 13h00 during spring (Figure 2.6). Clade A of *M. cuneirostris* was active throughout the day with activity that followed a bimodal pattern during both spring and autumn (Figure 2.6). Clade A of *M. cuneirostris* activity peak occurred between 10h00 and 11h00, and 14h00 and 15h00 during spring and between 07h00 and 08h00 and 13h00 and 15h00 during autumn such that no activity was recorded between 11h00 and 12h00. Clade B of *M. cuneirostris* also followed a bimodal pattern of activity with peak activity between 08h00 and 10h00 and around 14h00 during autumn. No activity for Clade B of *M. cuneirostris* was observed around 13h00 and the activity declined after 15h00. The peak activity for *M. anchietae* occurred approximately four hours after sunrise during spring as compared to approximately after one hour during autumn. Peak activity for Clade A of *M. cuneirostris* occurred approximately five hours after sunrise during spring and approximately after one hour during autumn. Peak activity for Clade B of *M. cuneirostris* occurred approximately three hours after sunrise during autumn. During spring, no lizards were active between 06h00 and 07h00 and a few lizards of both *M. anchietae* and Clade A of *M. cuneirostris* were active during sunset. During autumn, no lizards were active after sunset.



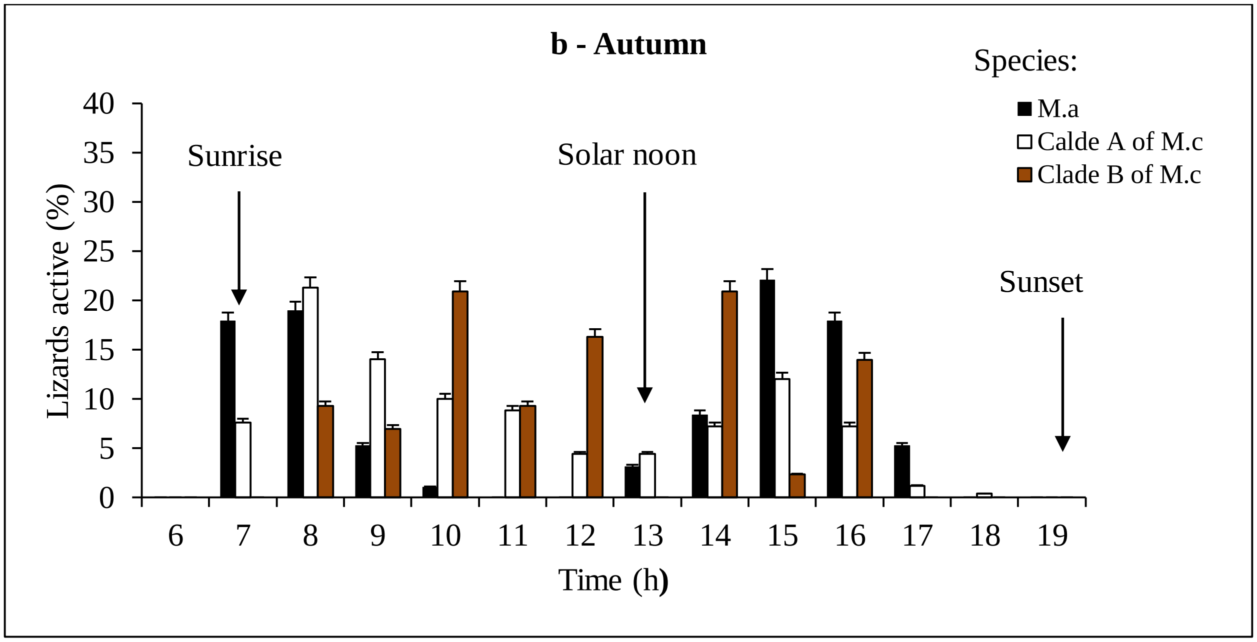


Figure 2. 6: Diurnal activity of *Meroles anchietae* (M.a - black: September (spring), *n* = 110; March-April (autumn), *n* = 95), Clade A of *M. cuneirostris* (Clade A of M.c - white: September (spring), *n* = 228, March-April (autumn), *n* = 292), and Clade B of *M. cuneirostris* (Clade B of M.c - brown: March-April (autumn), *n* = 43) from Namib Desert, Namibia. Data are presented as the percentage of total observations of active lizards across season within one-hour interval during: a) September (spring) 2016 and b) March-April (autumn) 2017.

2.4 Discussion

2.4.1 Molecular assessment

In as far as it could be established, the present study is the first to provide molecular evidence of genetic differences within and among populations of *M. cuneirostris* from the Namib Desert. In addition, the present study also had an interest in the genetic structure of the northern Namib populations of *M. anchietae* that are known to form two distinct monophyletic clades (Griffin 2003; Lamb & Bauer 2003), however, due to logistical constraints, the samples could not be sequenced, and the population will form part of a future study. The cytochrome *b* gene phylogeny recovered one clade for the central Namib Desert populations of *M. anchietae* and two clades of *M. cuneirostris,* one for the central Namib Desert(Clade A) and the other for the southern Namib Desert (Clade B).

Meroles anchietae (AY AY184401.1) clustered with the central Namib populations of *M. anchietae* (present study), indicating similar genetic structure. The *M. anchietae* sequence (AY AY184401.1) derived from Lamb & Bauer (2003) was sampled from the south bank of Kuiseb River near Rooibank Road, Walvis Bay District, Erongo Region, Namibia which is in the same vicinity with samples collected in this study, thus clustered and formed one clade. *Meroles cuneirostris* (AY184403.1 and JX962929.1) sampled from the north bank of Kuiseb River at Rooibank Road, Walvis Bay District, Erongo Region, and that from Grasplatz, Luderitz, Karas Region, Namibia (Lamb & Bauer 2003; Engleder *et al.* 2013), respectively, clustered with the central Namib population of *M. cuneirostris* (present study), also indicating similar genetic structure. The southern Namib population of *M. cuneirostris* (present study), however, formed a clade distinct from that of the central Namib, and was limited to one area of the population, thus suggesting further investigation to define the taxonomic status and genetic structure of the entire population of *M. cuneirostris* across the Namib Desert.

The divergence levels of 7.9% (cytochrome *b*) placed the genetic structure of the northern and southern Namib sand sea populations of *M. anchietae* (similar to the central Namib populations of *M. anchietae* of the present study) in accordance with observed allozymic variation (Nei distance > 0.25; Gordon & Griffin 1989; Lamb & Bauer 2003). *Meroles knoxii*, an ecological generalist was shown to be a sister taxon to other *Meroles* both genetically and morphologically (Branch 1998; Mayer & Richer 1990; Lamb & Bauer 2003). *Meroles ctenodactylus*, *M. cuneirostris* and *M. micropholidotus* collectively form a subgenus *Saurites* in accordance with 17 derived morphological and behavioural characteristics linked to functioning in loose sand, with *M. anchietae* (formerly *Aporosaura*) closely related to *Saurites* (Boulenger 1921; Lamb & Bauer 2003). Engleder *et al.* (2013) reported that *M. anchietae, M. cuneirostris, M. reticulatus, M. ctenodactylus* and *M. micropholidotus* form part of a highly specialized psammophilous group compared to the generalist group members, *M. suborbitalis* and *M. knoxii.*

Most of the molecular phylogenies are confirmed by morphological data (Arnold 1990). Some clades show several characters that can easily separate original and derived conditions (Arnold 1990). On the other hand, some clades may show few characters that makes it difficult to identify sub clades effectively. Two factors affect such differences; first, variation in phylogeny because of clades that are exposed to different environmental conditions during evolution. Similarly, populations of the same species may differ in morphology, physiology and behaviour because of environmental differences (Edwards & Kot 1995). The second factor is variation in the natural capacity to produce and keep the variety of derived conditions of morphological characters in order to restore definite phylogenies (Arnold 1990). Apart from large body sizes and genetic variation of Clades A and B of *M. cuneirostris*, the two clades occur in a similar habitat and indicate similar bimodal pattern of activity. These factors do not sufficiently separate the two clades to impose taxonomic status on them, therefore, sufficient data is required.

2.4.2 Morphology

This study is the first to report on the morphological differences between populations of Clades A and B of *M. cuneirostris*. The present study found that the snout-to-vent lengths (SVL) and body mass differed significantly between the three monophyletic groups, Clade A of *M. cuneirostris* being longer than both Clade B of *M. cuneirostris* and *M. anchietae*. The differences in body size between Clades A and B of *M. cuneirostris* may be directly related to the populations being geographically separated (*ca*. 800 km), occurring in different climates and vegetation types, indicating that seasonal abundance and availability of resources also differ, and therefore producing different selection regimes for these populations (Ferguson & Brockman 1980; Smith & Ballinger 1994). Another common pattern observed in lizards is a decrease in body size with an increase in elevation (Sears 2005; Pincheira-Donoso *et al.* 2008; Ramirez-Bautista *et al.* 2011), and the variation observed in body size between Clades A and B of *M. cuneirostris* is different to this pattern. This pattern however, may be affected by the combination of data for Clade A populations (at elevations of 30 m, 97 m, 486 m and 496 m) compared to 150 m for Clade B. Ectotherms behaviourally and physiology depend on their body temperature (Vitt & Caldwell 2009), such that small-bodied species living in cold environments enable fast heating to thermal optima (Garcia-Rosales *et al.* 2017). Therefore, species living in cold environments may not grow to large body sizes because of limitations on thermoregulation efficiency (Pincheira-Donoso *et al.* 2008).

Both Clades A and B of *M. cuneirostris* were similar in being sexually dimorphic, with males being longer and heavier than females. This confirms previous observations by Childers & Eifler (2015) of *M. cuneirostris* adult males being larger than adult females in mean SVL (males:

55.75 ± 5.61 mm; females: 50.63 ± 3.83 mm). Similarly, Goldberg & Robinson (1979) found that *M. cuneirostris* adult males (8.1g mass; 54 mm SVL) were significantly larger than adult females (4.7g mass; 49 mm SVL). Sexual dimorphism may be a result of resource and territory defence (Stamps 1983). Such examples are when larger males defend their territories from smaller male invaders (Stamps 1983), competition between males for mating partners (females; Shine 1978), and differences in feeding niches between males and females to reduce competition for food resources (Schoener *et al.* 1982; Hierlihy *et al.* 2013).

The present study also found that *M. anchietae* was not sexually dimorphic for both SVL and body mass. This observation was different from the study by Robinson (1989) of *Aporosaura anchietae* (*M. anchietae)* who found the species to be sexually dimorphic, with mean body mass of males being significantly heavier (5.10g) than that of females (2.93g). A study by Goldberg & Robinson (1979) also showed sexual dimorphism in *M. anchietae* with adult males being larger (4.5g mass; 49 mm SVL) than adult females (3.1g mass; 44 mm SVL). The differences in the results of the previous studies with the finding of the present study may be limited to morphological differentiate between male and female individuals of *M. anchietae*.

Lizard body size can influence the length of the breeding season and timing of reproduction (Goldberg & Robinson 1979). Smaller-sized female lizards have lower maintenance cost, which leads to high-energy accumulation for quicker egg production (Downhower 1976). This allows small body-sized females to respond rapidly to the unpredictable productivity flushes that characterize extreme desert environments such as the Namib Desert. In addition, small females can lay eggs more frequently; however, several consequences of counter-selectivity come with small-sized bodies of females (Goldberg & Robinson 1979). In Namib lacertids, the size of the clutch is proportional to the body mass in females (M.D. Robinson, unpublished). The inability of small body-sized lizards to consume large prey items reduces prey diversity, and as a result, individuals become less resistant to desiccation and starvation such that mortality increases during longer periods of low prey productivity and drought (Goldberg & Robinson 1979).

The study also revealed that Clade B of *M. cuneirostris* has a more solid reddish colour pattern compared to the lighter colour pattern of Clade A of *M. cuneirostris*. The interaction between genetic traits and environmental effects results in differences in phenotypes (Garcia-Rosales *et al*. 2017), and expression of some geographically variable traits such as variation in body colour are related to heritable variation in genes (Sinervo & Lively 1996). Body colours can also be temperature-dependent as a function of temperatures experienced during incubation (Randriamahazo & Mori 2005), or changes in thermal conditions for adults (Stephenson *et al*. 2016). The differences in body colour between Clade A and B of *M. cuneirostris* may therefore, be associated with the difference in environmental temperatures experienced by the two taxa during incubation. Body colouration plays a role in thermoregulation where darker animals heat faster than lighter ones (Trullas *et al*. 2007, 2008). In this study, lizard dorsal colouration is significantly darker in Clade B with lower body temperatures compared to the lighter Clade A of *M. cuneirostris* with higher body temperatures. Dark colouration could potentially protect lizards from the harmful influence of ultraviolet radiation (Porter & Norris 1969).

2.4.3 Microhabitat

This study is the first to investigate and compare seasonal microhabitat preferences between populations of Clades A and B of *M. cuneirostris*. However, the study by Murray & Schramm (1987) reported on the microhabitat comparison between *M. cuneirostris* and *M. anchietae* as species. During both seasons (autumn and spring), the present study found that Clades A and B of *M. cuneirostris* occupied a similar microhabitat; the vegetated dune base as the dominant substrate type used, that differed from the slipface as a preferred substrate type for *M. anchietae*. Murray & Schramm (1978) also found *M. cuneirostris* mainly on lightly vegetated dune base and *M. anchietae* mainly on dune slipface. Similarly, Louw & Holm (1972) observed the majority of the *M. anchietae* on the slipface (loose deep sand) and Childers & Eifler (2015) observed *M. cuneirostris* spending more time in vegetation cover as substrate type. Apart from the highly preferred substrate types, the taxa were also observed on bare dune base (*M. anchietae*) and on gravel dune base (Clade A of *M. cuneirostris*) similar to observations by Murray & Schramm (1978) of *M. anchietae* and *M. cuneirostris* on dune base or sandy interdune areas.

Lizards that live on dunes prefer linear or barchans dunes with steep slipface slope, and the crest and windward slope (Robinson & Barrows 2013). The slipface as the preferred microhabitat for *M. anchietae* provides the species with substrate to burrow and move across the steep dune complimenting burrowing adaptation characters of long toes with scales on the hands to increase traction on loose sand and a wedge-shaped head for easy penetration of the sand (Stebbins 1944, 1948; Norris 1958; Luke 1986; Arnold 1995; Robinson & Barrows 2013). The slipface has little or no vegetation with the base dominated by perennial plants such as the dune succulent, *Trianthema hereroensis*, the dune Bushman's grass, *Stipagrostis sabulicola*, *Cladoraphis spinosa*, *Acanthosicyos horridus*, the baboon food/pickle bush, *Augea capensis*, the box-thorn/desert-thorn, *Lycium cinereium*, the salt cedar, *Tamarix aphylla*, and the saltwort, *salsola sp.* such that the morphological adaptations of the three taxa complement the characteristics of the preferred microhabitat. Individuals of Clades A and B, and of *M. anchietae* took advantage of the rising sun in the mornings, sun basking before continuing a daily routine of essential functions such as feeding, finding mating partners and escaping from predators.

The interaction between microhabitat use and thermal conditions form an important component of behavioural thermoregulation (Paulissen 1988; Huey 1991). Lizards maintain their body temperatures for ecological functions in some microhabitats and avoid others (Waldschmidt & Tracy 1983; Christian & Tracy 1985). The use of microhabitat therefore, may have a direct effect on lizard survival (Christian & Tracy 1986; James & M'Closkey 2003). The use of microhabitat in lizards differ between age and body size resulting in activities such as territoriality (Schall 1974), avoiding of predators (Stamps 1983), variation in resting site selection (Moermond 1979), and food security (Henderson 1974). In terrestrial lizards, thermal relationships result in body size-specific microhabitats such as smaller lizards occupying warmer and more open microhabitats compared to larger lizards (Hillman 1969; Asplund 1974; Scheibe 1987). As for this study, juveniles were also observed more in open areas sun basking, whereas adult lizards were observed under vegetation as perfect cover from predators.

The body size of lizards can also be influenced by the change in microhabitat type and structure (Amor *et al.* 2007). Changing climate influences the availability of water and preferred thermal conditions for ectotherms such as lizards (Lourdais *et al.* 2004; Araujo *et al.* 2006). Changes in the availability of water can negatively influence the trophic interactions, animal activity (Voigt *et al.* 2003; Suttle *et al.* 2007), community dynamics and disrupting ecosystems (Voigt *et al.* 2003; Suttle *et al.* 2007; Smith *et al.* 2009; McCluney *et al.* 2012). A decrease in food quality may contribute to smaller body sizes because of slow growth and *vice versa* (Berrigan & Charnov 1994).

2.4.4 Thermal biology

This study is the first to compare the thermal biology between Clades A and B of *M. cuneirostris*, and *M. anchietae*, and little or no data are documented on the thermal preferences of the three monophyletic groups. Thermal conditions experienced during embryogenesis can induce phenotypic variation in animals (Brana & Ji 2000). Temperature, in particular, plays a significant role in determining the rates of development in ectotherms (Atkinson 1994; Johnston *et al.* 1996) and has a strong effect on morphological, behavioural and performance traits (Cossins & Bowler 1987; Huey & Berrigan 1996). In some lizards, females have lower body temperatures when pregnant (Van Damme *et al.* 1986; Tosini & Avery 1996a, b), suggesting that higher temperatures during incubation could have detrimental effects on hatchling phenotypes (Brana & Ji 2000). The lower body and air temperatures at sampling localities for Clade B of *M. cuneirostris* during spring may be related to preferred lower temperatures for biological processes in this taxon.

Hatchlings incubated at lower temperatures are smaller compared to those developed at higher temperatures and have lower body mass, reduced tail and limbs (Brana & Ji 2000). Clade A of *M. cuneirostris* had higher body temperatures and was observed at higher air and substrate temperatures compared to the other two taxa. These characteristics correspond with larger body sizes of Clade A of *M. cuneirostris*. The maximum body temperature of *M. anchietae* was 38.2° C (during both autumn and spring), compared to the findings of the study by Louw & Holm (1972) who reported on a maximum body temperature of 45.1° C. In the mornings, *M. anchietae* emerged from the sand at 20° C during spring and at 28.2° C during autumn compared to 30° C emerging temperature reported by Louw & Holm (1972). Individuals of Clade A of *M. cuneirostris* were active at higher substrate temperatures (54° C during autumn and 49° C during spring) compared to *M. anchietae* (48° C during autumn and 45° C during spring) and Clade B of *M. cuneirostris* (43° C during autumn).

Slipface are known for their high surface temperatures, and for this reason, lizards only had two escape tactics to prevent them from over-heating, by either burying or retreating to cooler slopes (Robinson & Barrows 2013). The body temperatures of *M. anchietae*, and Clades A and B of *M. cuneirostris* were lower than substrate temperatures at sampling localities during both seasons, suggesting that the species have adapted to regulating their body temperatures to ensure that they do not overheat. Previous studies reported that numerous strategies are identified on how lizards behaviourally thermoregulate by: 1) changing their time of activity (Heatwole *et al.* 1969; Porter *et al.* 1973; Huey *et al.* 1977; Childers & Eifler 2015); 2), moving between areas of lower surface temperatures (Heath 1964; Hammel *et al.* 1967; Spellerberg 1972; Childers & Eifler 2015), and 3) changing their posture (Bartholomew 1966; Barlett & Gates 1967; DeWitt 1971; Huey *et al.* 1977; Stevenson 1985; Bauwens *et al.* 1996). Individuals of *M. anchietae* were observed burying in deep sand as soon as surface temperatures became hotter than they could bear, confirming findings by Louw & Holm (1972), when surface temperatures go beyond 40° C and *M. anchietae* was observed diving swiftly beneath the soft sand to reach for cooler depths. On the other hand, individuals of Clades A and B of *M. cuneirostris* were observed running into vegetation cover and a few hiding in burrows of unknown animals.

The study revealed that the air temperature < body temperature < substrate temperature, suggesting that the body temperatures of the individuals were usually fitted between air and substrate temperatures, such that body temperature could be estimated from values of air and substrate temperatures provided. Murray *et al.* (2016) reported that the morphology and balances of convection, conductive and radiant heat transfer at lizard locations determines their body temperatures, such that when substrate temperatures were higher than body temperatures, the conductive and radiant heat transfer would have imposed more heat on the lizard’s body when in direct solar radiation. They further explained that when air temperature at sampling localities was below that of the body, lizards would have lost heat by convection (Murray *et al.* 2016). Air and substrate temperatures at sampling localities of *M. anchietae*, Clades A and B of *M. cuneirostris* indicated a dependent positive relationship.

2.4.5 Activity pattern

This study is the first to investigate the difference of daily activity patterns between Clades A and B of *M. cuneirostris*, and *M. anchietae*, and little or nothing has been documented on the timing of activity of the three monophyletic groups. In reptiles, activity patterns depend on factors such as habitat availability, population density, predation pressure, abundance and environmental temperature (Moreno-Rueda *et al.* 2009; Vidal *et al.* 2010). The thermal environment changes with altitude and thus lizard activity may vary along altitudinal gradients (Grant & Dunham 1990). The daily and seasonal activity period of lizards is narrow with increasing altitude due to reduced availability of optimum-temperatures (Zamora-Camacho *et al.* 2013). Moreover, reproductive phenology may also change with altitude (Doughty & Shine 1998; Diaz *et al.* 2005).

Dry conditions reduce lizard activity (Lorenzo *et al.* 1999) and in the Namib Desert, being one of the driest deserts in the world (Ward *et al*. 1983; Hartley *et al*. 2005; Herman & Branch 2013), lizards are faced with extreme dry conditions (Nagy 2004). Variation in thermal conditions influences the availability of suitable time for lizard activities such as feeding (Adolph & Porter 1993). In diurnal lizards, basking behaviour plays a significant role in the thermoregulation mechanism (Belliure & Carrascal 1998). The amount of time spent basking is relative to light intensity, with increasing basking time at wavelengths less than 540 nm (Tosini & Avery 1996a), and dermal light sensibility, that determines the ability to position under a heat source (Tosini & Avery 1996b). In this study, individuals of the three taxa were all observed emerging from the sand with the rising sun to heat up for energy. During the day when temperatures became hot, the individuals were observed in the shade of vegetation, as they cooled off.

A few individuals of *M. anchietae* were observed on the vegetated dune base of dunes facing north, and because of the sun's direction during sunrise and sunset, these received more sunlight. The differences in slipface directions could be because of differences in dune shape and direction due to blowing wind from different directions (Steven 1969). The majority of *M. anchietae* individuals however, were observed on dunes with inclined slipface facing in the eastern direction. A few individuals of Clade A of *M. cuneirostris* were observed on the slipface with vegetation and spend most of their time under vegetation. In addition, Clade A of *M. cuneirostris* was observed grubbing termites from their nests. Individuals of Clades A and B of *M. cuneirostris* were also observed actively searching for prey as they moved through the microhabitats and this confirms an observation on *M. cuneirostris* employing both active and ambush foraging tactics during the dietary study by Murray & Schramm (1987) and Childers & Eifler (2015).

2.5 Conclusion

The present study found that there are important differences in the genetics and morphology of *M. anchietae* and *M. cuneirostris*. Molecular analyses indicated genetic differences between *M. anchietae* and *M. cuneirostris*, recovering two clades (Clades A and B) within *M. cuneirostris*, supporting variation in phylogenies because of differences in environmental conditions (Arnold 1990; Edwards & Kot 1995). Individuals of these two clades of *M. cuneirostris* used similar microhabitat and indicated similar patterns of activity, however, expressed distinctive body length, mass and thermal preferences. Individuals of *M. anchietae* and *M. cuneirostris* (and its associated clades) expressed different body length and body mass, used different microhabitats and preferred different temperatures, however, showed similar pattern of activity. Thus, we accept the null hypothesis stating that there is a difference in the genetics and morphology among populations of *M. cuneirostris* because of ecological and geographical variations in their habitat and rejecting the null hypothesis stating that there are no genetic and morphological differences between populations of *M. anchietae* because of similarities in the ecology and geography of their habitat. In addition, we accept the null hypothesis, stating that there is seasonal variation in partitioning of time between populations of *M. anchietae* and *M. cuneirostris*, and accept the null hypothesis stating that there is seasonal variation in partitioning of space between populations of *M. anchietae* and *M. cuneirostris.*

To this end, the results of the molecular data, lizard morphology, dune morphology, thermal preference and daily activity pattern strongly suggest that the systematics and taxonomy of lacertid lizards of the genus *Meroles* from the Namib Desert need to be investigated further as the genus may be more diverse than currently considered. Consequently, the analyses and interpretations in the present study treated Clades A and B of *M. cuneirostris* as two monophyletic groups pending more detailed studies to establish the systematic and taxonomic status of *M. cuneirostris* in the Namib Desert and perhaps beyond. The present study provides new data that may allow insights into lizard responses to changing environments because of climate change. This is because the wide distribution of these species across the Namib Desert may allow the species to potentially serve as indicator species for change in climate and thus may result in increasing conservation initiatives of other Namib Desert species. The presence of

Clades A and B of *M. cuneirostris* may increase the number of species within the genus *Meroles* because of genetic differences between the central and southern populations of *M. cuneirostris*.

CHAPTER 3

Comparative feeding ecology of sympatric lacertid lizards (*Meroles anchietae* and *M. cuneirostris* and its associated clades) from the Namib Desert, Namibia

Abstract

Niche partitioning reflects a competitive interaction between species. Among several niche dimensions, trophic niche is the most commonly studied aspect because of the ability to allow species on different diets to co-exist. In this study, the feeding ecology of two sympatric lacertid lizards, the shovel-snouted lizard, *Meroles anchietae* and the wedge-snouted lizard, *M. cuneirostris* and its associated clades from the Namib Desert, Namibia is compared. Based on molecular data, a parallel study (Chapter 2) found that *M. cuneirostris* has two clades (designated Clades A and B) from the central and southern Namib Desert, Namibia, respectively. Pending a more detailed study to establish the systematic and taxonomic status of *M. cuneirostris*, the seasonal (autumn and spring) feeding ecology of these two clades (populations) is compared with that of populations of *M. anchietae.* Lizard activity is generally low during winter, thus sampling was not considered, while due to logistical constraints in summer, sampling was not possible. Diet was quantified using stable isotope of carbon and nitrogen, and validated with faecal pellet analysis. The carbon and nitrogen ratios for lizard tissues indicated that populations of *M. cuneirostris* were feeding at similar trophic levels that were different from that of populations of *M. anchietae.* Populations of *M. anchietae* occupied niches of higher carbon values than populations of *M. cuneirostris* that occupied niches of high nitrogen values. No faecal pellets were collected from lizard samples of the southern Namib Desert (Clade B of *M. cuneirostris*). Thus, for faecal pellet analyses, results were only compared between populations of *M. anchietae* and Clade A populations of *M. cuneirostris*. *Meroles anchietae* specialized on plant matter with seeds making up 80% of its diet and 59% of its faecal pellets, whereas Clade A of *M. cuneirostris* specialized on ants that made up 50% of its diet and 70% of its faecal pellets. Faecal analyses showed that Clade A of *M. cuneirostris* occupied a larger niche space, greater prey diversity, and a greater evenness of prey distribution within its diet than *M. anchietae*. The findings in this study add knowledge on lizard dietary niche and resource partitioning to allow better insights into the feeding ecology of lizards.

Keywords: *Meroles*, lacertid lizards, diet, feeding ecology, stable isotopes, faecal pellets, prey diversity, Namib Desert, Namibia

3.1 Introduction

Within a community, specific biotic and abiotic factors, and competition exist as part of a species' niche (Elton 1946; Hutchinson 1957; Patterson *et al.* 2003). Species that partition a niche indicate a competitive interaction among them (Pianka 1973; Patterson *et al.* 2003; Kartzinel 2015). Trophic niche is the most commonly studied aspect among several other niche dimensions, because of its ability to allow species on different diets to co-exist and because it influences the diversity of species (Simberloff & Dayan 1991; Goodyear & Pianka 2011; Mamou *et al.* 2016; Murray *et al*. 2016b). Species on the same dietary niche, however, may be either specialists or generalists, thus allowing the partitioning of their food niche (Futuyma & Moreno 1988). Several studies have shown that a habitat may support a greater number of specialist than generalist species because there is no overlap in resources used (Hutchinson 1957; Pianka 1973; Roughgarden 1974; Murray *et al.* 2016b). The theory of 'exclusion in competition' explains that two species may only co-exist if there is divergence into one or more niche dimensions to reduce competition (Hardin 1960; Pianka 1973; Reid *et al.* 2013; Parejo & Aviles 2015; Murray *et al*. 2016b). As such, two similar species on the same diet may co-exist by using different spatial and temporal niches (MacArthur 1958; Bowers & Brown, 1982).

Among several factors of ecology, similarities between species can be achieved by comparing their diet (Goodyear & Pianka 2011). Diet differs across the time at which species are active (Goodyear & Pianka 2011). The food and space niche of a lizard can be influenced by either the mode of foraging or the way in which a lizard uses space (Pianka 1973). Thus, widely foraging species typically have broader space niches than sit-and-wait species, while the latter often tend to have broader food niches than the former (Pianka 1973). For instance, lizard species that overlap along one niche dimension may have very low overlap along other niche dimensions (Pianka 1973). As an animals' diet composition is known to change with the density and abundance of prey (Pianka 1973), several other factors of an animal's biology such as behaviour, morphology, habitat preference, and physiology may influence the characteristics of the diet such as the size, type and amount of food consumed (Pyke *et al*. 1977; Houston & Shine 1993; Hawlena & Perez-Mellado 2009).

Arid ecosystems present ideal habitats to study niche partitioning between lizards because of their high lizard diversity (Pianka 1986; Murray *et al*. 2016b), and limited resources could potentially intensify the competition among species (MacArthur & Levins 1967; Murray *et al*. 2016b). Irrespective of the low availability of plant resources as food and shelter, the Namib Desert in Namibia is known to support high levels of lizard endemism (Murray & Schramm 1987; Hermann & Branch 2013; Murray *et al.* 2016b). Despite this, only a few studies on Namib Desert lizards have focused on resource partitioning (Robinson & Cunningham 1978; Murray & Schramm 1987; Murray *et al*. 2016b).

Several methods have been used to understand the feeding ecology of animals, such as stable isotope analysis of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) that is used to assess dietary variation of organisms in the wild (McKechnie 2004; Fisk *et al.* 2009; Murray *et al*. 2016b), stomach flushing (Herrel *et al.* 2006), faecal pellet analysis (Hawlena & Perez-Mellado 2009), stomach content analysis (Pough *et al.* 2004), and direct observation of lizards in the field as they forage (Saez & Traveset 1995). Most ecological studies currently use stable isotopes of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) as a method for assessing dietary variation of organisms in the wild (McKechnie 2004; Fisk *et al.* 2009; Murray *et al*. 2016b). The present study therefore attempts to address the trophic partitioning between populations of two sympatric lacertid lizards, the shovel-snouted lizard, *Meroles anchietae* and the wedge-snouted lizard, *M. cuneirostris* from the Namib Desert, Namibia, addressed through analyses of stable isotope and faecal pellet to understand how the species share the limited resources to reduce competition. The two species are similar morphologically, have similar diurnal activity pattern but differ significantly in their diet, habitat and reproduction (Goldberg & Robinson 1979).

Studies on stomach content analysis in the Namib Desert revealed that the shovel-snouted lizard, *Meroles anchietae* prefers an omnivorous diet, whilst the wedge-snouted lizard, *M. cuneirostris* prefers an insectivorous diet (Robinson & Cunningham 1978; Murray & Schramm 1987; Robinson 1987; Nagy & Shemanski 2009). Both lizards eat a wide range of arthropod species, consisting mainly of insects (Robinson & Cunningham 1978; Murray & Schramm 1987), but even though *M. anchietae* preys on insects of the same orders as those preyed upon by *M. cuneirostris*, seeds form the largest portion of their diet (Robinson & Cunningham 1978; Murray & Schramm 1987). As such, *M. anchietae* and *M. cuneirostris* are adapted to living in narrow sympatry with each other (Murray & Schramm 1987). Although there have been many studies on trophic ecology of *M. anchietae* and *M. cuneirostris*, there is very little documentation on the trophic levels at which these species are feeding, their isotopic niche occupancy, the dietary niche breadth, trophic niche evenness and the dietary species richness. The present study therefore, attempts to address this knowledge gap to better understand the trophic structure of Namibian lizards.

Stable isotopes

Stable isotopes have been used to gain insights into competitive interactions between similar species and relationships between predators and prey (Lattanzio & Miles 2016), and may also provide an estimation of the contribution of various food sources to an animal's diet (Wilson *et al*. 2010; Varela *et al*. 2011; Murray *et al*. 2016b). Depending on the type of tissue and species, assessed, stable isotopes can provide daily and annual dietary information of an organism (Dalerum & Angerbjo 2005; Fisk *et al.* 2009). Dietary information is important for monitoring and management of species (Hobson & Clark 1993; Fisk *et al.* 2009), despite very little being known on dietary preferences of reptiles (Fisk *et al*. 2009).

On average, δ^{15}N increases by ± 3.0‰ through each trophic level and this information may be useful to determine the trophic level at which a particular organism is feeding (DeNiro & Epstein 1981; Peterson & Fry 1987; Varela *et al*. 2011). On the other hand, δ^{13}C changes very little (± 1.0 ‰) through the trophic levels and this information may be used to trace the sources of food (carbon sources) (DeNiro & Epstein 1978; Peterson & Fry 1987; Murray *et al*. 2016b). Differences in photosynthetic pathways contribute to different δ^{13}C values in plants (Ehleringer *et al*. 1986, 1997; Murray *et al*. 2016b). The C_4 (i.e., grasses) or crassulacean acid metabolism (CAM) plants (i.e., succulents) yield significantly higher δ^{13}C values, between -9 and -17‰, compared to C_3 plants (i.e., trees) that yield between -20 and -32‰ (Tillberg *et al.* 2006), therefore, leading to lower δ^{13}C ratio in C_3 compared to C_4/CAM plants (Ehleringer *et al*. 1986).

These analyses result in values of δ^{13}C and δ^{15}N that are influenced by factors such as tissue-specific lipid content (Bodin *et al.* 2007). Compared to proteins, lipids are known to be depleted in ^{13}C because of lipid synthesis during fractionation of pyruvate oxidation to acetyl coenzyme A (DeNiro & Epstein 1977). For this reason, differences in lipid content may mislead diet interpretations (DeNiro & Epstein 1977; Post *et al.* 2007; Ricca *et al.* 2007; Oppel *et al.* 2010; Elliott & Elliott 2016). Extraction of lipids from samples is, therefore, required for stable isotope ratio measurements (Sweeting *et al.* 2004, 2006; Bodin *et al.* 2007; Kojadinovic *et al.* 2008; Kaufman *et al.* 2014; Elliott & Elliott 2016). Several methods of chemical extraction of lipids have been used, with chloroform-methanol commonly used as a solvent (Folch *et al.* 1957; Bligh & Dyer 1959; Elliott & Elliott 2016). Chloroform-methanol (polar solvent) serves as the best method for lipid extraction compared to other non-polar solvents (i.e., petroleum ether) because of its ability to result in more enriched ^{13}C values (Elliott & Elliott 2016).

Despite tissue-specific lipid content influencing the values of δ^{13}C and δ^{15}N (Bodin *et al.* 2007), there has been growing evidence that sample preparation such as acid washing, lipid extraction, water rinsing, storage and reservation, drying technique prior to isotopic analysis may also lead to biases in the values of δ^{13}C and δ^{15}N (Edwards *et al* 2002; Carabel *et al.* 2006; Bodin *et al.* 2007). Among marine and terrestrial invertebrates, there are contradictions on the effect of lipid extraction on δ^{13}C and δ^{15}N signatures (Chamberlain *et al.* 2004; Bodin *et al.* 2007; Mateo *et al.* 2008). Carbohydrates present δ^{13}C values similar to those of the whole body, whereas lipids are depleted by ± 4‰ and proteins are enriched by ± 2‰ relative to the whole body (DeNiro & Epstein 1978). Extraction of lipids should therefore result in δ^{13}C-enriched samples. The results of the study by Mateo *et al.* (2008) however, indicated significant δ^{13}C depletion in whole individual Gastropoda and Malacostraca, whereas the tissue samples from the same individuals indicated δ^{13}C enriched after extraction. In addition, the results of the study by Bodin *et al.* (2007) indicated no effect of lipid extraction on the δ^{13}C and δ^{15}N values of muscle tissue samples of invertebrates (3‰ w/w of lipids), but reported a significant increase in hepatopancres and gonads (1-3‰ for δ^{13}C and 1‰ for δ^{15}N). The effect of lipid extraction on δ^{15}N is large when dealing with tissue samples (Mateo *et al.* 2008). Other studies have also reported an increase in δ^{15}N values in lipid-rich tissues after extraction (Pinegar & Polunin 1999; Sweeting *et al.* 2006; Bennett & Hobson 2009). Certain lipid extraction methods such as the acetone-hexane method contributes to co-extraction of amino acids (Mateo *et al.* 2008), such that the increase in δ^{15}N observed in lipid extracted samples could be related to the removal of lipoprotein compounds that are depleted in δ^{15}N (Stiropoulos *et al.* 2004; Sweeting *et al.* 2006; Bodin *et al.* 2007).

The relative abundance of fatty acids in arthropods depends on the type of species (Hanson *et al.* 1985; Sushchik *et al.* 2003), the stage in life (Ogg & Stanley-Samuelson 1992; Sayah *et al.* 1997), the environmental conditions (Joanisse & Storey 1996), and the type of diet (Thompson 1973; Fernando-Warnakulasuriya *et al.* 1988; Graeve *et al.* 1994; Cripps & Atkinsonof 2000). In a natural environment, invertebrate metabolism is slow because of lower ambient temperatures (Neven 2000), and the process of carbon exchange will progress at slower rates (Chamberlain *et al.* 2004). The δ^{13}C values of lipids would therefore, reflect diet over a long period (Chamberlain *et al.* 2004). Moreover, soil invertebrates undergo periods of starvation (Joosse & Testerink 1977) which may affect the lipid content and the δ^{13}C values of the whole individual (Testerink 1981; Oelbermann & Schue 2002). Given the effects of biochemical processes on the δ^{13}C values and the high fluctuations of lipids in organisms, it is required to define the biochemistry of an organism, the point of isotopic fractionation and potential sources of carbon to better apply the compound-specific isotopic analysis to animal dietary studies (Chamberlain *et al.* 2004). This however, may be time and labour-intensive to achieve for individual animal species.

In addition, the analyses of carbon and nitrogen isotope ratios in tissues of a consumer require the use of consumer-resource (diet) discrimination factor (Caut *et al.* 2009; Boecklen *et al.* 2011). This is defined as the differences in ratios of stable isotopes between the resource and the consumer. The consumer-resource discrimination factor differs with digestion or fractionation during metabolism and assimilation processes, the quality of diet, tissues or individual species and growth rate (Caut *et al.* 2008; Boecklen *et al.* 2011). Time and labour-intensive feeding trials are required to define specific species discrimination factors (Gannes *et al.* 1997; Martinez & Carleton 2012).

For most terrestrial ecosystem studies involving stable isotope analysis, the focus has been mainly on mammals and birds (Kelly 2000) with little emphasis on reptiles (Struck *et al.* 2002; Warne *et al.* 2010). Reptiles however, are sensitive to seasonal, spatial and temporal variations in the availability of prey items that influence dietary selection and the isotopic composition of tissues (Pastro *et al.* 2013). In addition, reptiles exhibit different strategies of diet selectivity and trophic niche occupancy easily clarified with the use of stable isotope analysis (Seminoff *et al*. 2007).

Faecal pellets

Dietary studies based on faecal pellet analysis have been preferred over studies based on stomach content analysis (Marufu *et al.* 2017). This is because body parts of arthropods are more concentrated in the faecal pellet than in the stomach contents where items are likely to be stuck on the stomach wall (Black 1972; Hawlena & Perez-Mellado 2009; Perez-Mellado *et al.* 2011; Marufu *et al.* 2017). Faecal pellet analysis may, however, generate biased results for soft and small prey items that are usually broken down completely during the digestive process (Pincheira-Donoso 2008; Perez-Mellado 2009; Perez-Mellado *et al.* 2011). To reduce these biases, through the search for small and soft body parts (i.e., cuticles, head capsules, and mandibles) should be ensured (Perez-Mellado 2009; Murray *et al*. 2016a).

Based on molecular data, the results of Chapter 2 found that *M. cuneirostris* has two clades (designated Clades A and B) from the central and southern Namib Desert, Namibia, respectively. Pending a more detailed study to establish the systematic and taxonomic status of *M. cuneirostris*, the present study therefore aims to investigate the trophic variation between *M. anchietae* and *M. cuneirostris* (and its associated clades) from the Namib Desert, Namibia. The trophic structure is therefore assessed seasonally (autumn and spring) to determine whether the food niche dimension contribute to the separation of the microhabitat of the populations of the genetically defined taxa (Chapter 2). Because of low lizard activity during winter, sampling was not considered, while during summer, sampling was not possible due to logistical constraints. The present study hypothesize that the populations of *M. anchietae* and *M. cuneirostris* (and its associated clades) would prey on similar food items due to the occupancy of the same dune environment, and thus possibility for similar prey availability. This hypothesis is tested by comparing the diet preferences between the three taxa using stable isotope and faecal pellet analyses to evaluate the degree of dietary overlap.

3.2 Materials and Methods

Sampling of lizards (*M. anchietae* and Clades A and B of *M. cuneirostris*), plants and arthropods was conducted at five sites namely, Rooibank (RBK), Near Gobabeb site (NGS), Far Gobabeb site (FGS), Kuiseb Delta site (KDS) and Oranjemund (ORM) along the Namib Desert, Namibia (Chapter 1). Due to differences in the distributional range of the two sympatric lizard species across the Namib Desert, *M. anchietae* was sampled from three sites (RBK, NGS and FGS) and *M. cuneirostris* sampled from all five sites (Chapter 1). Trophic data were collected over two seasons only, during spring (September 2016) and autumn (March-April 2017). Spring and autumn were defined by the differences in daily average air temperature; spring daily average air temperature was 16.2 ± 3.0°C (daily average minimum air temperature was 9.5 ± 2.6° C and daily average maximum air temperature was 24.2 ± 4.5° C), whereas autumn daily average air temperature was 24.1 ± 3.7° C (daily average minimum air temperature was 17.4 ± 3.4° C and daily average maximum air temperature was 31.9 ± 4.1° C) (http://www.sasscalweathernet.org).

Meroles anchietae and Clades A and B of *M. cuneirostris* were sampled using cotton mesh bags (D.A. Eifler, unpublished) and noose poles (Murray *et al.* 2016a), respectively. The difference in sampling method is because of differences in lizard predatory behaviour, *M. anchietae* buries entirely in open sand (Robinson & Barrows 2013) and mesh bags are used to sieve the sand, leaving the lizard in the bag. On the other hand, Clades A and B of *M. cuneirostris* bury entirely in sand beneath vegetation and noose poles are used to sample them quietly to avoid burying (N. Iiyambo *pers. obs.*). To avoid re-sampling of individuals, a black cross was marked on the back with a non-toxic temporary marker for quick and easy recognition from a distance (Chapter 2). The identification of individual sex was determined among *M. anchietae* and *M. cuneirostris*. Because female and male *M. anchietae* are not easy to distinguish morphologically (*pers. obs.*), sex in *M. anchietae* individuals was determined by the presence or absence of the hemipenis in males and females, respectively (D.A. Eifler, unpublished). In young individuals, due to individuals not having reached sexual maturity, a probe was inserted into the cloaca. The male cloaca is usually deep and allows for the smooth entry of the probe to approximately 5 mm depending on the age of an individual whereas female cloaca is shallow. In *M. cuneirostris,* however, the females and males differ in colouration and pattern with the females possessing a distinct dark pink-orange lateral stripe that extends from the eye to the tail while the males lack this stripe and possess a more reticulated pattern (Branch 1998; Childers & Eifler 2015).

3.2.1 Sampling for stable isotope analyses

Lizard tissue sampling

For each individual, a tail tissue sample (approximately 5 mm) was sampled from the tail tip and stored in micro tubes at -5° C. Tail tissue was obtained from 17 males and 13 females (including 9 juveniles and 21 adults) of *M. anchietae,* and 19 males and 21 females (including 18 juveniles and 22 adults) of Clade A of *M. cuneirostris* during spring. During autumn, 14 males and 9 females (including 2 juveniles and 21 adults) of *M. anchietae,* 22 males and 18 females (including 4 juveniles and 36 adults) of Clade A of *M. cuneirostris,* and 3 males and 6 females (including 4 juveniles and 5 adults) of Clade B of *M. cuneirostris* were sampled.

Plant and arthropod tissue sampling

Plant material was sampled from each plant species at each site, and 37 samples were sampled from eight plant species. Plants from each species were chosen at random and sampling was conducted on leaves and stems. Plant sampling did not consider seasonality because the plant species were all perennials and the same plants were available for sampling during both spring and autumn. In cases where flowering was observed, however, flower buds were sampled separately to account for different plant parts that could be fed on. The dry plant samples were homogenized with a mortar and pestle, whereas fresh plant samples were sun-dried for periods long enough to ensure complete dryness (approximately two days of intense sunshine) and later homogenized. During sun drying, samples were covered with mesh bags to avoid arthropod infestation. A few succulent plant samples could not be homogenized with a mortar and pestle, and a BeadBug^{TM} Micro tube Homogenizer (Benchmark Scientific, New Jersey, U.S.A.) was used to further crush these plant samples. The bead bug micro tube homogenizer was used with 2 ml screw cap tubes and two standard Inotech IS-500-MS Glass Beads (Inotech Bioscience LLC, Maryland, U.S.A.) of 1.0 mm width at a speed of 380 revolutions per minute for 120 seconds, three times longer to ensure complete breakdown of samples into a homogenized powder. After crushing, all plant samples were stored in eppendorf tubes (at room temperature) awaiting analysis.

Individuals of each arthropod species observed at each site were sampled while walking through the habitat by hand capturing. Pit-fall traps were set out randomly within the microhabitat (open space and vegetated space) for unaccounted diurnal arthropods in areas where lizards were active. One hundred and seven arthropod samples of 29 known species and several unknown species such as beetles, flies, bees, wasps, moths, spiders, bugs and silverfish were sampled. An effort was made to ensure sampling of termites (termite mounds usually observed around grass hummocks) and ants as a key component of lizard diet (Murray *et al*. 2016b). Some arthropod samples could not be fully dried through sun-drying, as with plants, and the samples were stored in eppendorf tubes at -5° C, then oven-dried at 60° C for 24 hours and later homogenized with a mortar and pestle. A few arthropod samples with hard shells were further homogenized using the Bead Bug^{TM}micro tube homogenizer (Benchmark Scientific, New Jersey, U.S.A.). After crushing, all arthropod samples were stored in eppendorf tubes (at room temperature) awaiting analysis. Arthropods were identified to order, family or genus levels and to species level where possible using references on southern African insects and arthropods (Scholtz & Holm 1985; Picker *et al*. 2004; Murray *et al*. 2016b).

Stable isotope analyses

The frozen tail samples were treated with 5 mL of 2:1 chloroform-methanol solution for 24 hours to extract lipids (Halley *et al.* 2008). After 24 hours, the solution was removed from the micro tubes using a needle syringe. Tail samples were later dried in an oven at 60° C for 24 hours and a microbalance scale was used to weigh between 0.5 and 0.6 mg of sample that was placed into 6 x 4 mm tin capsules (Costech Analytical Technologies, California, U.S.A.) that have been pre-cleaned in toluene.

The dried plant and arthropod samples were also weighed for samples between 1.0 and 1.1 mg and divided into 6 x 4 mm tin capsules. Several random samples of tails, arthropods and plants were weighed in duplicates and mean values were recorded. The differences in weights of plant, arthropod and lizard tissues are because of lower concentrations of nitrogen than carbon in organic material (Malcolm & Durum 1976; Merriam-Powell 2007). Plants have lower nitrogen concentration than animals, thus nitrogen becomes the limiting factor in isotope measurements, meaning more sample is needed for plants and arthropods than animals (Malcolm & Durum 1976; Merriam-Powell 2007). For the present study, lipids were not extracted from the arthropods because of the contradictions on the effect of lipid extraction on $\delta^{13}C$ and $\delta^{15}N$ signatures (Chamberlain *et al*. 2004; Bodin *et al.* 2007; Mateo *et al.* 2008).

All samples from tails, plants and arthropods were analysed for carbon (δ^{13}C) and nitrogen (δ^{15}N) isotope ratios using a Delta V Plus stable light isotope ratio mass spectrometer (Thermo Fischer, Bremen, Germany). The mass spectrometer was coupled to a Flash EA 1112 series via ConFlo IV system (Thermo Fischer, Bremen, Germany) housed at the Stable Isotope Laboratory at the Mammal Research Institute (MRI), University of Pretoria, Pretoria, South Africa. After every 11 samples of analysis, there followed a blank sample and standards of known δ^{13}C and δ^{15}N ratios; Merck Gel δ^{13}C = -20.26‰; δ^{15}N = 7.89‰ and Deuterated Leucine Valine (DL-Valine) δ^{13}C = -10.57‰; δ^{15}N = -6.15‰. The standards were weighed into three different sample sizes of between 0.2 to 0.24 mg, 0.4 to 0.44 mg and 0.6 to 0.64 mg. The standards were used to ensure that analysis could be repeated to yield similar results and that the results are comparable across globally (Elliott & Elliott 2016). Merck Gel values were specifically used for data correction during each run and DL - Valine values were used to provide mass balance calculations (± error) for each run. All standards are calibrated against international standards based on the National Institute of Standards & Technology (NIST): NIST 1557b (bovine liver), NIST 2976 (muscle tissue) and NIST 1547 (peach leaves) (Ben-David & Flaherty 2012; Connan *et al.* 2018). The units of measurement are expressed in delta notation (δ) in parts per thousand (‰) referenced to international standards of Vienna Pee Dee Belemnite (VPDB; δ^{13}C) and atmospheric nitrogen (AIR; δ^{15}N) (Bond & Diamond 2009) as follows:

$$\delta\, X\,(‰) = \left(\left(\frac{Rsample}{Rstandard}\right) - 1\right) \times 1000$$

where δ is the isotopic notation of element *X* in its heavy form, and *R* is the ratio of heavy to light isotopes (e.g., ^{13}C/^{12}C or ^{15}N/^{14}N) for the sample and standard (Evans *et al.* 2003; Ben-David & Flaherty 2012; Murray *et al.* 2016b). For the present study, the poikilotherm consumer-resource discrimination factor mean $\Delta\delta^{13}$C (0.4‰, 91 studies) and the mean $\Delta\delta^{15}$N (2.3‰, 65 studies) were used to adjust the diet tissue δ^{13}C and δ^{15}N values (McCutchan et al. 2003). For comparison of trophic structure between populations of *M. anchietae* and *M. cuneirostris*, the following trophic niche metrics were assessed; the standard ellipse areas corrected for small sample size (SEA_C), the total area of the convex hull (TA), the mean distance to centroid of each species (CD), the mean nearest neighbour distance to each species (MNND) and the standard deviation of mean nearest neighbour distance (SDNND) (Layman *et al.* 2007).

3.2.2 Sampling for faecal pellet analyses

Faecal pellet sampling

Following Murray *et al.* (2016a), all lizards were kept overnight in cotton bags and released at their site of sampling the following morning. Any faecal pellets deposited in the bag were collected and stored in micro tubes at -5° C. When an individual lizard defecated, each defecation event was regarded as a single pellet (Murray *et al*. 2016a).

Faecal pellet analyses

The collected faecal pellets were dissected in 70% ethanol using a dissecting microscope to determine the types and number of prey items consumed (Suarez & Case 2002; Murray *et al*. 2016a). The arthropods observed in faecal pellets were identified to either class or order levels, and in some cases as far as the family level (Sneath & Sokal 1973; Carretero 2004; Cascio & Capula 2011). Authoritative taxonomic works of southern African insects and arthropods (Scholtz & Holm 1985; Picker *et al*. 2004; Murray *et al*. 2016a) were used for the identification of the arthropods. Sclerotized parts derived from the faecal pellets were counted using the minimum numbers criterion based on the analysis of wings, cephalic capsules, mandibles, and legs (Escarré & Vericad 1981; Carretero & Cascio 2010; Cascio & Capula 2011).

Diet was estimated by assessing the types of prey items (arthropod and plant matter) fed on and by calculating the contribution of each prey type on the diet of the species (prey abundance, %N) and the frequency of occurrence (%F) of each prey type within the faecal pellets (Murray *et al*., 2016a). The reciprocal of Simpson's diversity index ($1/N_2$) was used to estimate prey diversity through measurements of dietary niche breadth (B) (May 1975; Magurran 2004; Murray *et al*. 2016a) using the following equation:

$$B = \frac{1}{\sum_{i=0}^{n}(P_i^2)} = \frac{1}{\sum\left(\frac{n_i\,(n_i-1)}{N\,(N-1)}\right)}$$

where P is the comparative consumption of prey item i, and n the total number of prey categories and N the total number of individuals (Murray 2014; Murray *et al*. 2016a). A value of one indicates that a lizard species specializes on one prey type, whereas a higher value represents the use of all prey type by the same particular lizard species in a non-selective manner (Krebs 1999; Magurran 2004; Hooker 2009; Murray 2014). The Simpson's index of evenness ($E_{1 - D}$) was used to estimate the diet evenness (also known as species abundance and with reference to this study is the distribution of prey types on the diet of the two species; Smith & Wilson 1996) and was computed as follows (Magurran 2004):

$$E_{1-D} = 1 - B$$

where B is the dietary niche breadth of a particular species. The Simpson's index of evenness value ranges between zero and one, and the higher the value, the greater the evenness of prey types on the diet of a particular species (Smith & Wilson 1996; Krebs 1999). A community where species are equally abundant has high evenness and where species differ largely in abundance has low evenness (Smith & Wilson 1996). The symmetrical dietary niche overlap (O_{jk}) between species was estimated using Pianka's similarity index ($O_{kj} = O_{jk}$, Pianka 1973; Murray *et al*. 2016a) as follows:

$$O_{kj} = O_{jk} = \sum_{i=1}^{n} P_{ij}P_{ik} \Big/ \sqrt{\sum_{i=1}^{n} P^2{}_{ij} \sum_{i=1}^{n} P^2{}_{ik}}$$

where j and k representing the two lizard species for which the overlap is calculated, and P the comparative consumption of prey type I (Murray *et al*. 2016a). Niche overlap ranges between zero and one, with zero representing no resources used in common and one representing a complete overlap (Murray *et al*. 2016a).

No faecal pellets were collected from lizard samples of the southern Namib Desert (Clade B of *M. cuneirostris*). This observation may be related to variation in vegetation of geographically separated populations, suggesting differences in season and abundance of resources (Ferguson & Brockman 1980; Smith & Ballinger 1994). Thus, for faecal pellet analyses, results were only compared between populations of *M. anchietae* and Clade A of *M. cuneirostris*.

3.2.3 Statistical analyses

Stable Isotope Analyses package (SIAR; Parnell 2008; Jackson *et al.* 2011; Phillips 2012) and Stable Isotope Bayesian Ellipse (SIBER; Jackson *et al.* 2011) package in R statistical software (R version 3.4.1 © The R Foundation for Statistical Computing, Bell Laboratories, Murray Hill, New Jersey, U.S.A.) were used to compare isotopic niche space (widths) between populations of *M. anchietae* and *M. cuneirostris* (Murray *et al.* 2016b). Repeated-measures analysis of variance (ANOVA) was used to compare the carbon and nitrogen ratios using species and season as factors (Lattanzio & Miles 2016; Murray *et al.* 2016b). Mann-Whitney U-test was used to compare the number of prey items consumed between males and females (Murray *et al.* 2016a). A two-sample *t*-test was used to assess the amount of prey items consumed seasonally (Murray *et al.* 2016b). Values were reported as mean ± one standard deviation (± 1 SD) with a statistical significance level set at alpha (α) = 0.05. All statistical analyses were based on algorithms in R statistical software and Microsoft Excel 2016 (Microsoft Corp., Redmond, Washington, U.S.A.).

3.3 Results

3.3.1 Stable isotope assessment

Within *M. anchietae*, the carbon isotope ratios differed significantly between populations (repeated-measures ANOVA; population, δ^{13}C: $F_2 = 8.94$, $n = 59$, $P < 0.01$) with the FGS population occupying higher carbon niches than those of NGS and RBK. The RBK population occupied niches with significantly higher nitrogen (repeated-measures ANOVA; site, δ^{15}N: $F_2 = 16.97$, $n = 59$, $P < 0.01$) (Table 3.1). There was no significant difference in the carbon and nitrogen isotope ratios of the populations between season (repeated-measures ANOVA; season, δ^{13}C: $F_1 = 2.24$; $n = 59$, $P = 0.14$; δ^{15}N: $F_1 = 0.09$, $n = 59$, $P = 0.76$). The interaction between season and population was not statistically significant for both carbon and nitrogen ratios (repeated-measures ANOVA; season*population, δ^{13}C: $F_2 = 0.15$, $n = 59$, $P = 0.86$; δ^{15}N: $F_2 = 0.07$, $n = 59$, $P = 0.79$).

FGS population of *M. cuneirostris* occupied niches of significantly higher carbon than those of NGS, KDS, RBK and ORM (repeated-measures ANOVA; population, δ^{13}C: $F_4 = 8.08$, $n = 96$, $P < 0.01$), whereas KDS population occupied niches with significantly higher nitrogen than those of NGS, FGS, RBK and ORM (repeated-measures ANOVA; population, δ^{15}N: F_4 = 381.45, n = 96, P < 0.01). The carbon and nitrogen isotope ratios of populations did not differ significantly between season (repeated-measures ANOVA; season, δ^{13}C: F_1 = 0.03; n = 96, P = 0.87; δ^{15}N: F_1 = 1.49, n = 96, P = 0.23). The interaction between season and population was not statistically significant for carbon (repeated-measures ANOVA; season*population, δ^{13}C: F_3 = 0.21; n = 96, P = 0.89), however, it was significant for nitrogen (repeated-measures ANOVA; δ^{15}N: F_3 = 3.0, n = 96, P = 0.04) (Table 3.1). KDS and RBK populations of *M. cuneirostris* occupied niches with higher nitrogen in spring (one-way ANOVA; KDS season, δ^{15}N: F_1 = 5.16, n = 22, P = 0.04; RBK season, δ^{15}N: F_1 = 4.24, n = 22, P = 0.05). *Meroles cuneirostris* populations of NGS and FGS occupied niches with similar nitrogen in both seasons (one-way ANOVA; NGS season δ^{15}N: F_1 = 3.30, n = 22, P = 0.08; FGS season, δ^{15}N: F_1 = 0.00, n = 21, P = 0.96).

Table 3. 1: Mean (± 1 SD) δ^{15}N and δ^{13}C ratios of lipid-extracted tail tissue samples of populations of *Meroles anchietae* (FGS, NGS and RBK) and *M. cuneirostris* (FGS, NGS, RBK, KDS and ORM) from the Namib Desert, Namibia sampled between September (spring-2016), and March-April (autumn-2017). *n* = sample size. *n* = sample size.

Population isotopic ratios	*M. anchietae*		
	FGS (*n* = 22)	NGS (*n* = 17)	RBK (*n* = 20)
Mean δ^{13}C (‰)	-11.88 ± 0.51	-12.87 ± 0.45	-12.53 ± 0.96
Mean δ^{15}N (‰)	7.75 ± 0.79	5.52 ± 0.70	10.91 ± 0.87

Population isotopic ratios	*M. cuneirostris*				
	Clade A				Clade B
	FGS (*n* = 21)	NGS (*n* = 22)	RBK (*n* = 22)	KDS (*n* = 22)	ORM (*n* = 9)
Mean δ^{13}C (‰)	-12.36 ± 0.83	-12.47 ± 0.48	-14.57 ± 2.43	-14.66 ± 2.52	-13.86 ± 0.44
Mean δ^{15}N (‰)	8.76 ± 1.04	6.70 ± 0.81	14.03 ± 0.88	15.78 ± 0.85	10.80 ± 0.89

To investigate dietary partitioning between sympatric species using stable isotope analysis, the present study compares the differences in the food niche dimensions for Clade A of *M. cuneirostris* populations that occur sympatrically with *M. anchietae* populations and those that did not occur in sympatry. In areas where the two species occur sympatrically, on average, populations of *M. cuneirostris* occupied niches of significantly greater prey diversity (species richness) than those of corresponding populations of *M. anchietae* and similarly supported by larger SEA_c and TA dietary niches (Table 3.2; Figure 3.1). In areas where *M. cuneirostris* does not occur sympatrically with *M. anchietae*, the species occupied niches of significantly larger prey diversity for KDS population and niches of lesser prey diversity for ORM population. In addition, populations of *M. cuneirostris* expressed significantly greater CD than that of corresponding populations of *M. anchietae*. Both MNND and SDNND were similar for the three taxa (Table 3.2).

Table 3. 2: Trophic niche metrics based on the $\delta^{13}C$ and $\delta^{15}N$ ratios as estimated from lipid-extracted tail tissue samples of populations of *Meroles anchietae* (FGS, NGS and RBK) and *M. cuneirostris* (FGS, NGS, RBK, KDS and ORM) from the Namib Desert, Namibia sampled between September (spring-2016) and March-April (autumn-2017). The metrics; SEA_c, TA, CD, MNND and SDNND. *n* = sample size.

Niche metric	*M. anchietae*		
	FGS (*n* = 22)	NGS (*n* = 17)	RBK (*n* = 20)
Standard ellipse area			
SEAc	1.07	1.11	2.83
Layman niche metrics			
TA	3.33	3.63	6.04
CD	0.75	0.60	1.16
MNND	0.31	0.35	0.37
SDNND	0.46	0.41	0.27

Niche metric	*M. cuneirostris*				
	Clade A				Clade B
	FGS (*n* = 21)	NGS (*n* = 22)	RBK (*n* = 22)	KDS (*n* = 22)	ORM (*n* = 9)
Standard ellipse area					
SEAc	2.89	1.21	6.28	7.30	1.48
Layman niche metrics					
TA	9.02	4.36	14.25	18.13	1.98
CD	1.15	0.82	2.28	2.37	0.95
MNND	0.44	0.29	0.45	0.60	0.44
SDNND	0.43	0.26	0.36	0.49	0.19

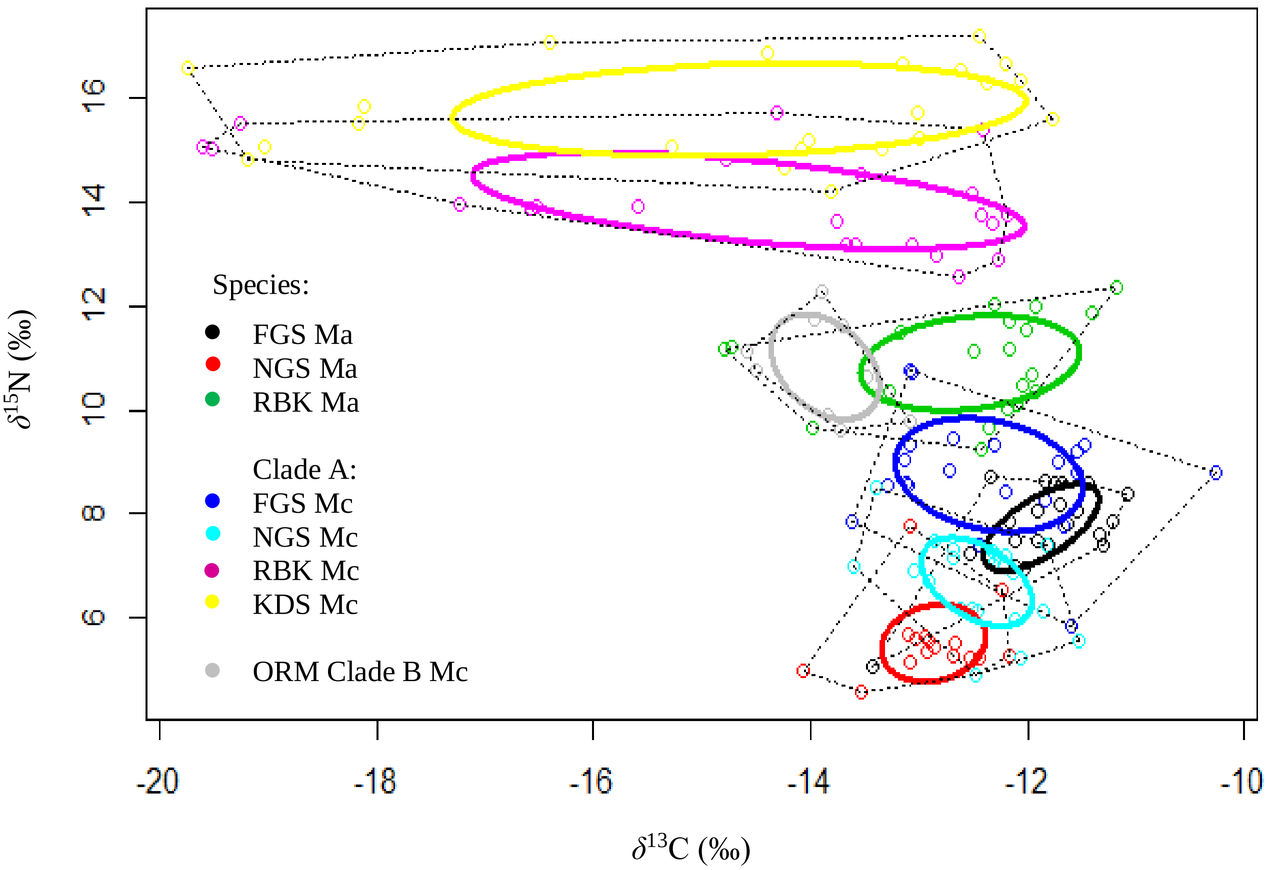


Figure 3. 1: Mean (± 1 SD) distribution of δ^{15}N and δ^{13}C ratios illustrating the standard ellipse areas (SEA_c) corrected for small sample sizes of populations of *Meroles anchietae* (black, red and green) and Clades A (dark and light blue, purple and yellow) and B (gray) of *M. cuneirostris* lipid-extracted tail tissue sampled between September (spring-2016) and March-April (autumn-2017) in the Namib Desert, Namibia.

Four plant species of both C_3 and C_4/CAM growing on site were analysed for isotopes and the results indicate non-overlapping carbon isotope ratios between the two groups. This observation allows the tracing of nutrient sources back to the plant functional groups. The mean carbon isotope ratios for the plant tissues were -13.59‰ ± 0.59‰ with a range of between -25.86‰ and -21.16‰ in C_3 and -21.49‰ ± 3.49‰ with a range of between -20.54‰ and -12.5‰ in C_4/CAM. The plant tissue mean nitrogen isotope ratios were 8.96‰ ± 1.89‰ with a range of between 8.02‰ and 14.36‰ in C_3 and 8.89‰ ± 3.53‰ with range of between 2.66‰ and 16.41‰ in C_4/CAM.

The arthropods available as potential prey for populations of *M. anchietae* and *M. cuneirostris* showed a statistically significant non-overlap in the carbon and nitrogen isotope niche (Table 3.3). The non-overlapping niche is evident by the significant difference in mean δ^{13}C ranging from -20.2‰ in *Stips* beetle of the family Tenebrionoidae to -12.1‰ in *Calognothus* beetle (Table 3.3). The arthropod prey categories occupied diverse trophic niche levels as confirmed by the statistically significant difference in the mean δ^{15}N with a range of 19.2‰ in wasps (from an unidentified family) to 2.64‰ in a cricket from the family Tettigoniidae. In addition, arthropods within the same order and family also showed a statistically significant difference in the tissue carbon and nitrogen isotope ratios, evident for the non-overlapping carbon and nitrogen ratios of beetles of the families Belidae and Meloidae beetle within the order Coleoptera) and beetles of the genera *Cauricura* and *Stips* (δ^{13}C)/ and the genera *Cauricura* and *Physadesmia* (δ^{15}N) within the Family Tenebrionoidae (Table 3.3).

Table 3. 3: Mean (± 1 SD) δ15N and δ13C ratios for arthropod as potential prey for populations of *Meroles anchietae* and *M. cuneirostris* from the Namib Desert, Namibia sampled between September (spring-2016) and March-April (autumn-2017). *n* = sample size.

Prey category	*n*	Mean δ^{13}C (‰)	Mean δ^{15}N (‰)
Araneae			
Spider	2	-13.4	13.2
Coleoptera			
Belidae	1	-14.3	7.1
Buprestidae	3	-17.3 ± 2.6	9.9 ± 4.9
Meloidae	2	-18.0	11.0
Scarabaeidae	3	-15.4 ± 1.1	9.7 ± 0.9
Tenebrionoidae			
Calognothus	2	-12.1	9.8
Cauricura	1	-12.8	8.3
Epiphysa	1	-17.5	16.8
Onymacris	8	-16.3 ± 2.3	13.1 ± 4.1
Physadesmia	2	-19.5	17.7
Stenocara	3	-20.0 ± 1.4	15.3 ± 1.6
Stips	2	-20.2	14.9
Zophosis	7	-14.9 ± 2.6	11.1 ± 2.3
unidentified beetle	2	-18.8	12.6
unidentified weevil	5	-14.9 ± 2.1	9.5 ± 3.2
Diptera			
unidentified fly	30	-16.6 ± 3.0	12.7 ± 3.6
Hemiptera			
unidentified true bug	3	-12.5 ± 0.6	11.2 ± 0.9
Hymenoptera			

Ants			
Formicidae	6	-16.3 ± 3.7	14.0 ± 3.7
Bee	3	-14.1 ± 0.1	10.1 ± 2.9
Wasp			
Unidentified wasp	2	-12.6	19.2
Mutillidae	7	-14.9 ± 1.1	18.8 ± 4.0
Blattodea			
Hodotermitidae	1	-13.4	4.8
Lepidoptera			
Butterfly	1	-13.6	18.1
Caterpillar	3	-17.4 ± 3.7	11.9 ± 2.3
Heterocera	3	-18.9 ± 5.7	13.6 ± 4.4
Mantodae			
Praying mantis	2	-12.4	10.5
Megadrilacea			
Earthworm	2	-13.0	10.9
Orthoptera			
Acrididae	1	-18.5	11.0
Pamphagidae	1	-14.2	3.8
Tettigoniidae	1	-13.9	2.6
Zygentoma			
Lepismatidae	1	-12.7	14.3

3.3.2 Faecal pellet assessment

Because no faecal pellets were collected from lizard samples of the southern Namib Desert (Clade B of *M. cuneirostris*), results on faecal pellet analyses were only compared between populations of *M. anchietae* and Clade A of *M. cuneirostris*. Among the 98 faecal pellets examined for diet composition of *M. anchietae* and Clade A of *M. cuneirostris,* two pellets were void of prey items and rather highly concentrated with dune sand particles. Eight hundred and fifty six prey items were identified from eight arthropods and one plant order. From 51 faecal pellets collected for *M. anchietae*, 13 were from females, 25 males, and 13 samples of unknown sex. Each *M. anchietae* pellet contained an average of 19.82 ± 17.57 individual prey items (Range = 1– 1). For *M. anchietae*, the number of prey items consumed did not differ between males (median = 15) and females (median = 9) (Mann-Whitney *U*-test: *U* = 128; d.f. = 1; *n* = 38; *P* = 0.30). For Clade A of *M. cuneirostris*, 482 individual prey items were identified from nine arthropods, one annelid and one plant order (Poales). From the 47 faecal pellets collected, 17 were from females, 20 males, and 10 samples of unknown sex. An average of 10.96 ± 14.83 individual prey items were contained per pellet of Clade A of *M. cuneirostris* that accounts for fewer individual prey items than that of *M. anchietae*. The range (1–51) of prey items per pellet for Clade A of *M. cuneirostris* was similar to those of *M. anchietae*. Similarly, the number of prey items consumed did not differ between males (median = 5.5) and females (median = 3) of Clade A of *M. cuneirostris* (Mann-Whitney *U*-test: $U = 145$; d.f. = 1; $n = 37$; $P = 0.46$). The number of arthropod prey items consumed did not differ significantly between seasons (two-sample *t*-test; season: $t_{71} = 1.59$; $n = 75$; $P = 0.12$). In addition, the number of plant matter prey items consumed differed significantly between seasons (two-sample *t*-test; season: $t_{48} = 3.09$; $n = 75$; $P < 0.01$), with more plant matter consumed during autumn than spring. The prey categories were divided into 11 groups (Table 3.4) for niche breadth and overlap estimations.

Table 3. 4: A comparison of prey consumption of *Meroles anchietae* ($n = 51$) and Clade A of *M. cuneirostris* ($n = 47$) faecal pellets from the Namib Desert, Namibia sampled between September (spring-2016) and March-April (autumn-2017). T = total number of individual prey items per prey type; %N = prey abundance (contribution of each prey type on the diet of *M. anchietae* and *M. cuneirostris* expressed as the percentage of total number of prey items of all prey types); and %F = frequency of occurrence of each prey type (number of individual lizards that have consumed a prey type, expressed as percentage of total number of pellets per species).

Prey item	*M. anchietae*			Clade A of *M. cuneirostris*		
	T	%N	%F	T	%N	%F
Coleoptera	15	13.72	1.75	47	44.68	9.8
Curculionoidae	-	-	-	3	6.38	0.62
Scarabaeidae	6	3.92	0.70	2	4.26	0.41
Tenebrionidae	9	9.80	1.05	42	34.04	8.71
Diptera	1	1.96	0.12	8	6.38	1.66
unidentified	1	1.96	0.12	8	6.38	1.66
Hemiptera	5	5.88	0.58	10	12.77	2.08
Belastomatidae	5	5.88	0.58	9	10.64	1.87
unidentified	-	-	-	1	2.13	0.21
Hymenoptera	102	54.89	11.92	242	70.22	50.21
Formicidae	92	43.13	10.75	209	51.07	43.36
adult	85	35.29	9.93	189	46.81	39.21
larvae	7	7.84	0.82	20	4.26	4.15
unidentified	9	9.80	1.05	33	19.15	6.85
Bee	1	1.96	0.12	-	-	-
Blattodea	25	11.76	2.92	62	36.17	12.86
Hodotermitidae	25	11.76	2.92	62	36.17	12.86
adult	2	3.92	0.23	12	19.15	2.49
larvae	23	7.84	2.69	50	17.02	10.37
Lepidoptera	4	7.84	0.47	2	4.26	0.41
Moth	3	5.88	0.35	2	4.26	0.41

Butterfly larvae	1	1.96	0.12	-	-	-
Mantodae	3	1.96	0.35	1	2.13	0.21
Praying mantis	3	1.96	0.35	1	2.13	0.21
Megadrilacea	-	-	-	3	2.13	0.62
Earthworm	-	-	-	3	2.13	0.62
Orthoptera	-	-	-	2	2.13	0.41
Grasshopper	-	-	-	2	2.13	0.41
Unidentified	14	9.8	1.63	2	4.26	0.41
unidentified arthropods	5	7.84	0.58	2	4.26	0.41
unidentified larvae	9	1.96	1.05	-	-	-
Plant matter	687	58.82	80.26	103	12.77	21.37
Leaves	542	56.86	63.32	100	12.77	20.75
Seeds	145	11.77	16.94	3	2.13	0.62
Total	856		100	482		100
Dietary niche breadth			**2.27**			**4.52**
Trophic niche evenness			**0.13**			**0.25**
Dietary niche overlap	**0.56**					

The diet of *M. anchietae* was primarily made up of plant matter that made up 80% of all individual prey items consumed and 59% of all faecal pellets composed of plant matter (Table 3.4). About 11% of the diet of *M. anchietae* was made up of ants, and composed 43% of all pellets (Table 3.4). *Meroles anchietae* also preyed on beetles (2% of the diet and 14% of faecal pellets) and termites (3% of the diet and 12% of faecal pellets). Dietary niche breadth (B) for *M. anchietae* was 2.27 (range of 1 to 11) with trophic niche evenness of 0.13. In contrast, Clade A of *M. cuneirostris* primarily preyed on ants that made up 50% of the diet with 70% of pellets containing ants (Table 3.4). Clade A of *M. cuneirostris* also preyed on termites (13% of the diet and 36% of faecal pellets) and beetles (10% of the diet and 45% of faecal pellets). Clade A of *M. cuneirostris* preyed on plant matter that made up 21% of their diet with only 13% of faecal pellets comprising plants (Table 3.4). The dietary niche breadth for Clade A of *M. cuneirostris* was 4.52 (range of 1 to 11) and trophic niche evenness was 0.25. The dietary niche overlap (O_{jk}) between *M. anchietae* and Clade A of *M. cuneirostris* was 0.56.

3.4 Discussion

The present study is the first to provide information on dietary variation between corresponding populations of *M anchietae* and *M. cuneirostris* using stable isotopes of carbon (δ^{13}C) and nitrogen (δ^{15}N) and through faecal pellet analyses. Analysing the structure of food webs and how species connect within a community is inadequate without considering differences in species interactions as an important component in determining how communities respond to major environmental changes (Goodyear & Pianka 2011). Among several factors, changes in the structure, growth and diversity of vegetation because of wildfires (Fyfe 1980; Braithwaite 1987; Masters 1996) and intense grazing may reduce the diversity and abundance of arthropod species (Gibson *et al.* 1992; McFerran *et al.* 1994; Kruess & Tscharnke 2002) as potential prey resources for lizards. Reduced arthropod diversity and abundance would mean less potential prey items to feed on.

Additionally, interspecific competition influences the trophic niche breadth of sympatric species (May & MacArthur 1972; Comas *et al.* 2014). That is, the trophic niche breadth decreases with an increase in competition for food (Gomez-Mestre & Tejedo 2002; Benard & Maher 2011; Comas *et al.* 2014). This is because the niche space of any given species may be limited by competition with a fellow sympatric species, thus these species may be forced to occupy smaller niches (Pianka 1974). Increased food competition may also contribute to decreased growth rate and body conditions (Jones & Barmuta 1998; Gomez-Mestre & Tejedo 2002; Benard & Maher 2011).

3.4.1 Stable isotopes

Several studies have documented the use of stable isotope to quantify dietary variation of organisms in the wild (McKechnie 2004; Fisk *et al.* 2009; Wilson *et al*. 2010; Varela *et al*. 2011; Lattanzio & Miles 2016; Murray *et al*. 2016b), with a few studies focusing on dietary variation of sympatric lizard species in the Namib Desert in Namibia (Murray *et al*. 2016b). The isotopic niche occupancy defines the resources used in that particular niche (Bearhop *et al.* 2004). The factors affecting the isotopic niche respond rapidly to changes in intra- and inter-specific competition and in prey abundance (Bearhop *et al.* 2004). These factors include the diversity of prey species consumed, the evenness of prey items in the diet, the range of trophic levels from which the prey consumed is drawn, the foraging location, variation in physiology of individuals, and the variation in the diet-tissue fractionation (Bearhop *et al.* 2004).

Generally, both the δ^{13}C and δ^{15}N ratios for lizard tail tissues were significantly similar between populations of *M. cuneirostris* suggesting that the populations are feeding at similar trophic levels that were different from those of *M. anchietae*. Species that consume a wide range of prey species exhibit a wider variation in their tissues isotopic signatures than those that consume a narrow range of prey species (Bearhop *et al.* 2004). A larger TA therefore indicates the ability of populations of *M. cuneirostris* to occupy more niche space (Layman *et al.* 2007) than populations of *M. anchietae*. This finding confirms the studies by Pianka (1986) and Vitt *et al*. (2003) who reported that lizard species that are active foragers are likely to have territories larger than specialist species and move greater distances through diverse habitats. *Meroles cuneirostris* employs both active and ambush foraging tactics (Murray & Schramm 1987; Childers & Eifler 2015) however, *M. cuneirostris* is more active compared to ambushing (*pers. obs.*), thus occupies more niche space. On the other hand, *M. anchietae* is more of a sit-and-wait predator with less active foraging patterns (*pers. obs.*), thus occupying smaller niche space compared to *M. cuneirostris*.

Species that consume a wide variable proportion of each of their prey items shows less variation in tissue stable isotope ratios compared to those consuming a constant proportion of each prey type (Bearhop *et al.* 2004). Hence, the greater the TA, the larger the prey diversity (species richness) (Layman *et al.* 2007). Populations of *M. cuneirostris* expressed diets of greater prey diversity and evenness compared to those of *M. anchietae*. Therefore, lizards employing active foraging mode spend more hours active as they move across large distances (Anderson & Karasov 1981; Huey & Pianka 1981; Murray *et al*. 2016b). The home range sizes of active foragers tend to be four times larger than that of sit-and-wait foragers (Anderson & Karasov 1981; Murray *et al*. 2016b). Habitat heterogeneity is positively related to foraging distances, the greater the heterogeneity the larger the foraging distance (Murray *et al*. 2016b). Thus, arthropod diversity is positively related to habitat heterogeneity (Liu *et al.* 2013). Active foragers are likely to encounter greater prey diversity and thus expressing larger trophic niches. Similarly, the SEA_c (as a metric for characterizing niches more robustly given a small sample size; Murray *et al*. 2016b) of populations of *M. cuneirostris* was significantly larger than that of populations of *M. anchietae* supporting the results from the TA. In addition, populations of *M. cuneirostris* had a CD greater than that of populations of *M. anchietae* suggesting a greater trophic diversity within the food web (Layman *et al.* 2007). The MNND and SDNND were similar for both populations of *M. anchietae* and *M. cuneirostris*, resulting in similar trophic redundancy and evenly distributed trophic niche (Layman *et al.* 2007).

In the present study, populations of *M. cuneirostris* occupied similar isotopic niches of C_3 and C_4/CAM plants and arthropods, however, their niches were different from those of populations of *M. anchietae*. Although populations of *M. anchietae* and *M. cuneirostris* use of plant and arthropod resources overlapped to some degree, there was a significant difference within the major prey elements. The use of plant and arthropod resources by populations of *M. cuneirostris* overlapped entirely. Populations of *M. anchietae* preyed predominantly on plant matter, whereas populations of *M. cuneirostris* preyed predominantly on arthropods. Both populations of *M. anchietae* and *M. cuneirostris* largely preyed on arthropods that fed to a lesser extent on C_3 plants.

The present study also found that populations of *M. anchietae* and *M. cuneirostris* acquired nutrients from C_4/CAM feeding arthropods, such that all species indicate considerably more isotopic signatures relative to C_4/CAM plants than C_3 plants. This finding may be related to the C_4 plants that are known to represent the most important sources of nutrients to food webs in arid ecosystems (Ehleringer *et al*. 1997; Still *et al*. 2003). With little differentiation between C_4 and CAM plants in the current study, CAM plants were minor components of the preferred habitats, whereas the C_4 grasses and shrubs constitute the majority of plant species as food web components in the diet of populations of *M. anchietae* and *M. cuneirostris*.

3.4.2 Faecal pellets

The present study found both *M. anchietae* and Clade A of *M. cuneirostris* to be omnivorous, feeding on plant matter and arthropods. The omnivorous diet of *M. anchietae* and Clade A of *M. cuneirostris* is similar to the findings of Robinson & Cunningham (1978), Murray & Schramm (1987) and Robinson (1987). *Meroles anchietae* fed on grass seeds, the dune succulent (*Trianthema hereroensis*), Hemiptera bugs, and thysanurans as the dominant prey consumed (Robinson & Cunningham 1978). The study by Robinson & Cunningham (1978) however, indicated the diet of *M. cuneirostris* to be strictly insectivorous and encountered little plant material during stomach content analysis, which was perhaps consumed unintentionally during capturing of arthropods as prey.

Although there is a significant overlap between *M. anchietae* and Clade A of *M. cuneirostris* in the prey items consumed, *M. anchietae* preyed more on plant matter compared to

Clade A of *M. cuneirostris* that preyed more on arthropods. This is similar to the findings of Murray & Schramm (1987) who reported that monocotyledonous seeds contributed the largest proportion to the diet of *M. anchietae*. Studies by Robinson & Cunningham (1978) and Murray & Schramm (1987) also found that ants (Formicidae), lepidopteron and tenebrionid larvae, hymenopterans, weevils (Curculionoidae) and termites contributed substantially to the diet of *M. cuneirostris*. Due to resource scarcity associated with desert ecosystems, *M. anchietae* also employs an opportunistic foraging tactic when abundance of insects is low with seeds still representing the major component of their diet, yet indiscriminately preying on arthropods when highly available (Robinson 1987). Fitzpatrick (2017) also observed *M. anchietae* feeding on termite alates.

In lacertid lizards, the consumption of plant matter differs between seasons (Cooper & Vitt 2002; Perera *et al.* 2006). In the present study, populations of *M. anchietae* fed on significantly more plant matter during autumn compared to spring. This finding may be related to seasonal processes associated with plant reproductive cycles. During dry periods, fresh fruits supply important amounts of water to the diet of lizards (Perez-Mellado *et al.* 1999). With reptiles, playing important roles as seed dispersers in ecosystems (Paine 1980), the seasonal variation in the number of seeds consumed suggests variation in the importance of lizards as seed dispersers (Rodriquez *et al.* 2008).

The present study is also the first to provide information on dietary niche breadth and diet evenness of *M. anchietae* and Clade A of *M. cuneirostris*. This study showed that the dietary niche breadth for *M. anchietae* (2.27) was narrower than that of Clade A of *M. cuneirostris* (4.52) suggesting that Clade A of *M. cuneirostris* had a greater diversity of prey types consumed than *M. anchietae*. A narrow niche breadth in *M. anchietae* may be related to the species being a specialised feeder (feeding significantly on one type of prey; plant matter), because the species may have specific behavioural and phenotypic characteristics that allows for the capture of a particular prey (Edwards *et al.* 2013). Whereas, generalized feeding species such as *M. cuneirostris* preys on a large range of food items, meaning it has a versatile morphology, allowing the processing of a large range of prey types (Edwards *et al.* 2013). Clade A of *M. cuneirostris* (0.25) also showed a greater diet evenness (greater abundance) of each prey type than that of *M. anchietae* (0.13). The greater diet evenness of Clade A of *M. cuneirostris* suggests a uniform distribution of prey items for each prey type compared to the diet of *M. anchietae*. The dietary niche overlap between *M. anchietae* and Clade A of *M. cuneirostris* was 0.56, suggesting that the resource utilization (diet) of *M. anchietae* and Clade A of *M. cuneirostris* is 56% similar. The microhabitats of the two species do not overlap significantly (Murray & Schramm 1987); however, the two species have been shown to prey on the same prey type.

Wind-blown decomposed plant matter and animals form part of the major source of food for *M. anchietae* as a slipface community species (Robinson & Barrows 2013). Seely (1978) also reported that the inter-dune grasslands produces biomass (approximately 10-20 kg per hectare) and the winds blow this material into the dunes. A complimentary study by Robinson & Seely (1980) reported that at Gobabeb, decomposed matter differs seasonally with more volume during late spring (November) to early autumn (March), with approximately 20%-48% coverage on the slipface, and thus corresponding with periods of high fog amounts and when many slipface species breed (Robinson & Barrows 2013). The present study found that there is considerable difference for plant matter preyed on seasonally. *Meroles anchietae* consumed significantly more plant matter during autumn (March – April 2017) than spring (September 2016). During autumn is when the plants shed and lose their leaves, thus plenty of plant matter is blown in and around the dunes to form part of food sources for the dune species.

In lizards, there is a negative relationship between body size and niche breadth (Costa *et al.* 2008).This relationship however, was attributed to the total frequency distribution of body size in lizards and little information is available on the direct link between lizard morphology and dietary niche breadth, and the associated variation in performance (Edwards *et al.* 2013). In the lizard genus *Nucras*, when diet was compared with morphology and performance, dietary niche breadth and the proportion of prey consumed was correlated with the shape of the cranium, although not when phylogeny was accounted for, suggesting that cranial shape is constrained by evolutionary history (Edwards *et al.* 2013). Consequently, further studies incorporating data on prey size and functional properties are required to better understand the evolution of body proportions in relation to diet in the Namib Desert lizards.

3.5 Conclusion

Trophic niche determines the diversity of species and allows similar species with different diets to co-exist within their niches (Simberloff & Dayan 1991; Murray *et al*. 2016b). Certainly, the present study found that there are variations in the diet diversity between *M. anchietae* and *M. cuneirostris* (and its associated clades). Stable isotope results indicated that Clades A and B of *M. cuneirostris* occupied similar dietary niches, suggesting that the two are feeding at a similar trophic level. *Meroles anchietae* however, showed distinctive isotopic niches and feed at different trophic levels from that of *M. cuneirostris* (and its associated clades). Faecal pellet results indicated that Clade A of *M. cuneirostris* occupied a larger niche space, had a greater prey diversity, and a greater evenness of prey distribution within its diet than *M. anchietae*. In addition, Clade A of *M. cuneirostris* fed on significantly more arthropods than *M. anchietae* that fed mainly on plant matter however; both monophyletic groups indicated an omnivorous diet.

The omnivorous diet of *M. anchietae* and Clade A of *M. cuneirostris* is confirmed by the 56% dietary overlap between the two monophyletic groups suggesting a possible availability of similar prey items within their different microhabitats. Thus, the present study accepts the null hypothesis stating that there is similarity in diet between populations of *M. anchietae* and *M. cuneirostris* (and its associated clades). These data may be useful in understanding partitioning of the trophic niche of sympatric species because of changing environments. The findings of this study are of conservation concern since the overlap in the diet of *M. anchietae* and Clade A of *M. cuneirostris* by more than 50% suggests a possibility of resource competition that may eventually contribute to the survival of a dominant taxon at the expense of the less dominant taxon.

Chapter 4

The influence of fog on the morphology and thermal biology of sympatric lacertid lizards, *Meroles anchietae* and *M. cuneirostris* (and its associated clade) from the Namib Desert, Namibia

Abstract

Fog is a major source of moisture in the Namib Desert, Namibia, and climate change may influence its availability. This study investigated the influence of fog density in this hyper arid environment on the morphology and thermal biology of sympatric lacertid lizards, the shovel-snouted lizard (*Meroles anchietae*) and the wedge-snouted lizard (*M. cuneirostris*). Molecular analysis in a parallel study found that *M. cuneirostris* has two clades (designated Clades A and B), and pending a detailed study to establish the systematic and taxonomic status of *M. cuneirostris*, the present study assessed the seasonal (autumn and spring) influence of fog density on the morphology and thermal biology of Clade A of *M. cuneirostris* and *M. anchietae*. Due to low lizard activity during winter sampling was not conducted, while sampling in summer was not possible due to logistical constraints. Clade B of *M. cuneirostris* was not considered due to the lack of fog data from the sampled area. Comparisons of morphology and thermal biology were made with reference to distance from the coast that included sampling sites located 9 km, 15 km, 60 km and 63 km. The results indicate that the coastal site received twice the amount of fog and number of fog events (days) compared to the inland site. Inland *M. anchietae* had longer body lengths than coastal *M. anchietae*, but this did not differ between coastal and inland Clade A individuals. Body mass did not differ between both coastal and inland *M. anchietae* and Clade A individuals. Body temperature did not differ between coastal and inland *M. anchietae*. Inland Clade A individuals showed higher body temperatures than coastal populations. Inland *M. anchietae* were active for longer periods daily than coastal *M. anchietae*. These results indicate that the density of fog in the Namib Desert affects coastal and inland *M. anchietae* and Clade A individuals differently, suggesting the need to investigate how climate change may influence the thermal behaviour and morphology of lizards in the Namib Desert.

Keywords: *Meroles*, lacertid lizards, fog, morphology, thermal biology, climate change, coastal/inland Namib Desert, Namibia

4.1 Introduction

Many recent studies have highlighted that the response of biodiversity to climate change is of great concern, because climate could potentially affect ecosystem structure and function, population dynamics, species abundance and distribution, and individual fitness (Parmesan *et al.* 2000, Dillon *et al.* 2010; Pereira *et al.* 2010; Beaumont *et al.* 2011; McMahon *et al.* 2011; Palmer & Di Falco 2012). Climate change predictions are important to scientists and decision-makers as it allows insights into how biodiversity responds to climate change, and these predictions contribute to the development of strategies to reduce the potential impacts (Pereira *et al.* 2010; Parmesan *et al.* 2011; Bellard *et al.* 2012). Even with limited evidence on extinction caused by climate change, it may be an extreme threat to biodiversity in future (Leadley *et al.* 2010). Species are known to respond to challenges caused by climate change by shifting their climatic niches in: 1) space (i.e., geographic range, shifting to different microhabitats; Parmesan 2006; Visser 2008); 2) time (i.e., phenology, shifting daily and seasonal activities such as change in reproductive life cycle events; Root *et al.* 2003; Parmesan 2006; Charmantier *et al.* 2008); and 3) organismal (i.e., physiology, by adapting to new climatic conditions rather than tracking their preferred optimal conditions; Johansen & Jones 2011; Bellard *et al*. 2012).

Despite change in geographic ranges and community composition as an effect of temperature, little is known about the direct effects temperature has on biological processes (MacDonald & Sertorio 1990; Wyman 1991; Peters & Lovejoy 1992; Kareiva *et al.* 1993; Root & Schneider 1993). In some reptile and amphibian species, unlike other vertebrates, sex determination depends on temperature, and they may provide an ideal model to test impacts of global temperature change on biological processes (Janzen & Paukstis 1991; Mrosovsky & Pieau 1991; Eggert 2004). The sex ratio of such temperature-dependent offspring may be affected by as little as a 1° C shift in incubation temperature (Paukstis & Janzen 1990). If change in climate has an impact on the behaviour and reproduction of reptiles, they may be at high risk of extinction because of unbalanced ratio of males and females (Fisher 1958; Paukstis & Janzen 1990; Conover & Van Voorhees 1990; Conover *et al.* 1992; Janzen 1994).

Recent studies have provided evidence of drastic increases in near-surface annual average temperatures in Africa over the past decades (Boko *et al*. 2007; Niang *et al*. 2014; Engelbrecht *et* *al*. 2015). Consequently, the Benguela Current responsible for most of the weather patterns and production of fog along the coastal west of the Namib Desert in Namibia is also experiencing increases in temperature (Belkin 2009; Haensler *et al.* 2011a, b). Based on climate predictions (Boko *et al*. 2007; Niang *et al*. 2014; Engelbrecht *et al*. 2015), increases in temperature of the Benguela Current may result in less fog production (Belkin 2009; Haensler *et al.* 2011a, b), and a decrease in the number of fog days (fog events) per year (Haensler *et al.* 2011a). In central Namib Desert, fog precipitation has been monitored in order to gain insights into the relationship between atmospheric moisture and desert organisms (Henschel & Seely 2008). Fog precipitation is a concern for desert life if its production continues to be variable and unreliable because of changing climate (Seely *et al*. 2016).

In 2014, the Namib Desert research-based institution, Gobabeb Research and Training Centre (23°33′S, 15°02′E), located in the central Namib Desert, Namib-Naukluft Park, began a sophisticated technological project called FogNet (Fog Network) aimed at assessing the influence of changing climate on the predicted decreasing fog in the Namib Desert coast due to the warming Benguela Current. The project provides comparative data for fog parameters recorded between 1960 and 1990 (Seely *et al*. 2016). The FogNet project is funded within the Southern African Science Service Centre for Climate Change and Adaptive Land Management (SASSCAL) weather network (Seely *et al*. 2016). SASSCAL is a joint program for Namibia, Botswana, Zambia, Angola, South Africa and Germany in order to gain insights into the impacts and challenges that climate change has on the fauna and flora in these countries and is sponsored by the German Federal Ministry of Education and Research (Seely *et al*. 2016).

Despite water scarcity as a challenge, deserts are home to many species of animals, and studies on desert species have shown their ability to survive and reproduce due to behavioural, physiological and morphological adaptations (Herrmann & Branch 2013; Murray *et al*. 2015). Nagy (2004) reported that there are concerns on how desert animals maintain their water balance and keep up with their body hydration levels given such scarcity of water, and further elaborates that desert animals have adapted to conserving water better by decreasing their output or obtaining more water each day by increasing their water input. Several studies on water economy have addressed water scarcity concerns by evaluating the water budget (i.e., water input *versus* output) of animals with constant body masses living freely in the wild by measuring rates of water flux (in ml/day) using water that is enriched with traceable isotopes. (Nagy 1983, 2004; Cooper & Robinson 1990; Nagy *et al*. 1991, 1993; Tielman & Williams 2000; Murray *et al*. 2014).

Based on molecular analysis in a parallel study (Chapter 2), it was found that *M. cuneirostris* has two clades (designated Clades A and B from the central and southern Namib Desert, respectively). Pending a detailed study to establish the systematic and taxonomic status of *M. cuneirostris*, the present study therefore, investigates whether there is seasonal (autumn and spring) variation in morphology and thermal preferences between the coastal and inland populations of the shovel-snouted lizard (*Meroles anchietae*) and the wedge-snouted lizard (*M. cuneirostris* - Clade A, hereinafter referred to as Clade A; see Chapter 2). Sampling in winter was not conducted because of low lizard activity, while sampling in summer was not possible due to logistical constraints. Clade B of *M. cuneirostris* was not considered due to the lack of fog data from the sampled area.

According to water budget measurements, *M. anchietae* yielded a water economy index (WEI) of 0.15 ml H_2O kJ^{-1}, and this species does not require extra drinking water from the surface apart from the water it obtains from the food it consumes (Cooper & Robinson 1990). Murray (unpublished) described *M. cuneirostris* as a drinking carnivore that requires additional drinking water from the surface with a WEI of 0.54 ml H_2O kJ^{-1}. These species obtain their water by either directly drinking from wet surfaces or indirectly by feeding on prey that used fog water in their diets. Many reptile species have adapted to drinking rainwater that has collected on their bodies, and this water acquisition method may likely be important for desert species (Repp & Scheutt 2008; Glaudas 2009). A few reptile species in the Namib Desert such as *M. anchietae* have shown a direct relationship with fog moisture by drinking fog droplets on vegetation (Louw 1972). Similarly, the side-winding adder (*Bitis perengueyi*) has been observed drinking fog droplets that have condensed on its body (Louw 1972; Robinson & Hughes 1978), while the horned adder (*B. caudalis)* drinks condensed fog water from its body (Murray & Irish 2015).

With the scarcity of water (Nagy 2004), further reduction in fog production within the Namib Desert may contribute to stressful events that may change the feeding ecology, physiological and behavioural adaptations of species (MacArthur 1972; Hoffman & Parsons 1997; Parmesan 2006). The present study therefore, hypothesized seasonal differences in the morphology and thermal biology between populations of *M. anchietae* and Clade A, driven by variation in fog density across the two sites (coastal and inland) in the central Namib Desert. This hypothesis is tested by comparing the seasonal variation in morphology and thermal biology between the populations in relation to fog density in order to gain insights into the influence of fog on the thermal behaviour and morphology of these species.

4.2 Materials and Methods

4.2.1 Fog precipitation

FogNet consists of nine fog stations namely Coastal Met (CM), Kleinberg (KB), Sophies Hoogte (SH), Marble Koppie (MK), Garnet Koppie (GK), Vogelfederberg (VF), Station 8 (S8), Aussinanis (AU), and Gobabeb Met (GBB_Met) (yellow pins; Figure 4.1), with five positioned in an east-west direction and four positioned in a north-south direction. A Juvik fog gauge, 40.6 cm long with a cylindrical fog capture area of 500 cm² (Mcknight & Juvik, 1975; Juvik & Ekern, 1978; Frumau *et al.* 2006; Holwerda *et al.* 2011) was used as an instrument to capture fog produced (mm) at an hourly interval. The Juvik was positioned 1.5 m above ground and contained a Juvik cylindrical gauge fitted onto a Young tipping gauge (Y52203, Young Company, Michigan, U.S.A.).

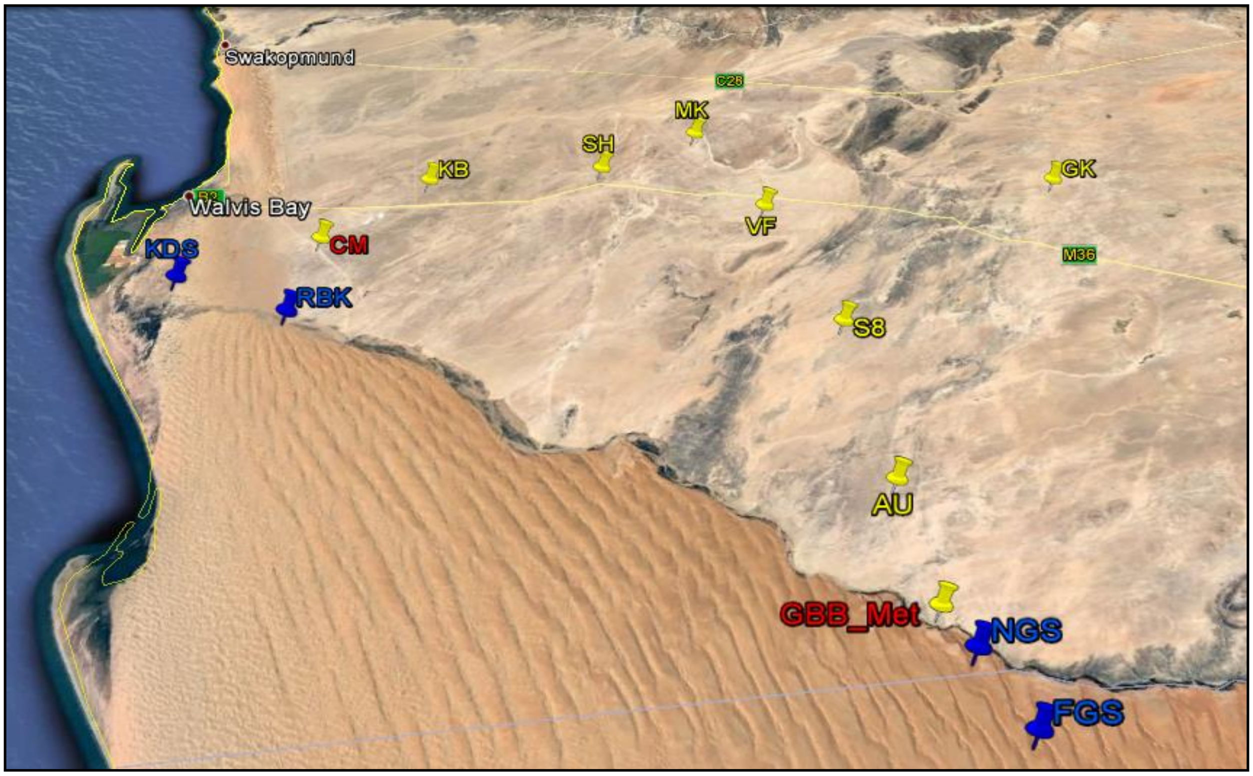


Figure 4. 1: The Namib Desert FogNet stations (yellow pins) that measured fog precipitation assessing the influence of changing climate on the predicted reducing fog at coastal Namib Desert, Namibia due to the warming Benguela Current. The blue pins show the study sites used to evaluate the influence of fog density on the morphology and thermal biology of lacertid lizards of the genus *Meroles*, with the red font sites indicating the FogNet stations for which fog data were used in the present study.

In the present study, only fog data (density) from CM and GBB_Met sites (hereinafter referred to as coastal and inland fog sites) were used to compare *M. anchietae* and Clade A data (morphology and thermal biology) across spring (September 2016) and autumn (March-April 2017). The coastal and inland fog sites were located at distances 15 km and 60 km from the coast, and 94 m and 406 m above sea level (a.s.l.), respectively (Figure 4.1, red font). The coastal fog sites' daily average air and surface temperature were 14.5 ± 2.3° C and 20.2 ± 1.4° C for spring, respectively; and 19.8 ± 3.1° C and 25.6 ± 1.7° C for autumn, respectively. The average air and surface temperatures at the inland fog site were 17.9 ± 3.7° C and 24.2 ± 2.1° C for spring, respectively; and 26.1 ± 2.7° C and 30.8 ± 2.0° C, for autumn, respectively (http://www.sasscalweathernet.org).

The fog data from the coastal fog site was linked with the species data from the Kuiseb Delta site (KDS) and Rooibank sites (RBK) (randomly selected 9 km and 15 km from the coast, and positioned at an altitude of 30 m and 97 m, respectively). Whereas, the fog data from inland fog site was linked with the species data from Near Gobabeb site (NGS) and Far Gobabeb site (FGS) (blue pins and font; Figure 4.1, also randomly selected 60 km and 63 km from the coast, and at an altitude of 496 m and 486 m, respectively). The sites NGS and FGS were named according to the distance from Gobabeb Research and Training Centre (NGS located 10 km southeast of Gobabeb and FGS site located 20 km south-east of Gobabeb), located in the central Namib Desert, in the Namib Naukluft Park, Namibia. The coastal fog site was 13 km and 11 km from KDS and RBK, respectively, whereas the inland fog site was 5 km and 12 km from NGS and FGS, respectively. The selection of the two coastal (KDS and RBK) and inland (NGS and FGS) species data sites were based on the distance of the fog sites (coastal and inland) closest to the dune environment as a preferred habitat for *M. anchietae* and Clade A.

4.2.2 Morphological analyses

Sampling of populations of *M. anchietae* and Clade A targeted four sites, namely, RBK, NGS, FGS and KDS along the Namib Desert, Namibia (Chapter 1). Due to differences in the distributional range of the two sympatric lizard species across the Namib Desert, *M. anchietae* was sampled from three sites (RBK, NGS and FGS) and Clade A sampled from all four sites (Chapter 1). Morphological data were collected over spring (September 2016) and autumn (March-April 2017) and the two seasons were characterized by the differences in daily average air temperature. Spring daily average air temperatures were 16.2 ± 3.0° C (daily average minimum air temperature was 9.5 ± 2.6° C and daily average maximum air temperature was 24.2 ± 4.5° C), whereas autumn daily average air temperatures were 24.1 ± 3.7° C (daily average minimum air temperature was 17.4 ± 3.4° C and daily average maximum air temperature was 31.9 ± 4.1° C) (http://www.sasscalweathernet.org).

Meroles anchietae and Clades A were sampled using cotton mesh bags (D.A. Eifler, unpublished) and noose poles (Murray *et al.* 2016a), respectively. The difference in sampling method is because of differences in lizard predatory behaviour where *M. anchietae* buries entirely in open sand (Robinson & Barrows 2013) and mesh bags are used to sieve the sand, leaving the lizard in the bag. On the other hand, Clade A buries entirely in sand beneath vegetation and noose poles are used to sample them quietly to avoid burying (N. Iiyambo *pers. obs*.). For each sampled individual, the snout-vent length (SVL; to the nearest mm) and tail length (mm) were measured using a standard millimetre ruler. Body mass (to the nearest g) was recorded using a spring scale (Pesola®, PESOLA AG, Feusisberg, Switzerland). The female and male *M. anchietae* are not easy to distinguish morphologically (N. Iiyambo *pers. obs*.), thus sex of *M. anchietae* was determined by squeezing the cloaca gently for the presence or absence of the hemipenis in males and females, respectively (D.A. Eifler, unpublished). For young individuals a probe was inserted into the cloaca because of the absence of a hemipenis due to individuals not having reached sexual maturity. The male cloaca is usually deep whereas female cloaca is shallow. In individuals of Clade A, however, the females and males differ in colouration and pattern with the females possessing a distinct dark pink-orange lateral stripe that extends from the eye to the tail while the males lack this stripe and possess a more reticulated pattern (Branch 1998; Childers & Eifler 2015).

To avoid re-sampling of lizard individuals, as a requirement for behavioural ecological studies, lizards were marked with different coloured plastic jewellery beads (Paramount Novelties, Los Angeles, California) (Chapter 2) when first sampled for identification (Fisher & Muth 1989). Four beads (2 mm thick x 2.5 mm in diameter) were stitched through the tail skin with surgical steel monofilament (Clinisut (Pty) Ltd, Port Elizabeth, South Africa). The resulting identification mark is about 2.5 mm long by 7 mm wide lying perpendicular to the long axis of the tail (Fisher & Muth 1989; D. A. Eifler, unpublished). The bead colours were read from left to right (Chapter 2), when holding the lizard on its belly in an upright position (D. A. Eifler, unpublished). The marking technique ensures minimal physical handling of the lizards, therefore allowing the identification of individual lizards by re-sighting rather than re-capturing (Fisher & Muth 1989).

4.2.3 Thermal biology

The body temperatures of lizards were recorded seasonally within 5 seconds after sampling using a thermocouple digital thermometer (± 0.2° C Omega HH202A Stamford, CT, U.S.A.) that was inserted approximately 5 mm into the cloaca (Murray *et al*. 2014; 2016). The body temperature of lizards that attempted to escape during capture was not recorded to minimize behavioural influence on the readings. Microhabitat air and substrate temperatures at sampling localities were recorded 10 mm above and below ground at all sampling and observation stations using a thermocouple digital thermometer (Murray *et al*. 2016). Air and substrate temperatures at all locations could not be measured simultaneously across the coastal and inland sites because it requires taking temperature readings at areas where the lizards are active. Potentially, ibuttons could have been used to record air and substrate temperatures to ensure simultaneous data collection. That however, would have meant recording temperature data on general habitat rather than the microhabitat at which the lizards were observed. The inability to record thermal data from different sites at the same time may therefore present limitations to the results and conclusions discussed in this study.

4.2.4 Statistical analyses

The amount of fog and number of fog events were compared between coastal and inland fog sites using a two-way analysis of variance (ANOVA; Murray *et al.* 2016) with site and season as factors. Two-way ANOVA (Murray *et al.* 2016) was also used to assess differences in body length and mass of populations of *M. anchietae*, with population and season as factors. One-way ANOVA (Murray *et al.* 2015) was used to assess body mass interaction with season between populations of *M. anchietae*. Body length and body mass were compared between populations of Clade A using a three-way ANOVA (Murray *et al.* 2015), with sex, population and season as factors. Two-way ANOVA (Murray *et al.* 2016) was used to assess differences in body and air temperature at lizard sampling localities of populations of *M. anchietae* and Clade A, with population and season as factors. Analysis of covariance (ANCOVA; Murray *et al.* 2014, 2015) was used to test for differences between season and body temperature, with air and substrate temperatures as covariates. Pearson's *R* (Murray *et al.* 2014) was used to assess the relationship between air and substrate temperature at lizard sampling localities of the populations of *M. anchietae* and Clade A. Analysis of partial correlation (Murray *et al.* 2015) was used to compare the individual effects of air and substrate temperatures on body temperatures of the populations of *M. anchietae* and Clade A. Values were reported as mean ± one standard deviation (± 1SD) with the statistical significance level set at alpha (α) = 0.05. All statistical analyses were based on algorithms in R statistical software (R version 3.4.1 © The R Foundation for Statistical

Computing, Bell Laboratories, Murray Hill, New Jersey, U.S.A.) and Microsoft Excel 2016 (Microsoft Corp., Redmond, Washington, U.S.A.).

4.3 Results

4.3.1 Assessment of fog precipitation

Because species data were recorded from mid-March to mid-April for the autumn sampling, the fog data for March and April were combined. The amount of fog received (Table 4.1; Figure 4.2) differed significantly between sampling sites (two-way ANOVA; site: $F_1 = 6.93$; $n = 12$; $P = 0.03$) with the coastal site receiving more fog than the inland site, and across seasons (two-way ANOVA; season: $F_1 = 5.62$; $n = 12$; $P = 0.05$), with spring receiving more fog than autumn. The interaction between site and season was not statistically significant (two-way ANOVA; site*season: $F_1 = 0.17$; $n = 12$; $P = 0.69$), indicating that during both seasons, the coastal and inland sites received similar amounts of fog.

Table 4. 1: A comparison of mean standard deviation (± SD) of total amount of fog (mm) and total number of days per year for which a fog event was experienced at the coastal and inland sites of the central Namib Desert, Namibia, between 01 July 2014 and 19 June 2017.

Trait	Coastal		Inland	
	Fog	Days	Fog	Days
2014	50.9 ± 4.1	62 ± 4.4	51.5 ± 7.1	38 ± 2.6
2015	410.0 ± 26.4	147 ± 5.3	101.0 ± 5.8	58 ± 3.0
2016	203.0 ± 12.0	99 ± 2.8	169.0 ± 14.7	64 ± 3.8
2017	59.8 ± 6.5	37 ± 2.9	18.1 ± 2.3	14 ± 2.1

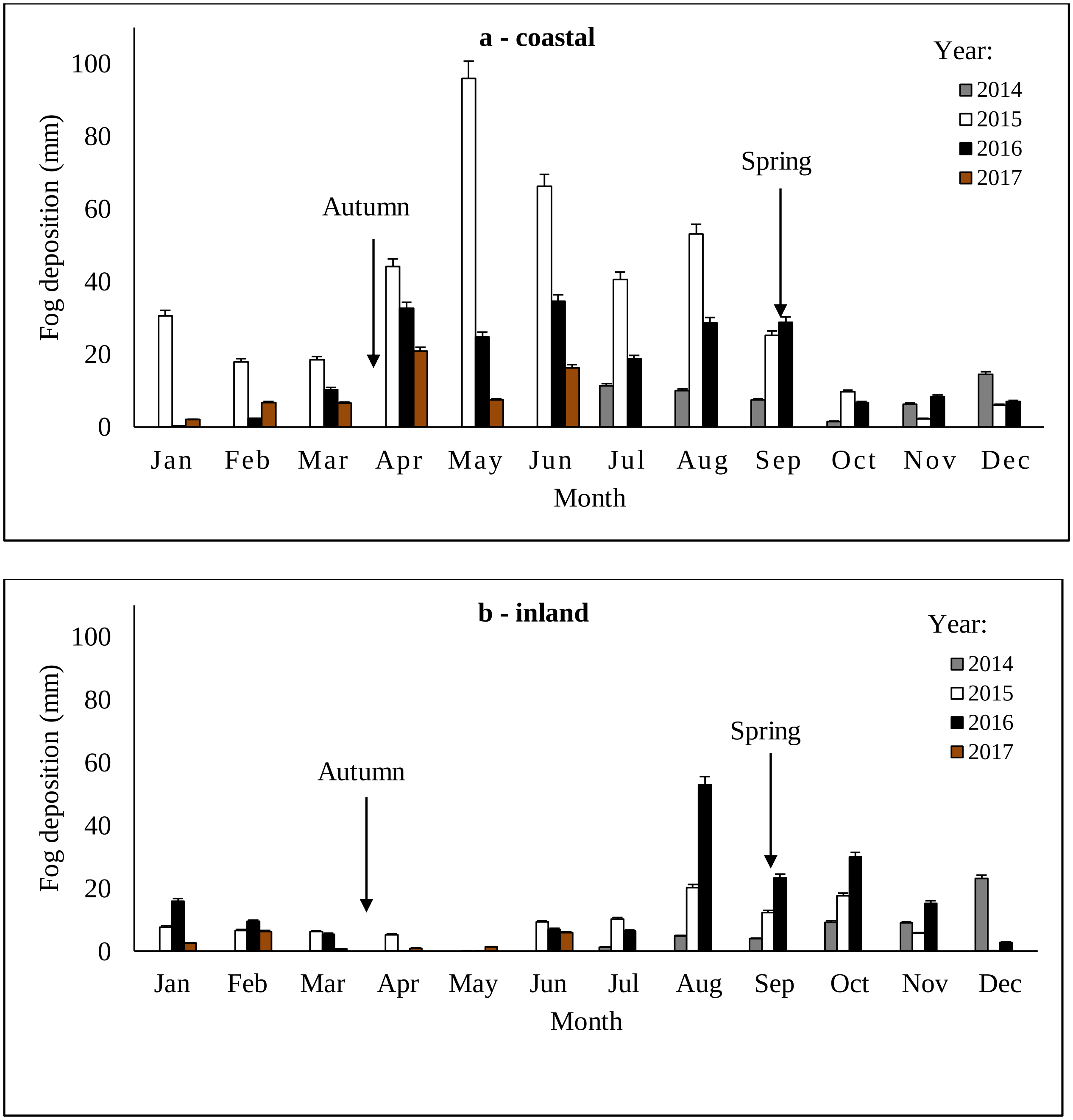
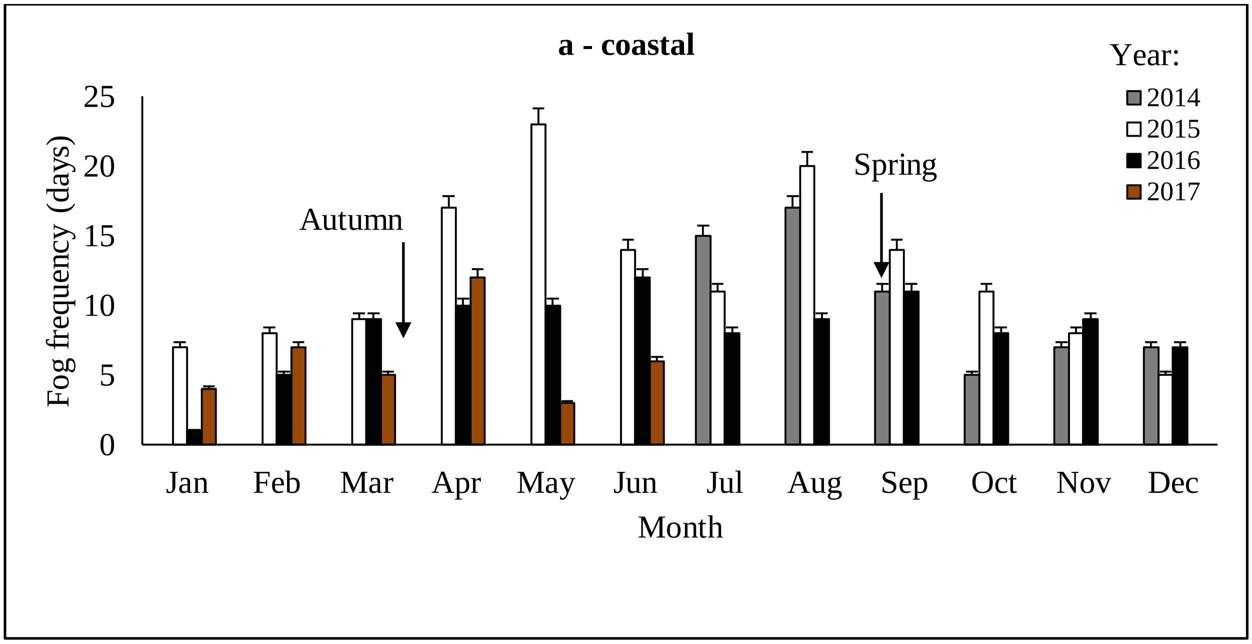


Figure 4. 2: The monthly fog deposition recorded at: a) coastal and b) inland sites of the central Namib Desert between 01 July 2014 and 19 June 2017. Data are presented as total amount of fog (mm) received per month.

The number of fog events (Table 4.1; Figure 4.3) differed significantly between sites (two-way ANOVA; sites: $F_1 = 11.83$; $n = 12$; $P < 0.01$), with the coastal site experiencing more fog events than the inland site. The number of fog events, however, did not differ significantly across seasons (two-way ANOVA; season: F_1 = 4.19; n = 12; P = 0.08). There was no statistically significant difference in the interaction between sampling site and season (two-way ANOVA; site*season: F_1 = 0.12; n = 12; P = 0.74), indicating that in both seasons, the coastal and inland sites received similar number of fog events. The average amount of fog received per day of any given fog event did not differ significantly between coastal and inland sites (two-sample t_5 = 0.12; n = 8; P = 0.91), coastal average was 1.82 mm of fog per day and inland average was 1.76 mm per day of any given fog event.



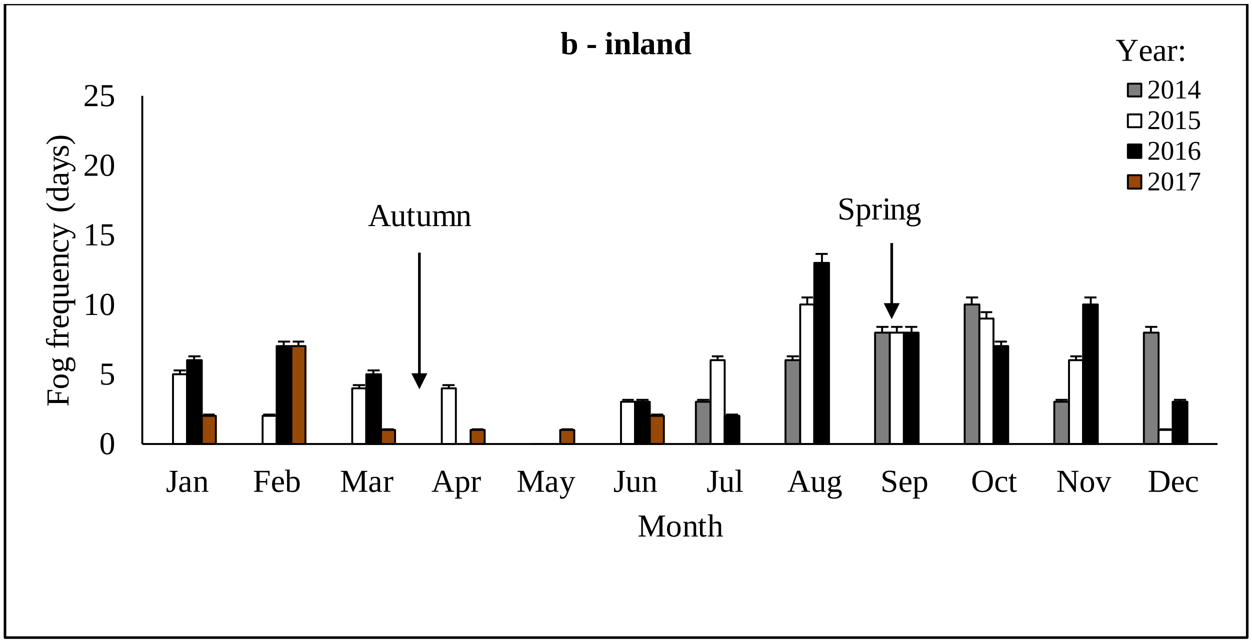


Figure 4. 3: The number of fog days per month for which a fog event was experienced and recorded at: a) coastal and b) inland sites of the central Namib Desert, Namibia between 01 July 2015 and 19 June 2017.

4.3.2 Morphological assessment

Meroles anchietae individuals sampled from RBK were treated as a single population representing the coastal population. On the other hand, populations of NGS and FGS were combined to represent the inland population of *M. anchietae* as they indicated no statistically significant differences in their morphology (two-sample; body length: t_{46} = -1.23 n = 48; P = 0.09; body mass: t_{46} = -1.98 n = 48; P = 0.06) and thermal biology (two-sample; body temperature: t_{54} = -1.30 n = 48; P = 0.20; air temperature at sampling localities: t_{53} = -0.12 n = 48; P = 0.91).

Clade A individuals from KDS and RBK did not show significant difference in morphology (two-sample; body length: t_{36} = 1.30 n = 52; P = 0.20; body mass: t_{42} = 1.49 n = 52; P = 0.14) and thermal biology (two-sample; body temperature: t_{64} = -1.11 n = 52; P = 0.27; air temperature at sampling localities: t_{61} = -0.59 n = 52; P = 0.56). Similarly, Clade A individuals from NGS and FGS did not indicate significant differences in morphology (two-sample; body length: t_{65} = -1.03 n = 71; P = 0.31; body mass: t_{68} = -1.12; n = 71; P = 0.27) and thermal biology (two-sample; body temperature: t_{61} = 1.29 n = 71; P = 0.20; air temperature at sampling localities: t_{66} = 0.55 n = 71; P = 0.59). Thus, data from KDS and RBK were combined to represent the coastal populations, and data from NGS and FGS combined to represent the inland populations of Clade A.

Thirteen individuals (six coastal and one inland *M. anchietae*, and four coastal, and two inland Clade A) captured during spring were re-captures from autumn, and these individuals were not included in the analyses for body mass and length. Additionally, the juvenile data were not considered for analyses of body length and body mass to avoid biased conclusions that may have resulted from frequent sampling of juveniles at some study sites over the others. Within the coastal and inland *M. anchietae*, there was no statistically significant difference in SVL between males and females (two-sample; sex: t_{36} = -0.85 n = 88; P = 0.40), thus male and female data were pooled in all subsequent analyses (Table 4.2). The SVL differed significantly between populations (two-way ANOVA; population: F_1 = 23.60; n = 88; $P < 0.01$), with inland *M. anchietae* being longer than coastal individuals, however, SVL did not differ across seasons (two-way ANOVA; season: F_1 = 2.38; n = 88; P = 0.13). The interaction between population and season was statistically significant (two-way ANOVA; population*season: F_1 = 23.63; n = 88; $P < 0.01$).

Table 4. 2: A comparison of mean and standard deviation (± SD) of snout-vent length (SVL; mm) and body mass (g) for coastal and inland *Meroles anchietae* during spring (September 2016) and autumn (March-April 2017). The dash (-) indicates non-significant results. *n* = sample size.

	M. anchietae			
Trait	Population		Season	
	Coastal (*n* = 40)	Inland (*n* = 48)	Autumn (*n* = 18)	Spring (*n* = 30)
SVL (mm)	42.20 ± 3.15	45.90 ± 4.55	-	-
Body mass (g)	-	-	3.12 ± 1.05	2.70 ± 1.07

Body mass of coastal and inland *M. anchietae* did not differ between males and females (two-sample; sex: t_{33} = -0.89; n = 88; P = 0.38), thus data for males and females were pooled in all subsequent analyses. Body mass did not differ significantly between populations (two-way ANOVA; population: F_1 = 0.44; n = 88; P = 0.51), however, it differed significantly across seasons (two-way ANOVA; season: F_1 = 4.93; n = 88; P = 0.03) with individuals being heavier during autumn than spring (Table 4.4). The interaction between population and season was statistically significant (two-way ANOVA; population*season: $F_1 = 8.82$; $n = 88$; $P < 0.01$). The coastal *M. anchietae* were heavier than the inland *M. anchietae* during autumn (one-way ANOVA; coastal *M. anchietae*: $F_1 = 27.6$; $n = 40$; $P < 0.01$). The body mass of inland *M. anchietae* did not differ significantly across seasons (one-way ANOVA; inland *M. anchietae*: $F_1 = 0.06$; $n = 48$; $P = 0.80$).

Body length of coastal and inland Clade A individuals differed significantly between males and females (three-way ANOVA; sex: $F_1 = 20.83$; $n = 123$; $P < 0.01$), with males being significantly longer than females and between populations (three-way ANOVA; population: $F_1 = 4.07$; $n = 123$; $P = 0.05$), with coastal longer than the inland. (Table 4.3). The interactions between sex, population and season were all not statistically significant (three-way ANOVA; population*season: $F_1 = 0.05$; $n = 123$; $P = 0.82$; population*sex: $F_1 = 3.61$; $n = 123$; $P = 0.06$; season*sex: $F_1 = 0.74$; $n = 123$; $P = 0.39$; and population*season*sex: $F_1 = 2.43$; $n = 123$; $P = 0.12$).

Table 4. 3: A comparison of mean standard deviation (± SD) snout-vent length (SVL; mm) and body mass (g) for males and females of Clade A of *Meroles cuneirostris* during September (2016) and March-April (2017). *n* = sample size.

Trait	Clade A			
	Sex		Population	
	Male ($n = 80$)	Female ($n = 43$)	Coastal ($n = 52$)	Inland ($n = 71$)
SVL (mm)	53.72 ± 5.68	49.39 ± 3.79	53.27 ± 5.12	51.42 ± 5.62
Body mass (g)	4.99 ± 1.97	3.70 ± 1.25	4.90 ± 1.82	4.28 ± 1.82

Body mass of coastal and inland Clade A individuals differed significantly between males and females (three-way ANOVA; sex: $F_1 = 15.37$; $n = 123$; $P < 0.01$), with males being significantly heavier than females and between populations (three-way ANOVA; population: $F_1 = 3.91$; $n = 123$; $P = 0.05$), with coastal individuals be significantly heavier than inland individuals (Table 4.5). Body mass did not differ significantly across seasons (three-way ANOVA; season: $F_1 = 0.00$; $n = 123$; $P = 0.98$). The interactions between sex, population and season were all not statistically significant (three-way ANOVA; population*season: $F_1 = 0.93$; $n = 123$; $P = 0.0.34$; population*sex: $F_1 = 3.72$; $n = 123$; $P = 0.06$; season*sex: $F_1 = 0.06$; $n = 123$; $P = 0.80$; and population*season*sex: $F_1 = 0.77$; $n = 123$; $P = 0.38$).

4.3.3 Assessment of thermal biology

The body temperature of coastal and inland *M. anchietae* did not differ between males and females (two-sample; sex: $t_{46} = 0.41$ $n = 108$; $P = 0.69$), thus male and female data were pooled in all subsequent analyses. Body temperature did not differ significantly between coastal and inland *M. anchietae* (two-way ANOVA; population: $F_1 = 1.07$; $n = 108$; $P = 0.30$), however, it differed significantly between seasons (two-way ANOVA; season: $F_1 = 13.74$; $n = 108$; $P < 0.01$), with body temperature being significantly higher during autumn than spring (Figure 4.4). The interaction between population and season was statistically significant (two-way ANOVA; population*season: $F_1 = 11.83$; $n = 108$; $P < 0.01$). Individuals of coastal *M. anchietae* had higher body temperatures during autumn than during spring (one-way ANOVA; coastal *M. anchietae*: $F_1 = 22.24$; $n = 108$; $P < 0.01$). The body temperatures of inland *M. anchietae* did not differ significantly across seasons (one-way ANOVA; inland *M. anchietae*: $F_1 = 0.003$; $n = 108$; $P = 0.96$).

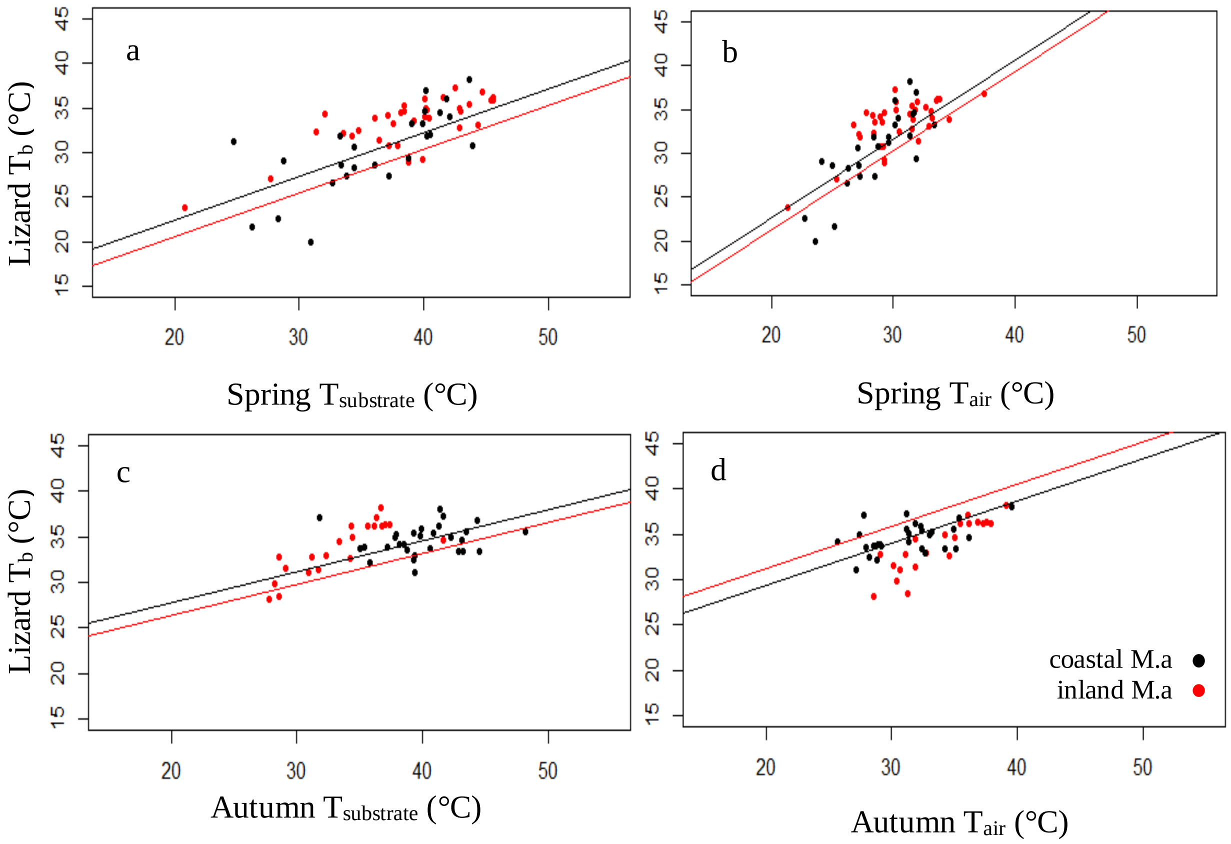


Figure 4. 4: The seasonal relationship between body temperature (T_b) of coastal (black circles) and inland (red circles) *Meroles anchietae* (M.a) and substrate (10 mm below ground) and air temperatures (10 mm above ground) at sampling sites in the Namib Desert, Namibia in spring (September) = a and b, and in autumn (March-April) = c and d. The regression line of the relationship is shown relative to a line of identity ($T_{body} = T_{substrate}$ or T_{air}).

The body temperature of the coastal and inland Clade A individuals did not differ between males and females (two-sample; sex: $t_{112} = -1.01$ $n = 154$; $P = 0.31$), thus male and female data were pooled in all subsequent analyses. Body temperature differed significantly between coastal and inland Clade A individuals (two-way ANOVA; population: $F_1 = 19.70$; $n = 154$; $P < 0.01$), with inland Clade A individuals having significantly higher body temperatures than coastal Clade A individuals, and across season (two-way ANOVA; season: $F_1 = 28.58$; $n = 154$; $P < 0.01$), with body temperature being higher during autumn than spring (Figure 4.5). The interaction between population and season was statistically significant (two-way ANOVA; population*season: $F_1 = 14.89$; $n = 154$; $P < 0.01$). Coastal Clade A individuals had higher body temperatures during autumn than during spring (one-way ANOVA; coastal Clade A: $F_1 = 28.19$;

n = 154; *P* < 0.01). Body temperatures of inland Clade A individuals did not differ significantly across seasons (one-way ANOVA; inland Clade A: $F_1 = 3.71$; *n* = 154; *P* = 0.06).

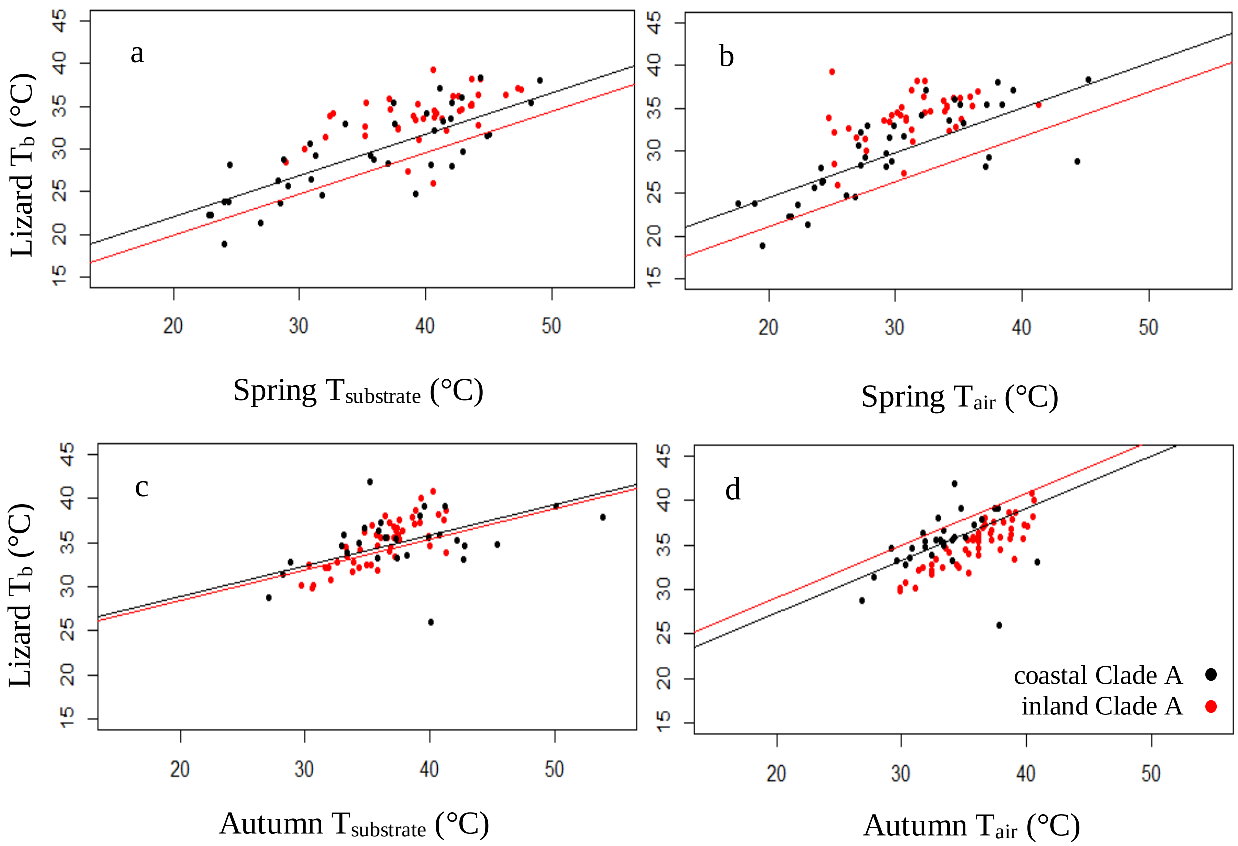


Figure 4. 5: The seasonal relationship between body temperature (T_b) of coastal (black circles) and inland (red circles) Clade A of *Meroles cuneirostris* and substrate (10 mm below ground) and air temperatures (10 mm above ground) at sampling sites in the Namib Desert, Namibia, during spring (September) = a and b, and in autumn (March-April) = c and d. The regression line of the relationship is shown relative to a line of identity ($T_{body} = T_{substrate}$ or T_{air}).

During spring, the relationship between body and substrate temperature at sampling locations of coastal *M. anchietae* ($T_b = 0.60 (T_{sub}) + 8.66$; $r^2 = 0.52$; d.f. = 1; *n* = 24; *P* = 0.06); (ANCOVA; $F_1 = 24.89$; *n* = 24; *P* < 0.01) had a higher slope and a lower intercept than the equivalent relationship in inland *M. anchietae* ($T_b = 0.41 (T_{sub}) + 17.57$; $r^2 = 0.56$; d.f. = 1; *n* = 35; *P* < 0.01); (ANCOVA; $F_1 = 45.01$; *n* = 35; *P* < 0.01). On the other hand, during autumn, the relationship between body and substrate temperature at sampling localities of coastal *M. anchietae* ($T_b = 0.08 (T_{sub}) + 31.45$; $r^2 = 0.03$; d.f. = 1; *n* = 28; *P* = 0.39); (ANCOVA; $F_1 = 0.76$; *n* = 28; *P* = 0.39) had a significantly lower slope and a significantly greater intercept than that of inland *M. anchietae* ($T_b = 0.63 (T_{sub}) + 12.46$; $r^2 = 0.69$; d.f. = 1; $n = 20$; $P < 0.01$); (ANCOVA; $F_1 = 41.73$; $n = 20$; $P < 0.01$).

The regression of body and substrate temperatures at sampling locality of inland Clade A during spring ($T_b = 0.33 (T_{sub}) + 20.48$; $r^2 = 0.29$; d.f. = 1; $n = 37$; $P < 0.01$); (ANCOVA; $F_1 = 15.05$; $n = 37$; $P < 0.01$) showed a significantly lower slope and a significantly greater intercept than in coastal Clade A individuals ($T_b = 0.53 (T_{sub}) + 10.59$; $r^2 = 0.65$; d.f. = 1; $n = 36$; $P < 0.01$); (ANCOVA; $F_1 = 66.16$; $n = 36$; $P < 0.01$). During autumn, the slope was significantly greater ($T_b = 0.20 (T_{sub}) + 27.72$; $r^2 = 0.13$; d.f. = 1; $n = 27$; $P < 0.01$); (ANCOVA; $F_1 = 4.13$; $n = 27$; $P = 0.05$) and the intercept significantly lower for the relationship between body and substrate temperatures at sampling localities of coastal Clade A individuals than that of inland Clade A individuals ($T_b = 0.72 (T_{sub}) + 8.89$; $r^2 = 0.54$; d.f. = 1; $n = 48$; $P = 0.01$); (ANCOVA; $F_1 = 56.8$; $n = 48$; $P < 0.01$).

The air temperature at sampling localities differed significantly between populations (two-way ANOVA; population: $F_1 = 4.40$; $n = 108$; $P = 0.04$) with inland *M. anchietae* found at areas of higher air temperatures than coastal *M. anchietae*, and across seasons (two-way ANOVA; season: $F_1 = 22.26$; $n = 108$; $P < 0.01$), with autumn having higher air temperatures than spring. The interaction between population and season was not statistically significant (two-way ANOVA; population*season: $F_1 = 0.02$; $n = 108$; $P = 0.90$), indicating that during both seasons, the coastal and inland populations of *M. anchietae* were found at areas of similar air temperatures. For Clade A, the air temperature at sampling localities differed significantly between populations (two-way ANOVA; population: $F_1 = 14.24$; $n = 154$; $P < 0.01$) with inland Clade A individuals being found at areas of higher air temperatures compared to those areas of coastal Clade A individuals, and across seasons (two-way ANOVA; season: $F_1 = 31.58$; $n = 154$; $P < 0.01$), with autumn having higher air temperatures than spring. The interaction between population and season was not statistically significant (two-way ANOVA; population*season: $F_1 = 0.66$; $n = 154$; $P = 0.42$), also indicating that during both seasons, the coastal and inland populations of Clade A were found at areas of similar air temperature.

During spring, the regressions of body and air temperature at sampling localities of coastal *M. anchietae* ($T_b = 1.23 (T_{air}) – 5.56$; $r^2 = 0.67$; d.f. = 1; $n = 23$; $P = 0.31$); (ANCOVA; $F_1 = 46.21$; $n = 23$; $P < 0.01$) had a higher slope and a significantly lower intercept than that of inland *M. anchietae* ($T_b = 0.66 (T_{air}) + 13.36$; $r^2 = 0.49$; d.f. = 1; $n = 34$; $P < 0.01$); (ANCOVA; $F_1 = 32.6$; $P < 0.01$). During autumn, the slope was significantly greater ($T_b = 0.79 (T_{air}) + 6.99$; $r^2 = 0.77$; d.f. = 1; $n = 19$; $P = 0.05$) (ANCOVA; $F_1 = 63.27$; $n = 19$; $P < 0.01$) and the intercept significantly lower for the relationship between body and air temperature at sampling localities of inland *M. anchietae* than that of coastal *M. anchietae* ($T_b = 0.23 (T_{air}) + 27.3$; $r^2 = 0.23$; d.f. = 1; $n = 27$; $P < 0.01$); (ANCOVA; $F_1 = 7.23$; $n = 27$; $P = 0.01$).

The relationship between body and air temperature at sampling localities for coastal Clade A individuals ($T_b = 0.31 (T_{air}) + 24.66$; $r^2 = 0.10$; d.f. = 1; $n = 27$; $P < 0.01$); (ANCOVA; $F_1 = 2.89$; $n = 27$; $P = 0.101$) showed a significantly greater slope and a lower intercept than in inland Clade A individuals during autumn ($T_b = 0.81 (T_{air}) + 5.90$; $r^2 = 0.67$; d.f. = 1; $n = 48$; $P = 0.05$); (ANCOVA; $F_1 = 98.3$; $n = 48$; $P < 0.01$). During spring, the relationship between body and air temperature at sampling localities for coastal Clade A individuals had a significantly higher slope ($T_b = 0.59 (T_{air}) + 12.26$; $r^2 = 0.62$; d.f. = 1; $n = 36$; $P < 0.01$); (ANCOVA; $F_1 = 57.41$; $n = 36$; $P < 0.01$) and a significantly lower intercept than for inland Clade A ($T_b = 0.33 (T_{air}) + 23.52$; $r^2 = 0.20$); (ANCOVA; $F_{1, 37} = 8.97$; $P = 0.005$).

Air and substrate temperatures at sampling localities were significantly correlated for coastal *M. anchietae* ($T_{substrate} = 0.50 (T_{air}) + 10.98$; Pearson correlation: $r_{52} = 0.71$; $n = 54$; $P < 0.01$) and inland *M. anchietae* ($T_{substrate} = 0.24 (T air) + 22.96$; Pearson correlation: $r_{55} = 0.36$; $n = 57$; $P = 0.01$). Similarly, for coastal and inland Clade A, both air and substrate temperature at sampling localities were significantly correlated ($T_{substrate} = 0.48 (T_{air}) + 13.87$; Pearson correlation: $r_{65} = 0.72$; $n = 67$; $P < 0.01$) and ($T_{substrate} = 0.20 (T_{air}) + 26.51$; Pearson correlation: $r_{87} = 0.20$; $n = 89$; $P = 0.061$), respectively. Body temperature for both coastal and inland *M. anchietae* and Clade A individuals showed statistically significant correlations with substrate temperature, partial correlation of body-substrate temperature at sampling localities of coastal *M. anchietae* (Partial correlation = 0.35; d.f. = 1; $n = 54$; $P = 0.01$), inland *M. anchietae* (Partial correlation = 0.58; d.f. = 1; $n = 57$; $P < 0.01$), coastal Clade A (Partial correlation = 0.43; d.f. = 1; $n = 67$; $P < 0.01$) and inland Clade A (Partial correlation = 0.44; d.f. = 1; $n = 89$; $P < 0.01$). Similarly, partial correlation of body-air temperature was significantly correlated for coastal *M. anchietae* (Partial correlation = 0.43; d.f. = 1; $n = 54$; $P = 0.001$), inland *M. anchietae* (Partial correlation = 0.66; d.f. = 1; $n = 57$; $P < 0.01$), coastal Clade A (Partial correlation = 0.56; d.f. = 1; $n = 67$; $P < 0.01$) and inland Clade A (Partial correlation = 0.61; d.f. = 1; $n = 89$; $P < 0.01$).

4.4 Discussion

4.4.1 Fog precipitation

The study found that the coastal site received more fog (average 180.9 ± 145.4 mm of fog and 86.3 ± 41.4 days per year) than the inland site (average 84.9 ± 43.5 mm of fog and 56.8 ± 19.6 days per year). This is similar to previous observations by Hachfeld (2000) who observed that the coastal site (15 km from the coast) receives 130 mm in a year compared to the inland site (60 km from the coast) that receives 62 mm in a year. Lancaster *et al.* (1984) and Hachfeld & Juergens (2000) also indicated that the number of fog days per year decreased significantly from coastal to inland regions and the study by Haensler *et al.* (2011a) indicated more than 100 days of fog per year occurring in the coastal region and 50 days a year in the inland region. When fog condenses at high altitude, areas of higher elevation receive more fog than those of lower elevation (Henschel *et al.* 1998). Nonetheless, the coastal fog site at 94 m above sea level (a.s.l.) received more fog than the inland fog site at 406 m a.s.l. Moreover, the coastal fog in the Namib Desert is highly influenced by the lower sea surface temperatures of the Benguela upwelling system (Olivier 1992; Henschel *et al.* 1998). This is supported by the present study when the coastal fog site with daily average surface temperature of 20.2 ± 1.4° C in autumn and 25.6 ± 1.7° C in spring, received more fog compared to the inland fog site with daily average surface temperature of 24.2 ± 2.1° C in autumn and 30.8 ± 2.0° C in spring. This finding indicates that the Namib Desert is not only influenced by altitude, but also distance from the coast, and surface temperature influence, such that the relationship between these factors is the key determinant of fog density.

Cool air holds less water vapour that condenses to dew point and remains suspended in the air as fog (Haensler *et al.* 2011a). When air is warmer, it holds more water vapour supporting more condensation, thus producing more fog (Olivier & Stockton 1989; Haensler *et al.* 2011a). In the present study, more fog was received in spring compared to autumn; however, the air was warmer in autumn than in spring, supporting the notion that other factors may influence the production of fog in the Namib Desert. Additionally, the present study found that the number of fog events did not differ with season, indicating that the frequency of fog events was the same seasonally. The results of the present study suggest that the coastal lizard populations may have access to more water compared to inland populations.

The winter months received more fog at the coastal site, whereas the inland site received more fog in spring between August and October. Hachfeld (2000) suggested the same for strong temporal concentration of precipitation in the Namib Desert during winter months from May to October. Haensler *et al.* (2011a) also stated that fog in the Namib Desert is more common at the coastal regions during winter (April to September), whereas at the inland regions most fog is received during early summer (October to March). Additionally, Lancaster *et al.* (1984) indicated that at the coast of Namibia (e.g., Swakopmund), fog was most common during winter months while further inland (e.g., Swartbank and Vogelfederberg) more fog was recorded during summer. No fog precipitation was recorded in May 2015 and from April to May 2016 (autumn) at the inland site, meaning no fog event was experienced during those months. The study also found that the average amount of fog received per day did not differ between coastal and inland sites such that the more fog events, the greater the fog density per site. Generally, this finding suggests that the number of fog events may potentially serve as one of the major contributing factors to the differences in fog density across the two sites.

4.4.2 Morphology

This study is the first to report on the influence of fog density on the morphology of coastal and inland *M. anchietae* and Clade A individuals by comparing morphological and thermal data to assess the impacts of climate change on these aspects. Little to no data on differences between coastal and inland *M. anchietae* and Clade A individuals are available. A few similar studies have modelled data obtained on lizard species (i.e., habitat use, species abundance, and reproductive performance) in relation to rainfall (Dickman 1999; Marquis *et al.* 2008). The present study was limited to comparing fog data spanning a three-year period (01 July 2014 to 19 June 2017) to data spanning two/three months (September and March-April) representing two seasons (spring 2016 and autumn 2017). A seven- and 16-year period of monthly fog and activity data as suggested by Dickman (1999) and Marquis *et al.* (2008) were not available in the present study because recordings of fog in the central Namib Desert by FogNet stations is a fairly new initiative and thus the present study acts as a baseline investigation to understand the potential effects of fog on lizard ecology of populations of *M. anchietae* and Clade A in the Namib Desert, Namibia.

Based on morphological data, a parallel study (Chapter 2) found that the body length of Clade A individuals was significantly longer than that of *M. anchietae*. For comparison of body length between coastal and inland populations of *M. anchietae* and Clade A individuals, the present study found that the body length of inland *M. anchietae* was significantly longer than that of coastal *M. anchietae*. This finding is linked to less fog received at the inland site compared to the coastal site, indicating that the body length of inland *M. anchietae* is negatively correlated with fog density. Dunham (1978) and Stamps & Tanaka (1981) reported that precipitation may have beneficial effects by increasing water availability and in turn contributing to greater prey abundance, suggesting that the greater the prey abundance, the larger the lizard bodies as a result of more food availability. In present study, however, prey abundance per site (coastal and inland sites) was not determined, as this aspect did not form part of the research questions being addressed in the present study.

In addition, less fog precipitation would suggest fewer available prey resources, leading to smaller lizard bodies. The inland *M. anchietae* however, showed longer body length with less fog availability, suggesting that other factors (i.e., growth rate; Andrew 1982) may play significant roles in longer body lengths of inland *M. anchietae*. Body size and age at maturity are two important life-history characters that effect fecundity and survival of organisms, thus determining growth rate (Andrew 1982; Ballinger 1983; Stearns 1992; Roff 2002). There are phenotypic differences of growth rate in all organisms and numerous ecological factors contribute to phenotypic plasticity for growth rate (Lee & Roh 2010). Temperature and nutrition are the prevailing ecological factors affecting growth and other biological processes (i.e., thermoregulation and reproduction) in organisms (Mattson 1980; Slansky 1993; Casey 1993; Sinervo & Adolph 1989; Huey & Berrigan 2001; Lee & Roh 2010). In lizards, the interaction between behaviour and physiology in their thermal environment affects growth rate (Porter & Tracy 1983; Sinervo & Adolph 1989). Individual variation in body temperature influences variation in growth rate because lower body temperatures decrease rates of physiological processes that contribute to growth in reptiles (Dawson 1975; Hutchinson & Maness 1979;

Andrew 1982); however, both coastal and inland *M. anchietae* indicated similar body temperatures.

To maintain body temperatures, lizards depend on environmental temperature to allow normal activity, and thus thermal constraints limit the activity time of lizards daily and seasonally (Porter & Tracey 1983). Variation in latitude and elevation influences change in thermal environments, thus contributing to differences in the time available for activity, thus affecting growth rate (Avery 1979; Porter & Tracey 1983; Grant & Dunham 1988; Tsuji 1988). A greater amount of time for activity suggests more prey consumed and thus larger body sizes (Tinkle 1972; Tinkle & Ballinger 1972; Avery 1984; Sinervo & Adolph 1989). Inland *M. anchietae* were active for two hours longer than coastal *M. anchietae* in both seasons, supporting the greater body lengths. Lizards are less active when the air is drier (decreased air humidity) because of constrains on sunbasking and foraging activities, suggesting decreased body sizes (i.e., body length and mass) (Lorenzo *et al.* 1999). Inland *M. anchietae* was found in areas of higher air temperatures, supporting longer body lengths.

In addition, based on morphological data, a parallel study (Chapter 2) found that the body mass of Clade A individuals was significantly heavier than that of *M. anchietae*. As for comparison of body mass between coastal and inland *M. anchietae* and Clade A individuals, the present study found that the body mass of coastal and inland *M. anchietae* was significantly heavier during autumn than spring, indicating a negative correlation with fog density. Robinson & Seely (1980) reported that at Gobabeb, decomposed plant matter, a major source of food for *M. anchietae* (Robinson & Barrows 2013), differs seasonally with more volume during late spring (November) to early autumn (March), with approximately 20% - 48% coverage on the slipface (Robinson & Seely 1980). This would suggest greater prey abundance, and thus larger body sizes. The present study also found that the body mass of coastal *M. anchietae* was heavier than inland *M. anchietae* during autumn, indicating a negative correlation with fog density. This finding is further supported by more fog received at the coastal site, suggesting that coastal *M. anchietae* has access to more water than the inland populations of the species. Consequently, increased water availability contributes to greater prey abundance and thus larger body-sized lizards because of more food availability (Dunham 1978; Stamps & Tanaka 1981). The study also found that the body mass of males was significantly heavier than that of females for coastal and inland Clade A individuals, indicating sexual dimorphism (Chapter 2).

4.4.3 Thermal biology

This study is the first to assess the thermal biology of coastal and inland *M. anchietae* and Clade A. Other studies reported that the temperatures experienced during embryonic development influence the morphology, physiology and behaviours of neonate reptiles (Shine & Harlow 1993; Shine & Downes 1999; Massot *et al*. 2002). The study found that the body temperature was higher during autumn compared to spring for both coastal *M. anchietae* and Clade A, and body temperatures was higher for inland Clade A compared to coastal Clade A, indicating a negative correlation with fog density. This finding indicates that the less fog received, the higher the body temperature for these populations, which corresponds with warmer ambient temperatures from less fog received.

Lizards rely on their environmental temperature (i.e., air and substrate temperature) to allow normal activities, and regulate their body temperatures through behavioural adjustments (i.e., moving between areas of sun and shade) (Cowles & Bogert 1944; Porter & Tracey 1983). Despite air temperature fluctuations, such behavioural adjustments enable lizards to maintain high and relatively constant body temperatures, and the higher the environmental temperatures, the higher the body temperatures (Huey 1982). The inland *M. anchietae* individuals experienced higher body temperatures because of higher environmental temperatures at their sampling locations and in turn larger body sizes (Huey 1982; Lorenzo *et al*. 1999). In lizards, the body size affects the rates of cooling and heating (Martins *et al.* 1995). Individuals with small bodies' heat up faster compared to those with large bodies (Garcia-Rosales *et al.* 2017). Consequently, because of limitations on thermoregulation efficiency, species living in cold environments may not adapt to large bodies (Pincheira-Donoso *et al.* 2008). Distinctively, coastal Clade A individuals indicated larger body sizes regardless of cold environments. The larger body sizes in coastal Clade A individuals may be related to more water availability, thus greater prey abundance.

In addition, based on thermal data, a parallel study (Chapter 2) found that Clade A individuals were active at higher substrate temperatures (54° C for autumn and 49° C for spring) compared to *M. anchietae* (48° C for autumn and 45° C for spring). A comparison of substrate temperatures at sampling localities between coastal and inland *M. anchietae* revealed that in the mornings, coastal *M. anchietae* emerged from the sand at 26° C during spring and at 32° C during autumn compared to inland *M. anchietae* emerging at 21° C during spring and at 28° C during autumn. This finding indicates that the daily activity of inland populations of *M. anchietae* begun at cooler substrate temperatures (and cooler during spring than autumn) compared to coastal populations. This finding is further explained by the inland populations relying heavily on the substrate for heat conduction to raise body temperature, suggesting thigmothermy, whereas the coastal populations depends on short wavelength solar radiation, suggesting heliothermic mechanisms (Louw & Holm 1972). On the other hand, the daily activity of inland populations of Clade A begun at warmer substrate temperatures (at 29 °C in spring and at 30 °C during autumn), suggesting heliothermic mechanisms compared to the coastal populations (at 23 °C in spring and at 27 °C in autumn), suggesting thigmothermy mechanisms. With increasing surface temperatures because of climate change (Boko *et al.* 2007; Niang *et al.* 2014; Engelbrecht *et al.* 2015), the inland populations of *M. anchietae* and the coastal populations of Clade A may be affected because of very hot substrate temperatures and thus reduced amount of time for activity, further contributing to reduced body sizes. The study also found that substrate temperatures were higher than body temperatures, suggesting that conductive and radiant heat transfer would have imposed more heat on the lizard body when in direct solar radiation (Murray *et al.* 2016). In addition, the air temperature at sampling locations was below that of the body temperature, suggesting that lizards would have lost heat by convection (Murray *et al.* 2016).

Slipface are known for their high surface temperatures, and for this reason, lizards only had two escape tactics to prevent them from over-heating, either burying or retreating to cooler slopes (Robinson & Barrows 2013). The body temperatures of coastal and inland *M. anchietae* and Clade A individuals were lower than substrate temperatures at sampling localities during both seasons, meaning the individuals have adapted to regulating their body temperatures to ensure that they do not overheat. Previous studies identified numerous strategies used by lizards to behaviourally thermoregulate by: 1) changing their time of activity (Heatwole *et al.* 1969; Porter *et al.* 1973; Huey *et al.* 1977; Childers & Eifler 2015); 2) moving between areas of lower surface temperatures (Heath 1964; Hammel *et al.* 1967; Spellerberg 1972; Childers & Eifler 2015); and 3) changing their posture (Bartholomew 1966; Barlett & Gates 1967; DeWitt 1971; Huey *et al.* 1977; Stevenson 1985; Bauwens *et al.* 1996). Populations of *M. anchietae* were observed burying in deep sand as soon as surface temperatures became hotter than they could bear, whereas individuals of Clade A were observed running into vegetation cover and a few getting into burrows of unknown animals.

The influence of fog density on the coastal and inland *M. anchietae* and Clade A individuals indicate both positive and negative correlations with the morphology and thermal biology. Several studies have documented that rainfall drives population fluctuations in many species in arid Australia (Newsome & Corbett 1975; Schodde 1982; Dickman 1993; Dickman *et al.* 1999) and other deserts (Brown & Heske 1990; Meserve *et al.* 1995). After rain, species response to changes in resources (i.e., food and shelter) results in population differences (Dickman *et al.* 1999), however, important biotic factors (i.e., predation and competition) may also contribute significantly to the dynamics of populations (Thompson *et al*. 1991; Heske *et al.* 1994; Meserve *et al.* 1996). On the other hand, the density of fog in the present study may as well contribute significantly to the differences in lizard populations across the arid Namib Desert in Namibia.

Water plays a significant role in many physiological processes (Lorenzo *et al.* 1999). Climate change influence the availability of water and temperature in ectotherms (i.e., lizards; Lourdais *et al.* 2004; Araujo *et al.* 2006). The influence of rainfall on life history traits and population dynamics of reptiles is related to the effects of temperature and other climatic variables (Marquis 2008). There is an increase in evaporation with increasing temperatures, indicating a strong relationship between water balance and thermoregulation in ectotherms (Mautz 1982). In habitats with limited water, rainfall can improve growth, food availability and neonate success through changes in vegetation cover (Dunham 1978; Stamps & Tanaka 1981; Dickman *et al.* 1999). On the other hand, higher amounts of rainfall may negatively influence insolation, thus pressuring thermoregulation and food intake and therefore, reducing lizard activity (Avery 1971). In the bronze anole lizard (*Anolis aenus*), the growth rate of juveniles is related to water availability such that water scarcity contributed to limited growth rate during the dry season (Stamps & Tanaka 1981). Whereas some lizards express lower body temperatures in relation to water shortage therefore, modifying their activity patterns (Huey & Webster 1976; Jones *et al.* 1987).

In a dry environment, such as that of the present study, lizards may experience high risk of dehydration (Lorenzo *et al.* 1999). Lizards could potentially avoid or reduce dehydration through: 1) reducing respiratory water loss by decreasing their activity level (Mautz 1982); 2) spending less time in areas of higher temperatures as it can reduce water loss through the skin (Waldschmidt & Porter 1987); and 3) selecting non-dehydrating conditions through the use of high-humidity microhabitats when inactive (Mautz 1982). Geographic and seasonal variation in temperature affects the foraging of lizards at their preferred body temperature (Grant & Dunham 1988; Adolph & Porter 1993). Activity level is directly related to the amount of time spent at a preferred temperature and the more time spent at such temperature, the most effective and efficient the growth processes (i.e., digestion, metabolism and assimilation; Waldschmidt *et al.*1986; Van Damme *et al.* 1991). Biologically, it is more important to avoid dehydration than lowering the growth rate (Lorenzo *et al.* 1999).

4.5 Conclusion

Availability of water during gestation affects reproductive traits in lizards (Marquis 2008). The temperature experienced during embryonic development influences morphology, behaviour and physiology of neonate reptiles (Shine & Harlow 1993; Massot *et al.* 2002). Fluctuations in temperature significantly changes the phenotype of neonate and the morphology in viviparous snakes (Lourdais *et al.* 2004). Generally, populations of the same species may differ in morphology, physiology and behaviour because of environmental differences (Edwards & Kot 1995). The present study confirms that the fog density and seasonality affects the morphology and thermal biology of the coastal and inland *M. anchietae* and Clade A individuals, both positively and negatively. Thus, we accept the null hypothesis stating that there is variation in morphology and thermal preferences between coastal and inland *M. anchietae* and Clade A individuals because of difference in the amount of fog received between the coastal and inland sites.

As a baseline study on understanding the influence of fog on lizard morphology and thermal biology, considering consequences of future climate change, the comparison of species data from only two sites (coastal and inland) might have constrained the conclusions of this study. Moreover, the species data sites could not be selected on preferred intervals of > 20 km along a fog gradient in the direction of coast to inland because there were no FogNet stations in a close vicinity of the dune environment to better link their recordings of fog to the species data. The present study therefore, suggests further investigations that would require installations of more fog measuring stations along the dunes of the Namib Desert to provide additional data that may allow further insights into lizard responses to variation in fog density because of climate change. This is because the wide distribution of these species across the Namib Desert may allow the species to potentially serve as indicator species for change in climate and thus may result in increasing conservation initiatives of other Namib Desert species.

CHAPTER 5

General discussion

5.1 Introduction

A species' niche is influenced by biotic and abiotic factors, resource use and competition (Elton 1946; Hutchinson 1957), and a competitive interaction among species potentially leads to niche partitioning which can be determined by analysis of ecological niches in sympatric animals (Pianka 1973; Ricklefs 2008; Kartzinel 2015; Parejo & Aviles 2015). Niche partitioning is known to occur in three fundamental dimensions, namely, spatial, temporal and trophic (Schoener 1968; Pianka 1973; Vitt *et al*. 1981; Vitt & Carvalho 1995; Kronfeld-Schor & Dayan 2003; Luiselli 2008). Species may thus differ in the time at which they are active, the space they make use of, and/or the food they eat (Pianka 1973). The differences in such activities may therefore, result in niche separations, reduced competition, and most likely allow co-existence of a variety of species (Hutchinson 1957; MacArthur 1972).

To understand partitioning of resources between sympatric species, knowledge on the ecological variation between these species is required (Hillis & Wiens 2000). Genetic and morphological analyses have been used to understand ecological differences among populations of the same species (Hillis & Wiens 2000). Hence, the aim of the present study was to investigate the seasonal (autumn and spring) ecological niche differences between populations of two sympatric lizard species, the shovel-snouted lizard, *Meroles anchietae* and the wedge-snouted lizard, *M. cuneirostris* from the Namib Desert, Namibia. This was undertaken by comparing of seasonal variation of the three niche dimensions, with specific focus on the significant separation in microhabitat of the populations of the two species. The study also investigated the seasonal effects of fog density on morphology and thermal biology to assess the potential impacts of climate change on the behavioural ecology of the populations of the two species. Sampling during winter was not considered because of low lizard activity while during summer, sampling was not possible due to logistical constraints.

5.1.1 Morphology

The first part of the study (Chapter 2) focused on assessing the genetic and morphological profiles of populations of the two sympatric lacertid lizards, *M. anchietae* and *M. cuneirostris* from the Namib Desert, Namibia, and the associated microhabitat preferences, thermal biology, and daily activity patterns of these lizards. In this chapter, the genetic and seasonal variation in morphology, the partitioning of time (activity) and space (microhabitat) niche dimensions between populations of *M. anchietae* and *M. cuneirostris* were assessed to evaluate the degree of overlap in resource use between the populations of these lizards. Genetic and morphological variation in populations of *M. anchietae* and *M. cuneirostris* across their distributional range are understudied. However, populations of *M. anchietae* are known to vary genetically and morphologically between individuals from the northern and southern parts of the Namib Desert (Griffin 2003; Lamb & Bauer 2003), but due to logistical constraints, the northern Namib populations could not be sequenced, and the population will form part of further studies on this group of lizards.

In this study, the central Namib Desert populations of *M. anchietae* were genetically similar across their distributional range. A similar pattern was reported between populations of the Mongolia racerunner, *Eremias argus* and the Ordos racerunner, *E. brenchleyi* from China, which showed similar genetic patterns across their distributional range (Zhao *et al.* 2011). The findings of the present study indicate that populations of *M. anchietae* occurred across similar geographical ranges, thus exhibiting less geographically structured genetic diversity. Differently for *M. anchietae*, the present study recovered two clades for populations of *M. cuneirostris* (designated Clades A and B), indicating genetic differences between the central and southern Namib Desert populations that are geographically separated by *ca.* 800 km. These findings are consistent with observations by Garcia-Rosales *et al.* (2017) on population differences in the Minor lizard, *Sceloporus minor* from central Mexico as a result of geographic separation. The climate and vegetation of geographically separated populations may differ, suggesting differences in season and abundance of resources, thus generating different genetic and morphological regimes in these populations (Ferguson & Brockman 1980; Smith & Ballinger 1994; Hewitt 1996, 1999, 2000, 2004; Avise 2000).

Genetic variation in populations of the same species potentially contributes to speciation and eco-geographical trends (i.e., variation in body size) of an organism across longitude and latitude (Meiri & Dayan 2003; Pincheira-Donoso *et al*. 2008). Edwards & Kot (1995) also stated that variation in environmental conditions between similar populations influences the differences in morphology, physiology and behaviour of these populations. Similarly, the present study revealed morphological differences in body mass and length between Clades A and B of *M. cuneirostris* (from the central and southern Namib Desert, Namibia, respectively). Clade A of *M. cuneirostris* was 54% heavier and 12% longer than Clade B of *M. cuneirostris*, further supporting the genetic variation between the two clades. Genetic similarities in populations of *M. anchietae* are also supported by similar body masses and lengths. Traditionally, reptile taxonomy has largely used morphology to describe new taxa (Smith & Taylor 1966) and has more recently been augmented by DNA sequencing (Hillis & Wiens 2000; Marshall *et al.* 2006). Although the genetic identity and morphological profiles of the two-lizard species was confirmed, the findings in the present study suggest further investigations of genetic variation, particularly in *M. cuneirostris* from the southern-most areas of its geographical range, is needed to determine the systematic and taxonomic status of these clades. Thus, the null hypothesis that there are genetic and morphological differences linked to variation in environmental factors and activity patterns among populations of *M. cuneirostris* is accepted, while the null hypothesis that there are genetic and morphological differences linked to environmental factors among populations of *M. anchietae* from the Namib Desert, Namibia, is rejected.

Colouration in animals serves multiple functions such as thermoregulation, camouflage and social signalling (Smith *et al.* 2016). In ectotherms, exposure to direct sunlight is required to reach and maintain the active body temperatures necessary for essential daily routine functions including feeding, finding mating partners, and escaping from predators (Dunham *et al.* 1989; Seebacher & Franklin 2005), yet by exposure to direct sunlight in open spaces simultaneously increases exposure to predators and thus camouflage is used as a compromise (Endler 1978). Populations of the same species may exhibit intraspecific variation in camouflage because of genetic adaptation to different local environments (Rosenblum *et al.* 2004; Marshall *et al.* 2006; Rosenblum 2005; Hoekstra *et al.* 2006; McLean *et al.* 2014). The external assessment of morphology in the present study showed Clade B of *M. cuneirostris* to possess a more solid reddish colour pattern associated with dark red coloured dunes of the southern Namib Desert and

Clade A of *M. cuneirostris* possessing a lighter red colour pattern associated with the central Namib Desert dunes. These findings are supported by Branch (1998) who reported that the colouration of *M. cuneirostris* matches sand colour. On the other hand, populations of *M. anchietae* indicated similar colouration, corresponding with dune sand colour in their habitat.

Despite Clades A and B of *M. cuneirostris* sharing a similar habitat, namely the sand dunes of the Namib Desert, the two clades also shared similar microhabitat, the base of the dune which is covered with vegetation (i.e., vegetated dune base). The microhabitats of the two populations comprised of similar vegetation cover namely the !nara plant (*Acanthosicyos horridus*), the spiny love grass/Ostrich grass (*Cladoraphis spinosa*), and the saltwort (*Salsola sp.*). Similar to what has been observed in other studies, the base of the central Namib dunes was also covered by perennial plants such as the dune succulent (*Trianthema hereroensis*), the dune Bushman's grass (*Stipagrostis sabulicola*), the box-thorn/desert-thorn, (*Lycium cinereium*), and the salt cedar (*Tamarix aphylla*) (Robinson & Cunningham 1978; Murray & Schramm 1987; Childers & Eifler 2015), whereas the base of the southern Namib dunes was also covered by the baboon food/pickle bush (*Augea capensis*).

Among other factors, habitat preference also affects genetic diversity between populations (Bohonak 1999) and use of different microhabitats by sympatric species facilitates co-existence (Zhao 1999). The present study revealed that Clades A and B of *M. cuneirostris* preferred the similarly vegetated dune base microhabitats, which differed from the slipface as a preferred microhabitat for *M. anchietae*. These findings indicate that *M. anchietae* and *M. cuneirostris* (inclusive of its associated clades) co-exist because of inhabiting different areas. Thus, we accept the null hypothesis stating that there is a significant contribution of space niche dimension to the microhabitat separation of the populations of *M. anchietae* and *M. cuneirostris* (and its associated clades). This is supported by previous observations by Goldberg & Robinson (1979) and Murray & Schramm (1987) who suggested that the slipface and vegetated dune base microhabitats of *M. anchietae* and *M. cuneirostris*, respectively, differ.

Lizard activity can be influenced by the type of foraging, with active foragers being active for fewer hours of the day compared to sit-and-wait foragers (Anderson & Karasov 1981; Huey & Pianka 1981; Murray *et al*. 2016). The present study revealed that *M. cuneirostris* (and its associated clades) employed both active and ambush foraging tactics (Murray & Schramm

1987); Childers & Eifler 2015) compared to *M. anchietae* which is a sit-and-wait predator with less active foraging patterns. Distinctively, these findings indicate that *M. cuneirostris* is active for longer hours daily as it can shift between active and ambush foraging tactics compared to *M. anchietae*. Being active for more hours may explain the extreme exposure to prevailing weather conditions of *M. cuneirostris* (and its associated clades) that were active at 6° C higher substrate temperature than *M. anchietae*. In addition, Clade A of *M. cuneirostris* was active at substrate temperature 11° C higher than that of Clade B of *M. cuneirostris*, indicating that the two populations behaviourally thermoregulate differently to meet their preferred body temperatures necessary for essential daily functions.

Competition between sympatric lizard species can be reduced through temporal division of activities (Pianka 1973). Division of activities between diurnal and nocturnal lizards, which are completely non-overlapping in time, is the most noticeable temporal separation (Pianka 1973). Influence of climate variation suggests changes in daily and seasonal activity. The present study revealed that *M. anchietae* and *M. cuneirostris* (and its associated clades) are diurnal species, which are active at the same time of the day. They also expressed a bimodal activity pattern with a decrease in activity around solar noon, a pattern similar to that of desert lizards during hot times of the year (Grant 1990; Seely *et al.* 1990; Adolph & Porter 1993). Thus, we reject the null hypothesis stating that there is no significant contribution of time niche dimension to the separation of the populations of *M. anchietae* and *M. cuneirostris* (and its associated clades) in their microhabitat.

5.1.2 Diet

The second part of the study (Chapter 3) investigated seasonal variation in diet between *M. anchietae* and *M. cuneirostris* (and its associated clades; see Chapter 2) through stable isotope and faecal analyses. The comparison between the diet of *M. anchietae* and *M. cuneirostris* based on stomach content analyses has previously been extensively studied (Robinson & Cunningham 1978; Murray & Schramm1987; Robinson 1987; Nagy & Shemanski 2009). The present study demonstrated that both species have an omnivorous diet, feeding on plant matter and arthropods, which was supported by Murray & Schramm (1987) and Robinson (1987). The study by Robinson & Cunningham (1978) indicated *M. cuneirostris* to be strictly insectivorous and observed little plant material during stomach content analysis, which could have been consumed unintentionally during the capturing of arthropod prey. The differences observed in the diet in the present study and that by Robinson & Cunningham (1978) may be due to the lack of documentation of the direct observation of *M. cuneirostris* feeding on plant matter. The analyses of faecal pellets in the present study however, indicated the presence of plant matter in the diet of *M. cuneirostris*.

The ability of a species to specialize or generalize its diet enables partitioning of its food niche (Futuyma & Moreno 1988). Even with a similar omnivorous diet between *M. anchietae* and *M. cuneirostris*, the two species differed in their major diet constituents. *Meroles anchietae* preyed more on plant matter compared to *M. cuneirostris* (and its associated clades) that preyed more on arthropods. A previous study indicated that *M. anchietae* employs an opportunistic foraging tactic when the abundance of insects is low with seeds still representing the major component of its diet, yet indiscriminately preying on arthropods when frequently available (Robinson 1987). The opportunistic feeding strategy in *M. anchietae* may be related to the scarcity of resources associated with desert ecosystems.

Trophic niche enables species on different diets to co-exist and thus influences the diversity of species (Simberloff & Dayan 1991; Murray *et al*. 2016). In order to gain insights into diet diversity in *M. anchietae* and *M. cuneirostris* (and its associated clades), the present study reported on trophic niche space and levels at which the species are feeding as well as the dietary niche breadth, niche overlap, and diet evenness. The mode of foraging is known to influence the food niche such that actively foraging species often tend to have a broader food niches than sit-and-wait species (Pianka 1973).

The present study revealed that both clades of *M. cuneirostris* occupy similar isotopic niches and δ^{13}C and δ^{15}N ratios, indicating that the two are feeding at the same trophic level, different from that of *M. anchietae*. The present study, however, also recovered a larger total area of the convex hull (TA) for Clade A of *M. cuneirostris* as a widely foraging species, indicating more niche space occupancy compared to a similarly active foraging Clade B of *M. cuneirostris*, and the sit-and-wait forager, *M. anchietae*. These findings are similar to studies by Pianka (1986) and Vitt *et al*. (2003) who reported that active foraging lizard species are likely to have larger territories than sit-and-wait species and move greater distances through diverse habitats. In addition to a wider isotopic niche for Clade A of *M. cuneirostris*, the present study also revealed a higher trophic diversity among these individuals compared to Clade B of *M. cuneirostris* and *M. anchietae*. These findings suggest that when lizards forage across wide niche spaces, they encounter a wider range of prey items to feed on compared to other species of narrow niche spaces that may feed on one type of diet. This is supported by previous observations by Liu *et al.* (2013) who showed that foraging distance is positively related to habitat heterogeneity, thus the greater the heterogeneity (i.e., arthropod diversity), the larger the foraging distance (Murray *et al.* 2016). With predicted changing environments because of climate change, species with a low trophic diversity may be at a high risk of reduced food sources, with possible reduction of populations and a risk of extinction. On the other hand, species with higher trophic diversity have the ability to focus their diet on several prey items to ensure survival.

Meroles anchietae and Clade A of *M. cuneirostris* preferred different microhabitats (slipface and vegetated dune base, respectively), however, their diet overlapped by 56%, indicating that the two species are feeding on the same prey items in different microhabitats. Feeding on similar prey in different locations means the prey consumed by the two species is available in both microhabitats. Results from dietary niche breadth indicated that Clade A of *M. cuneirostris* (niche breadth = 4.52) had a greater diversity of prey types consumed compared to *M. anchietae* (niche breadth =2.27), as also supported by the larger Total Area of the convex hull (TA) in Clade A of *M. cuneirostris*, indicating a larger niche occupancy for actively foraging species. Clade A of *M. cuneirostris* (0.25) also indicated a greater diet evenness of each prey type than *M. anchietae* (0.13), suggesting a uniform distribution of prey items for each prey type. Thus, we reject the null hypothesis stating that there is no significant seasonal difference in food niche dimension to the separation of the populations of *M. anchietae* and *M. cuneirostris* (and its associated clades) in their microhabitat.

Lizards are known to be selective feeders, and do not necessarily feed on prey that is frequently available (Pianka 1986; Vitt *et al.* 2003). Microhabitat selection in desert lizards may be based on the availability of preferred prey in that particular microhabitat (Vitt & Pianka 2007). In the present study, prey availability per microhabitat was not estimated and thus evaluations of prey availability where *M. anchietae* and Clade A of *M. cuneirostris* foraged could not be undertaken. It is evident; however, that the two species in this study did not choose their microhabitats based on preferred prey availability because the same prey items were available in both microhabitats. Similar to what has been observed in other studies, *M. anchietae* prefers habitats with loose deep sand on the inclined dune steep slipface, and on rare occasions may venture into the nearby dune bases (Louw & Holm 1972; Robinson & Seely 1980; Robinson & Barrows 2013), and Clade A of *M. cuneirostris* prefers to sprints between tufts of vegetation on sand hummocks and has also been observed sun basking on the dune slipface on cold sunny periods (Robinson & Cunningham 1978; Murray & Schramm 1987; Branch 1998; Childers & Eifler 2015). Microhabitat selection of *M. anchietae* and Clade A of *M. cuneirostris* could be due to sand-diving morphological adaptations to burrow and move across sand. These include: 1) long toes with scales on the hands to increase traction on loose sand; 2) a wedge-shaped head for easy penetration of the sand; 3) closure valves on nasal openings to block sand: 4) large eyelids to prevent damage to the cornea and reduced size of the scales on the body; and 5) reduced femoral pores (Stebbins 1944, 1948; Norris 1958; Luke 1986; Arnold 1995; Robinson & Barrows 2013).

5.1.3 Fog

The third part of the study (Chapter 4) investigated seasonal influence of fog density on the morphology and thermal biology of coastal and inland populations of *M. anchietae* and *M. cuneirostris* (and its associated Clade A; see Chapter 2). Potential responses of biodiversity to changing climate has been widely studied (Dillon *et al*. 2010; Pereira *et al*. 2010; Beaumont *et al*. 2011; McMahon *et al*. 2011; Palmer & Di Falco 2012) to gain insights into impacts on their survival (Bellard *et al*. 2012), and contribute in reducing potential impacts of climate change (Pereira *et al*. 2010; Parmesan *et al*. 2011; Bellard *et al*. 2012).

As a result of increasing surface temperatures in Africa (Boko *et al.* 2007; Niang *et al.* 2014; Engelbrecht *et al.* 2015), the cold Benguela Current responsible for most of the weather patterns along the coastal west of the Namib Desert in Namibia is experiencing an increase in temperature (Belkin 2009; Haensler *et al.* 2011a, b). Warming of the Benguela Current may result is less production of fog precipitation which acts as the major source of moisture for desert organisms (Schulze 1969; Seely & Stuart 1976; Seely 1979; Lancaster *et al.* 1984; Seely *et al.*

1998; Haensler *et al.* 2011a). Due to scarcity of water, like any other desert (Nagy 2004), the Namib Desert may face stressful events that may contribute to changes in the feeding ecology, and physiological, and behavioural adaptations of species (MacArthur 1972; Hoffman & Parsons 1997; Parmesan 2006) to ensure species survival and reproduction.

In the central Namib Desert, fog precipitation has been well monitored since the 1960s, and in 2014, a sophisticated FogNet project was initiated to investigate the influence of changing climate on the predicted reduction of fog of the Namib Desert coast due to the warming Benguela Current. In this chapter, with reference to distance from the coast, fog precipitation was compared between coastal and inland fog-monitored sites (located 15 km and 63 km from the coast, respectively) to gain insights into the variation in fog density. Similar to what has been observed in other studies, the present study indicated that the coastal fog-monitored site received twice the amount of fog and number of fog events (days) compared to the inland fog-monitored site (Lancaster *et al.* 1984; Hachfeld 2000; Hachfeld & Juergens 2000; Haensler *et al.* 2011a). In addition, the study showed that the average amount of fog received per day on any given fog event did not differ between coastal and inland fog-monitored sites, indicating that the more fog events, the greater the fog density per fog-monitored site. Generally, these findings suggest that the number of fog events may serve as one of the major contributing factors to the differences in fog density across the two fog-monitored sites.

Species are known to respond to challenges of climate change by shifting their climatic niches in space (i.e., range, shifting to different microhabitats; Parmesan 2006; Visser 2008), time (i.e., phenology, shifting daily and seasonal activities such as change in life cycle events of reproduction; Root *et al.* 2003; Parmesan 2006; Charmantier *et al.* 2008), and physiology (i.e., by adapting to new climatic conditions rather than tracking their preferred optimal conditions; Johansen & Jones 2011; Bellard *et al.* 2012). In the present study, the comparison of the influence of fog density on lizard behavioural ecology was made with reference to distance from the coast that included coastal and inland species sampling sites located 9 km, 15 km, 60 km and 63 km from the coast. Species sampling sites were further classified into coastal and inland sites representing the species population's closer inland and those further inland, respectively. As the first study to report on variation in morphology, microhabitat and thermal preferences, and activity pattern in relation to fog density between coastal and inland *M. anchietae* and Clade A of

M. cuneirostris, the present study revealed both positive and negative correlations. These correlations suggest that when fog density increases so do morphological dimensions, thermal biology, and the duration of daily activity time) and *vice-versa*.

The present study indicated that the body length and air temperature at sampling locations of coastal *M. anchietae* were lower with more fog received, indicating a positive correlation with fog precipitation. Furthermore, the body and air temperatures at sampling localities of coastal Clade A of *M. cuneirostris* were also lower with more fog received, indicating a positive correlation with fog precipitation. The present study also showed that with more fog received during spring compared to autumn, the lower the body temperature and air temperature at sampling localities. In addition, the air temperature at sampling localities of coastal and inland Clade A of *M. cuneirostris* decreased during spring, indicating a negative correlation with fog precipitation. Thus, the null hypothesis that the seasonal density of fog influences the morphology and thermal biology of the populations of *M. anchietae* and *M. cuneirostris* from the Namib Desert, Namibia, is accepted.

Variation in the times at which species are active, the space they use, and/or the food they consume (Pianka 1973) results in niche separation, reducing competition, and most likely allow the co-existence of a range of species (Hutchinson 1957; MacArthur 1972). *Meroles anchietae* and *M. cuneirostris* (and its associated clades) were active at the same time of the day, used different microhabitats, and fed on similar plant and arthropod resources. The difference in the microhabitat use between them may have allowed them to co-exist; however, an overlap in resource use (i.e., the time of activity and food consumed) may have resulted in competition between them. Thus, the null hypothesis that there are resource use overlap between the populations of *M. anchietae* and *M. cuneirostris* from the Namib Desert, Namibia, is accepted.

The results of the present study highlight the significance of understanding how changes in the environment (e.g., desert ecosystems) may affect the morphology, behaviour, microhabitat and thermal biology of lizard species considering the consequences of future climate change. More knowledge on temporal, spatial and trophic ecology, with reference to climate change in Namib Desert lizard species, may be useful for allowing insights into climatic food web dynamics for the conservation and monitoring of biodiversity. The ability of diverse lizard species to occupy the same area includes sharing of the food niche as well as differences in space and time at which the lizard species are active (Pianka 1973; Barbault & Maury 1981).

5.2 Conclusions

The present study demonstrates that the southern populations of *M. cuneirostris* differ genetically and morphologically from the northern population. Clade A of *M. cuneirostris* (from the central Namib Desert, Namibia) had longer body length and heavier mass than Clade B of *M. cuneirostris* (from the southern Namib Desert, Namibia). These results further confirm that the two clades use similar microhabitats, forage on similar diet, and have similar activity patterns. Because of the differences in the distributional range of the two sympatric lizard species, *M. anchietae* and *M. cuneirostris* across the Namib Desert, conclusions on niche partitioning considered the central Namib Desert populations of *M. cuneirostris* (Clade A) that overlapped in the distributional range with *M. anchietae*. In addition, it appears that partitioning of the space niche plays a significant role in the niche separation of *M. anchietae* and *M. cuneirostris* (and its associated clades). The sympatric lacertid lizards from the Namib Desert use different microhabitats, forage on similar plant and arthropod resources, and have similar activity patterns with distinct thermoregulations. *Meroles anchietae* predominantly forages across the slipface and *M. cuneirostris* prefers the vegetated dune base. These lizards prey on plants and arthropods, and forage during the day (Chapter 2). *Meroles cuneirostris* was active at higher substrate and air temperatures compared to *M. anchietae* (Chapter 2). These sympatric lizards are able to co-exist by not occurring in the same ecological space (Chapter 2).

5.3 Recommendations

Given the above, the present study recommends that:

1. Home range studies be undertaken in order to gain better insights into the activity patterns of *M. anchietae* and *M. cuneirostris* (and its associated clades) as sympatric taxa;
2. There is a critical need for future studies on impacts of dune direction (slipface) in relation to sunshine for the microhabitat preferences of *M. anchietae* and *M. cuneirostris* (and its associated clades);

3. There is a need for a more comprehensive study on impacts of fog on *M. anchietae* and *M. cuneirostris* (and its associated clades) as indicator species for changing climate in the Namib Desert;
4. There is a critical need for studies to define the genetic structure of populations of *M. anchietae* and *M. cuneirostris* (and their associated clades) across their entire distributional range in the Namib Desert in Namibia, extreme north-west Western Cape Province in South Africa, and the extreme southern tip of Angola; and
5. There is a critical need for the conservation of *M. anchietae* and *M. cuneirostris* (and their associated clades), and other Namib Desert species because of extreme environments associated with changing climates, particularly given the potential of the presence of undefined taxa within this hyper arid ecosystem.

5.4 References

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APPENDICES

Appendix 1: Animal ethics permit issued by Animal Ethics Committee of the University of Pretoria, South Africa.

UNIVERSITEIT VAN PRETORIA
UNIVERSITY OF PRETORIA
YUNIBESITHI YA PRETORIA

Animal Ethics Committee

PROJECT TITLE	**Ecological niche partitioning of the two sympatric lacertid lizard species in the Namib Desert, Namibia**
PROJECT NUMBER	**EC036-16**
RESEARCHER/PRINCIPAL INVESTIGATOR	**NK Liyambo**

STUDENT NUMBER (where applicable)	**UP_16284225**
DISSERTATION/THESIS SUBMITTED FOR	**MSc (Zoology)**

ANIMAL SPECIES	***Meroles anchietae***	***Meroles cuneirostris***
NUMBER OF ANIMALS	**150/ season**	**150/ season**
Approval period to use animals for research/testing purposes		**May 2016 –May 2017**
SUPERVISOR	**Prof. CT Chimimba**	

KINDLY NOTE:

Should there be a change in the species or number of animal/s required, or the experimental procedure/s - please submit an amendment form to the UP Animal Ethics Committee for approval before commencing with the experiment

APPROVED	Date 14 June 2016
CHAIRMAN: UP Animal Ethics Committee	Signature

Appendix 2: Animal ethics permit extension no.1 issued by Animal Ethics Committee of the University of Pretoria, South Africa.

UNIVERSITEIT VAN PRETORIA
UNIVERSITY OF PRETORIA
YUNIBESITHI YA PRETORIA

Animal Ethics Committee

Extension No. 1

PROJECT TITLE	**Ecological niche partitioning of the two sympatric lacertid lizard species in the Namib Desert, Namibia**
PROJECT NUMBER	**EC036-16**
RESEARCHER/PRINCIPAL INVESTIGATOR	**NK Liyambo**

STUDENT NUMBER (where applicable)	**UP_16284225**
DISSERTATION/THESIS SUBMITTED FOR	**MSc (Zoology)**

ANIMAL SPECIES	***Meroles anchietae***	***Meroles cuneirostris***
NUMBER OF ANIMALS	**150/ season**	**150/ season**
Approval period to use animals for research/testing purposes		**January 2017-January 2018**
SUPERVISOR	**Prof. CT Chimimba**	

KINDLY NOTE:

Should there be a change in the species or number of animal/s required, or the experimental procedure/s - please submit an amendment form to the UP Animal Ethics Committee for approval before commencing with the experiment

APPROVED	Date 15 March 2017
CHAIRMAN: UP Animal Ethics Committee	Signature

S4285-15

Appendix 3: Research permit issued by Ministry of Environment and Tourism, Namibia.

MINISTRY OF ENVIRONMENT AND TOURISM

RESEARCH/COLLECTING PERMIT

Permit Number 2171/2016
Valid from 28 June 2016 to 31 May 2017

Permission is hereby granted in terms of the Nature Conservation Ordinance 1975 (Ord. 4 of 1975) to:

Name: **Ms N.K. Iiyambo**
Address: **University of Pretoria**
Department of Zoology and Entomology
Pretoria
South Africa
Coworkers: **Prof. C. Chimimba, Dr. J.L. de Cries, R. Gottlieb and S. Iiyambo**

Sympatric lacertid lizard species, *Meroles anchietae* and *Meroles cuneirostris* in the Namib Desert, Namibia: Ecological niche partitioning, home-range overlap-competition for resources at Namib Naukluft NP, Gobabeb dunes, Tsau//khaeb (Sperrgebiet) NP and Skeleton Coast NP, subject to attached conditions.

IMPORTANT: This permit is not valid if altered in any way.

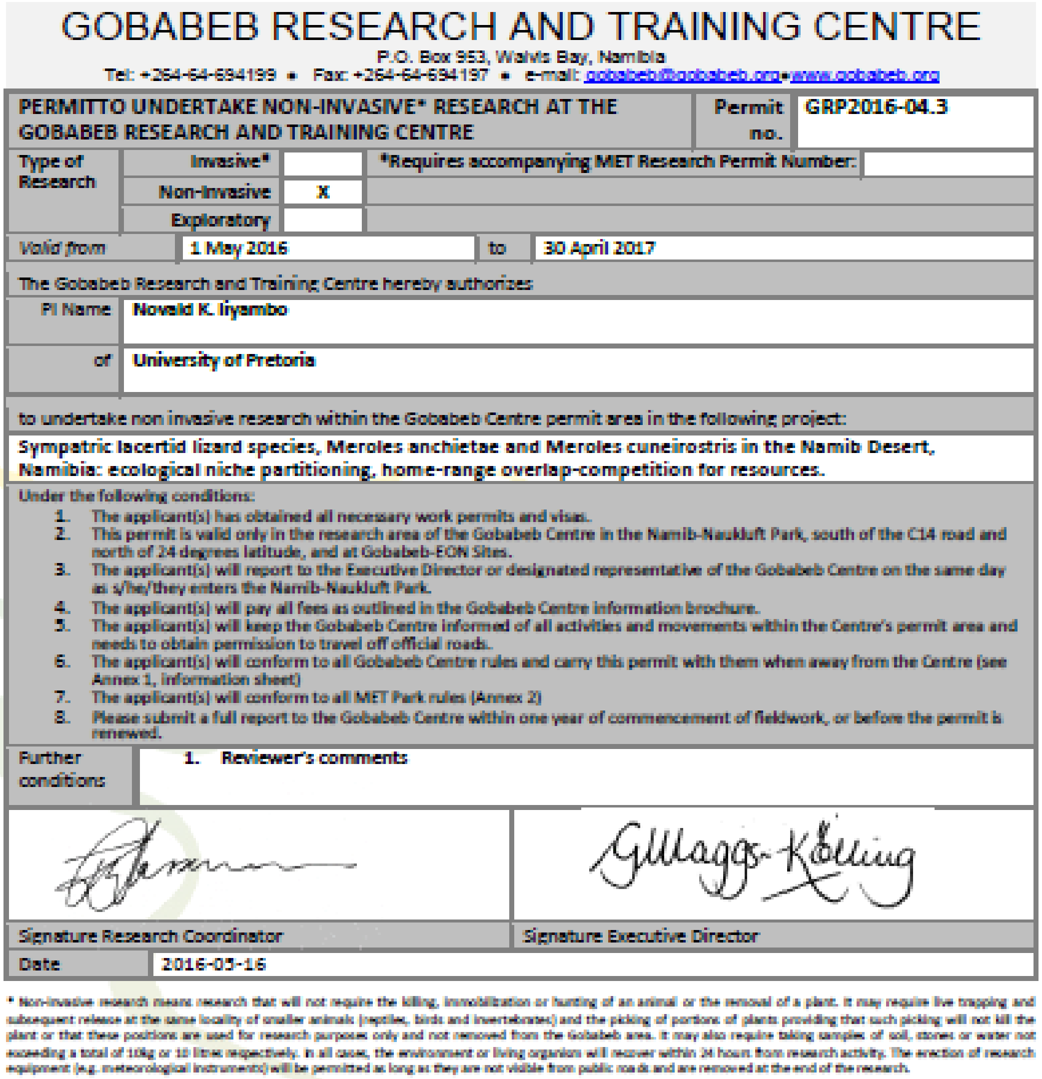
MINISTRY OF ENV
AND TOUR
REPUBLIC OF
10 OCT 2016
WINDHOEK
Private Bag 13304, W
Tel: 2842111 • Fax: 25

Authorising Officer

IMPORTANT
This permit is subject to the provisions of the Nature Conservation Ordinance, 1975 (Ordinance 4 of 1975) and the regulations promulgated thereunder, and the holder is subject to all such conditions and regulations.

Enquiries: Conservation Scientist, email ita.matheus@met.gov.na
Private Bag 13306, Windhoek, Namibia

Appendix 4: Research permit issued by Gobabeb Research and Training Centre, Namibia.



GOBABEB RESEARCH AND TRAINING CENTRE

P.O. Box 953, Walvis Bay, Namibia
Tel: +264-64-694199 • Fax: +264-64-694197 • e-mail: gobabeb@gobabeb.org • www.gobabeb.org

PERMITTO UNDERTAKE NON-INVASIVE* RESEARCH AT THE GOBABEB RESEARCH AND TRAINING CENTRE			**Permit no.**	**GRP2016-04.3**
Type of Research	**Invasive***		***Requires accompanying MET Research Permit Number:**	
	Non-Invasive	**X**		
	Exploratory			
Valid from	1 May 2016	to	30 April 2017	

The Gobabeb Research and Training Centre hereby authorizes

PI Name	**Noveld K. Iiyambo**
of	**University of Pretoria**

to undertake non invasive research within the Gobabeb Centre permit area in the following project:

Sympatric lacertid lizard species, Meroles anchietae and Meroles cuneirostris in the Namib Desert, Namibia: ecological niche partitioning, home-range overlap-competition for resources.

Under the following conditions:

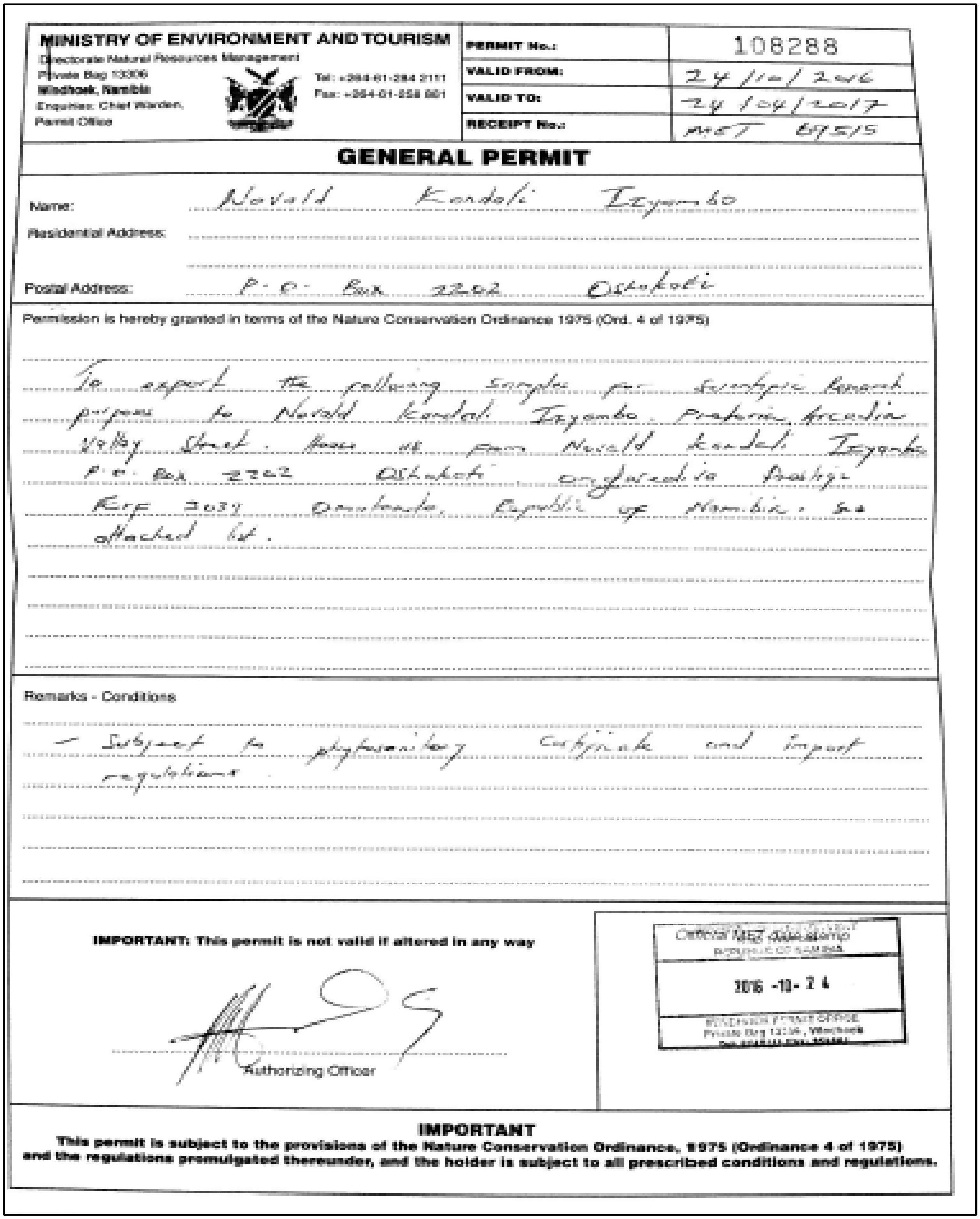
1. The applicant(s) has obtained all necessary work permits and visas.
2. This permit is valid only in the research area of the Gobabeb Centre in the Namib-Naukluft Park, south of the C14 road and north of 24 degrees latitude, and at Gobabeb-EON Sites.
3. The applicant(s) will report to the Executive Director or designated representative of the Gobabeb Centre on the same day as s/he/they enters the Namib-Naukluft Park.
4. The applicant(s) will pay all fees as outlined in the Gobabeb Centre information brochure.
5. The applicant(s) will keep the Gobabeb Centre informed of all activities and movements within the Centre's permit area and needs to obtain permission to travel off official roads.
6. The applicant(s) will conform to all Gobabeb Centre rules and carry this permit with them when away from the Centre (see Annex 1, information sheet)
7. The applicant(s) will conform to all MET Park rules (Annex 2)
8. Please submit a full report to the Gobabeb Centre within one year of commencement of fieldwork, or before the permit is renewed.

Further conditions	1. Reviewer's comments

	GMaggs-Kölling
Signature Research Coordinator	Signature Executive Director
Date	2016-05-16

* Non-invasive research means research that will not require the killing, immobilisation or hunting of an animal or the removal of a plant. It may require live trapping and subsequent release at the same locality of smaller animals (reptiles, birds and invertebrates) and the picking of portions of plants providing that such picking will not kill the plant or that these portions are used for research purposes only and not removed from the Gobabeb area. It may also require taking samples of soil, stones or water not exceeding a total of 10kg or 10 litres respectively. In all cases, the environment or living organism will recover within 24 hours from research activity. The erection of research equipment (e.g. meteorological instruments) will be permitted as long as they are not visible from public roads and are removed at the end of the research.

Appendix 5: Export permit issued by Ministry of Environment and Tourism, Namibia.



MINISTRY OF ENVIRONMENT AND TOURISM
Directorate Natural Resources Management
Private Bag 13306
Windhoek, Namibia
Enquiries: Chief Warden,
Permit Office
Tel: +264-61-284 2111
Fax: +264-61-258 861

PERMIT No.:	108288
VALID FROM:	24/10/2016
VALID TO:	24/04/2017
RECEIPT No.:	MET 69515

GENERAL PERMIT

Name: Novald Kondali Izyambo

Residential Address:

Postal Address: P.O. Box 2202 Oshakati

Permission is hereby granted in terms of the Nature Conservation Ordinance 1975 (Ord. 4 of 1975)

To export the following samples for scientific Research purposes to Novald Kondali Izyambo, Pretoria, Arcadia Valley Street. [illegible] [illegible] from Novald Kondali Izyambo P.O. Box 2202 Oshakati, Ongwediva [illegible] Erf 3039 [illegible], Republic of Namibia. See attached list.

Remarks - Conditions

- Subject to phytosanitary certificate and import regulations.

IMPORTANT: This permit is not valid if altered in any way

Authorizing Officer

Official MET date stamp
REPUBLIC OF NAMIBIA
2016 -10- 24
WINDHOEK PERMIT OFFICE
Private Bag 13306, Windhoek

IMPORTANT
This permit is subject to the provisions of the Nature Conservation Ordinance, 1975 (Ordinance 4 of 1975) and the regulations promulgated thereunder, and the holder is subject to all prescribed conditions and regulations.

Appendix 6: Import permit issued by Department of Agriculture, Forestry & Fisheries, South Africa.

agriculture,
forestry & fisheries

Department:
Agriculture, Forestry and Fisheries
REPUBLIC OF SOUTH AFRICA

Page 1

Directorate Plant Health

Permit No. P0080298

PERMIT FOR THE IMPORTATION OF CONTROLLED GOODS

In terms of the provisions of section 3(1) of the Agricultural Pests Act, 1983 (Act 36 of 1983) and subject to the conditions stated here under, authorisation is hereby granted to-

NOVALD KANDALI LIYAMBO **Tel No:**

P.O. BOX 2202
OSHAKATI
NAMIBIA

to import into the Republic the following controlled goods **ORGANISMS FOR RESEARCH**

ORGANISMS AS PER ATTACHED **2000** **GRAM (S)**

Name and address of foreign supplier **NAMIBIA**

Conditions **1. AS ATTACHED**

Port of Entry : **O R TAMBO INTERNATIONAL AIRPORT**

Import authorized from **2016/12/02** TO **2017/12/02**

IMPORTANT : This permit does not exempt the holder from the provisions of any other Act, ordinance or agreement

DEPARTMENT OF AGRICULTURE
FORESTRY AND FISHERIES
DIRECTORATE PLANT HEALTH
2016 -12- 05
DIRECTORATE PLANT HEALTH
P.O. BOX 40024, ARCADIA, 0007

Date

Executive Officer

Reference Number **9/16/280**

INQUIRIES : TEL.: (012)319 6102 (Solomon Matsa) **FAX: (012)319 6370**