The Relationship between Niche Breadth and Geographic Range Size in African Horseshoe Bats (Rhinolophidae, Chiroptera)

A thesis presented by

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ABSTRACT

There is tremendous variation in the geographic range sizes of individual species. The cause(s) of this variation is a fundamental question in ecology and a large number of factors have been proposed to explain it. Niche breadth is one of the more commonly cited determinants of a species' range. According to Brown's hypothesis, generalists have high niche breadth and can tolerate a wide variety of environmental conditions resulting in large geographic range sizes. Conversely, specialists have low niche breadth and small range sizes. I tested this hypothesis using African Horseshoe bats to determine if differences in niche breadth can explain variation in geographic range size. I predicted that rhinolophid species with a wide niche breadth would be widely distributed and rhinolophid species with low niche breadth would be narrowly distributed i.e. there should be a positive relationship between niche breadth and geographic range size. I characterised niches for 12 species of Horseshoe bat using biological and environmental variables and, using diversity indices and the Ecological Niche Factor Analysis (ENFA), quantified niche breadth. Niche breadth was then correlated with geographic range size using a polynomial regression. I found that African rhinolophids tend to have low niche breadth overall selecting marginal habitats and showing restricted niches in terms of climate, topography and vegetation. Most species also show low diversity regarding microhabitat use, diet and roost use. Niche breadth measured using environmental variables correlated with geographic range size in African Horseshoe bats supporting Brown's hypothesis. With the exception of diversity in roost use, which was positively correlated with range size, biological variables did not explain variation in geographic range size. My results suggest that variation in geographic range size in African rhinolophids is influenced by niche breadth and niche position (i.e. resource availability) with respect to environmental variables and roosts. This is the first study to test Brown's hypothesis using bats and it adds to the diversity of taxa for which positive relationships have previously been found suggesting some generality to Brown's idea.

AUTHORS DECLARATION

I know the meaning of plagiarism. The work contained in this thesis, save for that which is properly acknowledged, is the result of my own research. No part has been submitted to any other university in fulfilment of a degree or diploma. The University of Cape Town is encouraged to reproduce for the purpose of research any portion of the contents of this thesis.

Jonathan Aronson

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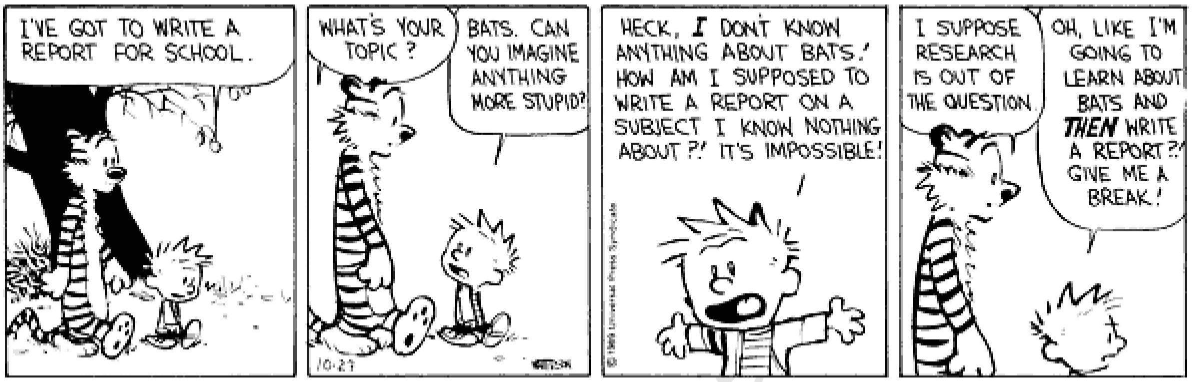


“Calvin and Hobbes”, by Bill Watterson, *The Indispensable Calvin and Hobbes*, 1992

INTRODUCTION

A fundamental question in ecology is why some species have larger geographic range sizes than others (Lester et al. 2007). There is tremendous variation in the sizes of the geographic range of individual species, even among closely related taxa (Brown et al. 1996). For example, the barn owl *Tyto alba* is regarded as the most widely distributed terrestrial bird, occurring on all major land masses and on many islands. In contrast, some species are confined to habitat patches with a very limited spatial extent such as the Soccoro Isopod *Thermosphaeroma thermophilum* which is confined to a single freshwater spring (Brown et al. 1996; Lester et al. 2007). The frequency distribution of geographic range sizes among species in a clade or taxonomic group has a distinctive shape (Brown et al. 1996; Gaston 1996). Most species have small to medium-sized geographic ranges while a few have large geographic range sizes which results in a right-skewed frequency distribution. This pattern has been observed in many taxa including seaweeds, freshwater fish, birds and mammals (Brown et al. 1996; Gaston 2003). Understanding the reason(s) for variation in geographic range size of species is important because this variation drives large-scale spatial patterns of biodiversity such as the latitudinal gradient in species richness and patterns of biodiversity hotspots (Gaston 1998). The size of a species geographic range is also a proxy for the probability of extinction (Bohning-Gaese et al. 2006; Jones et al. 2003) and plays a key role in the prioritization of species for conservation effort. For example, approximately 47% of the species on the IUCN Red List of Threatened Species™ are listed on the basis of geographic range size criteria (Gaston and Fuller 2009). Understanding the factors that determine geographic range size is also important in aiding predictions of how species may respond to global climate change (Calosi et al. 2008).

Answering the fundamental question of what determines the geographic range size of a species is difficult because it can be determined by a large number of ecological and evolutionary factors (Bohning-Gaese et al. 2006; Calosi et al. 2010). These factors include current species-specific traits (body size, niche breadth or environmental tolerance, habitat selection, abundance and dispersal ability), historic species-specific traits (phylogenetic age of the lineage) or environment-related biogeographic factors such as latitude (Bohning-

Gaese et al. 2006; Brown 1984; Gaston 2003; Kunin and Gaston 1997; Lester et al. 2007; Pyron 1999). Attempts have therefore concentrated on searching for biological correlates of range size to discover causal explanations for patterns in geographic range size (Beck and Kitching 2007; Kunin and Gaston 1997).

Niche breadth is one of the more commonly cited biological determinants of a species' range (Gaston 1996). Grinnell (1924) introduced the word 'niche' into the ecological literature defining it as the 'ultimate distributional unit of one species'. His definition emphasized that the niche is the potential area within which a species can live as opposed to the area in which it actually lives (Vandermeer 1972). At the same time, Elton (1927) introduced his concept of an organism's niche as an animal's place in the environment in relation to food and enemies or an animal's place in a community or ecosystem. His definition differed from Grinnell's in that it emphasized a species' actual place in nature as opposed to its potential place. These two definitions, referring to an organisms place in a community or environment, became inadequate and it was Hutchinson (1957) who formalized the niche concept by providing a new, quantitative definition (Giller 1984; Pulliam 2000). This was necessary because it was perceived that the definitions of the niche according to Grinnell and Elton were too vague (Vandermeer 1972).

Hutchinson defined the niche as an '*n*-dimensional hypervolume', every point in which corresponds to a state of the environment which would permit a species to exist indefinitely (Hutchinson 1957). According to this definition, a niche is the total range of environmental variables to which a species must be adapted to survive and reproduce (Giller 1984; Pulliam 2000). For example, a species will only be able to survive and reproduce within a certain range of temperatures. This temperature range is one dimension of the species' ecological niche. When a second or third variable are considered, then the niche becomes two- or three-dimensional respectively. However, there are many biotic (e.g. competition) and abiotic (e.g. precipitation) factors that influence a species' survival and the number of dimensions likely exceeds three. If there are *n* dimensions, we can consider a species' ecological niche to be an *n*-dimensional hypervolume (Figure 1; Begon et al. 1996). Hutchinson's concept differed fundamentally from that of Grinnell and Elton in that his definition, instead of using the term niche in reference to places in the environment that could support a species, emphasized that species, not environments, have niches (Pulliam 2000).

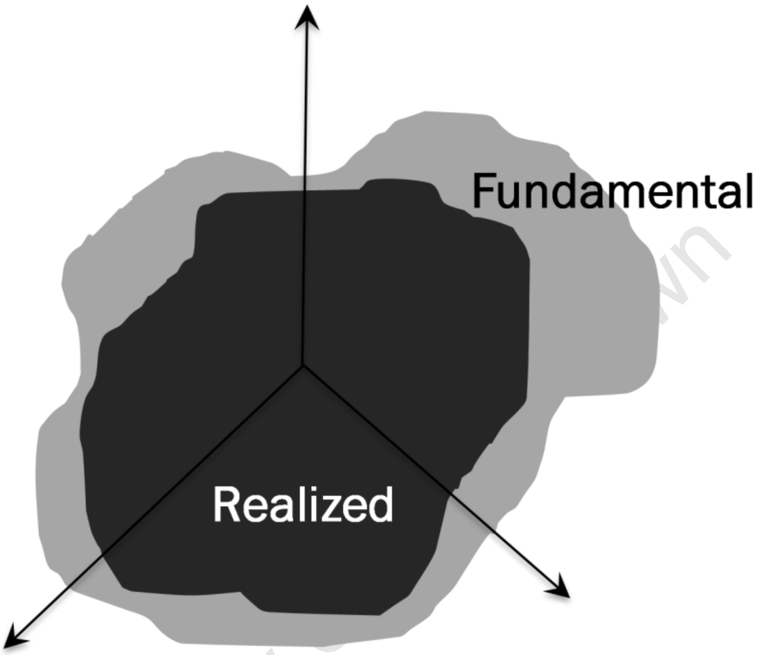


Figure 1: Representation of the ecological niche according to Hutchinson (1957). The arrows are environmental variables (e.g. temperature) which define the *n*-dimensional hypervolume. The fundamental and realized niches differ because of biotic interactions (e.g. competition).

Niche breadth can determine the size of a species geographic range according to Brown's hypothesis (Brown 1984). This hypothesis states that species with broad environmental tolerances or those which use a wide variety of resources will be able to achieve high local densities and survive in more places over a larger area. In contrast, species with narrow tolerances using only a narrow range of resources will be unable to achieve high local densities or become widespread. Species which have broad environmental tolerances and use a wide range of resources are referred to as generalists while species which have narrow environmental tolerances and use a narrow range of resources are referred to as specialists (Brown 1984). Because generalists can tolerate a wide variety of environmental conditions, they should have larger geographic range sizes than specialists (Brown 1984).

Brown's hypothesis predicts that there should be a positive relationship between niche breadth or environmental tolerance and geographic range size such that generalists should have large range sizes while specialists should have small range sizes. Some studies have found positive relationships between these two variables. For example the diversity of habitats exploited by herbaceous flora in Britain is a good predictor of range size (Thompson et al. 1999) and widespread species of European diving beetles (the *Agabus brunneus* group) have greater thermal tolerance levels than restricted species (Calosi et al. 2008). Similarly, there are strong positive correlations between range size and niche breadth (habitat breadth and dietary breadth) in African primates (Eeley and Foley 1999). Other studies have found similar relationships for African large mammals (Fernandez and Vrba 2005), stream insects in Finland (Heino 2005), North American suckers and sunfishes (Pyron 1999), European carabid beetles (Kotze et al. 2003), hawkmoths from the Indo-Australian tropics (Beck and Kitching 2007) and European tree species (Köckemann et al. 2009). Nevertheless, the evidence for a positive relationship between niche breadth and geographic range size is equivocal. Burgman (1989) found no difference between the environmental tolerances of rare and ubiquitous plant species and Gaston and Spicer (2001) found little support for Brown's hypothesis in *Gammarus* amphipods. Often studies that report on this relationship are confounded by sample size effects (Gaston 1994b; Thompson and Ceriani 2003; Thompson et al. 1998). For example, Burgman (1989) and Kolb et al. (2006) found that a positive relationship between niche breadth and range size disappeared when they accounted for sample size effects. This could occur if the niche breadths of widespread species are measured for larger numbers of individuals or sites than for narrowly distributed species (Gaston and Spicer 2001; Thompson and Ceriani 2003).

Despite some evidence for Brown's hypothesis, few studies have directly tested the relationship between niche breadth and the extent of the distribution of a species (Gaston and Spicer 2001). The failure of studies that have been conducted to find positive relationships may, at least in part, be because these studies are not measuring the relevant niche axes (Gaston et al. 1997b; Hobbs et al. 2010). Either the appropriate axes have not been measured at all or the wrong combinations of axes have been considered. This highlights the difficulty with fully defining the niche of a species and according to Brown et al. (1996), no study has quantified the entire niche of a species and then tested the ability of this complete characterization to predict geographic range size. Although Hutchinson's *n*-dimensional niche concept is a powerful heuristic tool, it is impossible to make it fully operational (Colwell and Futuyma 1971) which essentially makes Brown's hypothesis difficult to evaluate directly (Gaston et al. 1997b; Thompson et al. 1999). However, it should be possible to reliably characterize the niche of certain taxa if the relevant niche axes can be identified. For example, in bats wing morphology and echolocation characteristics clearly define the niche and foraging behaviour of different species (Racey and Entwistle 2003). Roost sites are also important characteristics of bat niches and their availability is a key ecological factor influencing bat survivorship and distribution (Bell et al. 1986; Churchill 1991; Kunz 1982; Kunz and Lumsden 2003). Bats may thus lend themselves to a direct test of Brown's hypothesis. Despite the idea having been investigated for a wide range of taxa (Gaston et al. 1997b), no studies have tested it using data for bats. Brown’s hypothesis predicts that both distribution and abundance will be affected in similar ways by niche breadth (Brown 1984; Hobbs et al. 2010). Because population abundance is difficult to accurately measure in bats (Arita 1993) I focus solely on the prediction related to distribution.

Bats belong to the order Chiroptera and, with approximately 1116 species, are the second most taxonomically diverse group of mammals after the Rodentia (Simmons 2005). They are nocturnal animals and the suite of morphological, physiological and behavioural adaptations needed to overcome the perceptual challenges imposed by the night-time environment has contributed to bats becoming the most ecologically diverse group of mammals (Schnitzler and Kalko 2001; Schnitzler et al. 2003). In particular, the evolution of flight and echolocation are key factors that has led to the diversity and evolutionary success of bats (Jones and Teeling 2006; Schnitzler and Kalko 2001). These two characters are intimately linked to the ecology of bats and can be considered as a single adaptive complex dictating their foraging habitats, foraging strategies and diets (Arita and Fenton 1997).

One of the most important ecological constraints on foraging by bats is clutter which can be defined as obstacles that a bat must detect and avoid while commuting and foraging (Fenton 1990). Clutter presents both perceptual and mechanical problems for bats in that they need to both distinguish between echoes from the target and from structural clutter as well as avoid collisions with obstacles. Perceptually, a bat's ability to forage in clutter therefore depends on its tolerance for overlap in echoes and its ability to detect and define echoes from several sources including prey and obstacles. Mechanically, a bats ability to forage in clutter is dependent on how manoeuvrable and agile the bat is which is largely determined by its wing morphology (Aldridge and Rautenbach 1987; Fenton 1990; Norberg and Rayner 1987).

Different classifications of clutter conditions have been used to divide bats into three functional groups: open-air, clutter-edge and within-clutter feeders (Fenton 1990; Neuweiler 1989; Norberg and Rayner 1987; Schnitzler and Kalko 2001; Schnitzler et al. 2003). Bats in the open-air functional group forage for insects in uncluttered areas such as open spaces, high above the ground and far from vegetation. Open-air bats need to overcome the problem of detecting prey that are distributed over a wide area and hence, occurring typically at low densities and thus difficult to find. Their echolocation call characteristics are therefore adapted for long-range prey detection e.g. low frequency (< 30 kHz), long duration and narrowband. They are adapted for fast, agile flight provided by wings which are long and narrow (high aspect ratio) with high wing loading (ratio of weight to wing area; Fenton 1990; Norberg and Rayner 1987; Schnitzler et al. 2003).

Clutter-edge bats hunt insects near the edges of vegetation, between and along vegetation and in vegetation gaps. These bats need to distinguish between echoes from insects and background echoes and avoid collisions whilst navigating. Bats foraging in edge space overcome these problems by using mixed signals with both broadband and narrowband components (Fenton 1990; Schnitzler and Kalko 2001; Schnitzler et al. 2003). The narrowband components are well suited for prey detection while the broadband, frequency modulated (FM) signals are better suited to localize and characterize background targets. High aspect ratio and low wing loading are typical of clutter-edge bats (Fenton 1990).

The clutter functional group comprises bats that search and capture insects in highly cluttered space close to vegetation or the ground where echoes from clutter often mask prey echoes (Schnitzler et al. 2003). Like bats in the clutter-edge functional group, these bats need to discriminate between echoes from insect prey versus clutter and be able to pinpoint their position relative to the clutter to avoid collisions whilst commuting and foraging. Two strategies have evolved to solve these problems. Bats using the first strategy glean prey from surfaces and make use of prey-generated sounds to detect, classify and localize the position of potential prey. They use broadband uni- or multiharmonic FM signals of low intensity for spatial orientation and clutter detection (Schnitzler and Kalko 2001; Schnitzler et al. 2003). The second strategy is used by flutter-detecting bats which emit long, constant frequency (CF) signals followed by a FM terminal sweep. These bats can detect echoes or acoustic glints from the wings of fluttering insects by using Doppler shift compensation and a specialised hearing system (Schnitzler and Denzinger 2010; Schnitzler and Kalko 2001; Schnitzler et al. 2003). Clutter bats have wings characterized by low aspect ratio and low wing loading which result in the wings being short and broad which is necessary for slow, manoeuvrable flight in highly cluttered environments (Fenton 1990).

It is clear that bats foraging in similar habitats with similar foraging modes and for similar prey must solve similar problems (Schnitzler et al. 2003). Common adaptations to overcome these ecological constraints especially with regards to echolocation signals and wing design has facilitated the division of bat species into three functional groups which can be interpreted as their niche along the microhabitat axis according to Hutchinson’s (1957) definition. Along with differences in microhabitat use, other factors combine to define the niche of bat species including roosts and diet.

Bats occupy a wide variety of roosts ranging from caves, rock crevices, dis-used mines, tombs, buildings, bridges, tree-cavities, under bark and within foliage (Kunz and Lumsden 2003). Bats use roosts for a number of reasons (Altringham 1996; Kunz and Lumsden 2003) but mainly because they provide a stable microclimate and protection from predators (Churchill et al. 1997). The associations between bats and specific roost structures range from being obligatory to opportunistic. Morphological and physiological specialization has meant that some species are dependent on certain types of roosts and therefore have a narrow niche along the roost axis. For example, the disk-winged bat, *Thyroptera tricolor* (Thyropteridae), roosts on the inner surfaces of leaves and attaches itself with adhesive disks on its feet and wrists (Findley and Wilson 1974). Roosts are also important for bats because their distributions are largely determined by the availability of suitable roosting sites (Maree and Grant 1997). Opportunistic species which have generalized roosting habits (or niches) tend to have wider geographic distributions (Kunz 1982). For example, Churchill (1991) found that species using roosts with a broad range of humidity's occupied a larger geographic range that those with more specific requirements.

Bats show a high level of dietary diversity. They feed on a wide range of foods including fruit, nectar, fish, insects and blood (Patterson et al. 2003). In general, bats seem to feed opportunistically (Norberg and Rayner 1987) and have a wide dietary breadth (Racey and Entwistle 2003). Specialization appears to be rare although it has been reported for some species. For example, studies on the golden-tipped bat *Kerivoula papuensis* (Vespertilionidae) suggest that this species is a spider specialist (Schulz and Wainer 1997). Similarly, the short-eared trident bat, *Cloeotis percivali*, appears to be a moth specialist (Black 1979; Jacobs 2000). Therefore, habitat use, roosts and diet are three important niche axes that can be combined to form an *n*-dimensional hypervolume to characterize bat niches. This renders bats useful models to test Brown's hypothesis.

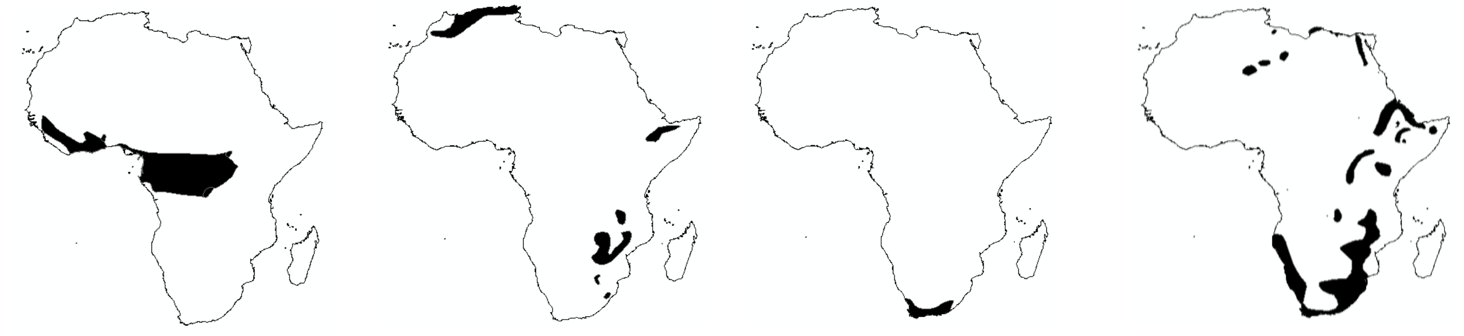
One group of bats, the Rhinolophidae or Horseshoe bats may be particularly ideal for testing Brown's hypothesis. Horseshoe bats belong to the genus *Rhinolophus,* the second largest genus of bat with 77 currently recognized species (Simmons 2005) and the only genus in the monophyletic family Rhinolophidae (Mao et al. 2007; Stoffberg et al. 2010). The geographic distribution of the genus is restricted to the Old World (Csorba et al. 2003). They occur in a variety of habitats including rainforest, dry savanna and various temperate habitats (Siemers and Ivanova 2004). Rhinolophids have a highly specialised auditory system consisting of an acoustic fovea which is able to exploit Doppler-shifted echoes to detect fluttering prey. The acoustic fovea is a region of the cochlea with an over-representation of neurons sensitive to a unique frequency (Schuller and Pollak 1979). During flight, the dominant constant-frequency component of their echolocation calls is shifted as a result of Doppler effects (Metzner et al. 2002; Schnitzler 1973). The bats compensate for these Doppler shifts by lowering the frequency of subsequent calls which ensures that the returning echo falls within the range of the acoustic fovea (Schnitzler 1968). Horseshoe bats are therefore capable of emitting and receiving signals simultaneously as they separate the emitted pulse and returning echo in frequency rather than by time (Fenton et al. 1995). This system is also used in the family Hipposideridae and in one New World species, *Pteronotus parnellii*, from the family Mormoopidae. All rhinolophids are high duty cycle echolocators i.e. the duration of their calls are long relative to the time between consecutive calls (Fenton et al. 1995). High duty cycle bats emit calls with a long constant-frequency (CF) component, high frequencies and a short frequency-modulated (FM) component at the beginning and/or end of the call.

The echolocation system used by Horseshoe bats enables them to forage in highly cluttered environments. Their echolocation calls are specifically adapted to detect echoes from the wings of fluttering insects in clutter (Arita and Fenton 1997; Schnitzler and Denzinger 2010; Siemers and Ivanova 2004). Rhinolophids use two main feeding strategies to hunt insect prey. Firstly, they hunt for insects while flying and secondly, they use feeding perches from which individual bats scan the environment and fly out to catch prey as the they fly past (Csorba et al. 2003; Siemers and Ivanova 2004). Rhinolophids are therefore capable of echolocating while stationary (Speakman et al. 2004) and their rib cages are adapted for this by a pectoral ring which is formed by the fusion of the manubrium to the first two ribs. The ribs are also flattened and extended and together with the pectoral ring make the rib cage more rigid (Csorba et al. 2003; Eick et al. 2005). The deformation of the rib cage during the expulsion of echolocation pulses by muscle contraction is therefore more efficient but at the same time less energetically costly. Their wings are short and rounded with low aspect ratio (Norberg and Rayner 1987; Skinner and Chimimba 2005) which allows for manoeuvrable flight in clutter and some species are able to hover (Csorba et al. 2003). There is considerable uniformity in skeletal morphology within the family (Csorba et al. 2003; Mao et al. 2007) and they appear to be adapted for hunting in clutter (Heller and von Helversen 1989; Schnitzler and Denzinger 2010).

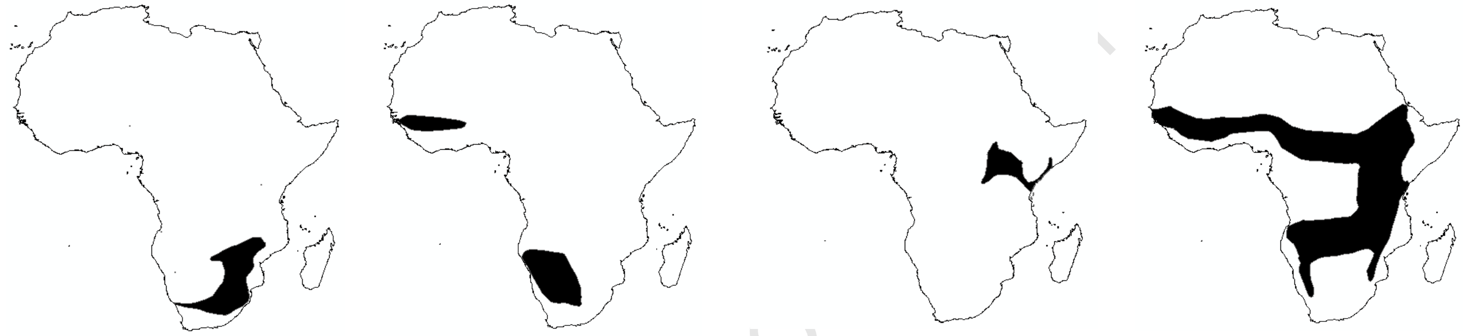
Closely related, ecologically similar species differ substantially in only one or a very small number of niche dimensions (Brown 1984). Owing to their ecological similarity, rhinolophids are ideal model species to test Brown's hypothesis. They are ideal because their niches can be reliably characterized along a small number of niche dimensions. In addition, using species from the same genus controls for differences in phylogeny that could also result in a positive relationship between niche breadth and geographic range size (Blackburn et al. 1998; Gaston et al. 1997a; Pyron 1999).

Using rhinolophids also controls for the effect dispersal ability may have on the relationship between niche breadth and geographic range size. Dispersal ability has been hypothesised to influence geographic range size in a wide range of taxa (Beck and Kitching 2007; Lester et al. 2007). Species with greater dispersal ability tend to be more widely distributed and there is generally a positive relationship between dispersal ability and geographic range size. In bats, wing morphology has been found to be an important predictor of a number of ecological characteristics including dispersal ability and home range size (Norberg and Rayner 1987). Bat wings with a high aspect ratio result in more efficient flight than wings with a low aspect ratio. Bats with high aspect ratio wings are therefore better dispersers (Altringham 1996; Miller-Butterworth 2003; Norberg and Rayner 1987). Since rhinolophids have wings with low aspect ratio, adapted for manoeuvrable flight in cluttered environments, they should all have restricted dispersal abilities. Therefore, it is expected that the differences in geographic range size among rhinolophids should not be overly influenced by differences in dispersal ability.

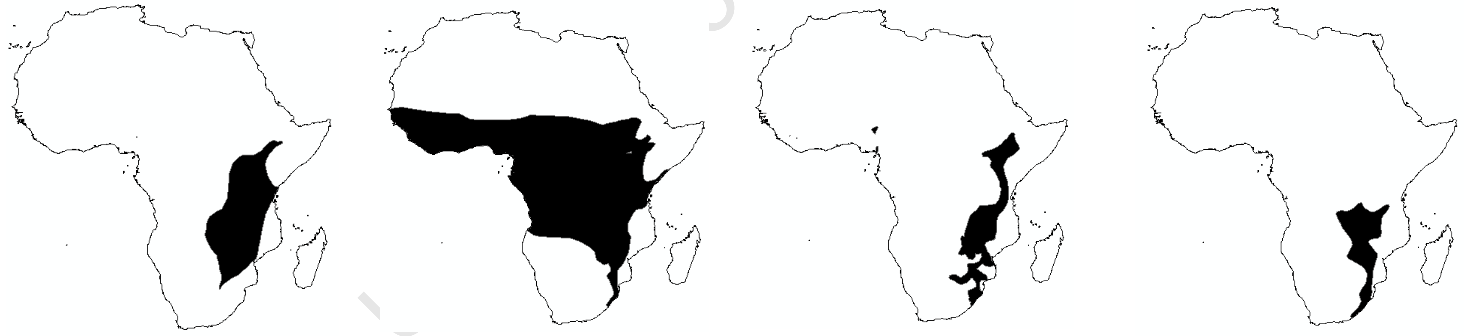
There are 21 currently described species of rhinolophid bats in Africa (Csorba et al. 2003) and most have small to medium sized geographic ranges while relatively few have large geographic ranges, a pattern consistent with other taxa (Gaston 2003). In Africa, the majority of species in the genus are listed as Critically Endangered (CR), Data Deficient (DD), Endangered (EN), Near Threatened (NT) or Vulnerable (V) on the IUCN Red List of Threatened Species™. Twelve species (Figure 2) are all listed as Least Concern (LC). There is a large amount of interspecific variation in geographic range size in these 12 species; some (e.g. *R. landeri*) have extensive distributions across the continent and others (e.g. *R. capensis* and *R. eloquens*) have extremely narrow distributions. These 12 species are excellent models with which to test Brown's hypothesis because of the variation in geographic range size.



R. alcyone *R. blasii* *R. capensis* *R. clivosus*



R. darlingi *R. denti* *R. eloquens* *R. fumigatus*



R. hildebrandti *R. landeri* *R. simulator* *R. swinnyi*

Figure 2: Extent of occurrence in Africa of 12 common *Rhinolophus* species.

The aim of my study was to determine if differences in niche breadth can explain variation in geographic range size using African Horseshoe bats to test Brown's hypothesis. Based on this hypothesis, I predicted that rhinolophid species with a wide niche breadth would also be widely distributed and rhinolophid species with low niche breadth would be narrowly distributed i.e. there should be a positive relationship between niche breadth and geographic range size.

METHODS

Since Hutchinson (1957) published his niche concept there have been numerous attempts to define niches of various species (Griffiths 1986). Niches are often defined by assessing the diversity of resources used by a species, or its niche breadth, along various dimensions. Niche breadth is often quantified along these dimensions by using indices of diversity such as the Shannon-Weiner Index of Diversity or Simpson's Diversity Index (Costa et al. 2008; Martins et al. 2006; Nicholson et al. 2006). I quantified niche breath using three biological variables namely microhabitat use, diet and roost use which are three important factors that have been argued to be good proxies for bat niches.

I also characterised horseshoe bat niches using environmental variables with the Ecological Niche Factor Analysis (Hirzel et al. 2002). The ENFA is a species distribution model based on Hutchinson’s (1957) niche concept which takes place in a multivariate statistical framework (Ayala et al. 2009; Hirzel et al. 2002). Species distribution models use an environmental envelope approach and allow the ecological requirements of a species to be estimated (Araújo and Guisan 2006; Guisan and Zimmermann 2000). The ENFA takes as input data, species presence localities and quantitative data from predictor variables (Hirzel et al. 2002). The ENFA compares, in the multidimensional space of the predictor variables, the distribution of the localities where the focal species was present to the distribution of the entire study area. The ENFA compares these two distributions with respect to their mean and variance.

Similar to a Principle Components Analysis, this factor analysis transforms the original predictor variables into new, uncorrelated factors which have ecological relevance (Hirzel et al. 2002). The first factor extracted is called “Marginality”, which expresses the departure of the ecological niche from the average available habitat. The remaining factor(s) extracted are called “Specialisation” which express the narrowness of the niche with respect to the overall distribution of the predictor variables (Hirzel et al. 2002). The Specialisation factor(s) describe how selective a species is in terms of the predictor variables

(Dolan et al. 2008). The ENFA therefore allows the quantification of the ecological niche along any of its axes.

The ENFA also provides overall indices of Marginality and Specialisation which are computed over all the predictor variables and can be used for multi-species comparisons (Hirzel et al. 2002). The Marginality index ranges mostly from 0 to 1 and values close to 1 indicate that the species lives in a very particular habitat relative to the reference set (Basille et al. 2008; Hirzel et al. 2002). The higher the Marginality, the further the species' niche departs from the mean conditions. The Specialisation index ranges from 0 to infinity and is less easy to interpret. For this reason, an index termed Tolerance has been devised which is the inverse of overall Specialisation (Hirzel et al. 2002; Sattler et al. 2007). The Tolerance index ranges from 0 to 1 with low values indicating a specialist and high values a generalist. Any value below 1 indicates some form of specialisation.

To test Brown's hypothesis, the niche breadth of the 12 focal species of African Horseshoe bat must be related to geographic range size. There are two major methods to quantify geographic range size; extent of occurrence or the area of occupancy (Gaston 1991; Gaston 1994a; Gaston and Fuller 2009). The extent of occurrence is the distance/area between the outer most limits of the occurrence of a species. The area of occupancy is the area over which the species is actually found and is therefore a more accurate measure of geographic range size. However, most field guides and taxonomic texts depict species distributions as extent of occurrence (Gaston 1991). I therefore, used extent of occurrence to quantify geographic range size because such data are readily available as opposed to data for area of occupancy.

Rhinolophus species range size distribution

Distribution maps of the extent of occurrence for the 12 focal species of African rhinolophids were obtained from the IUCN Redlist 2008 Global Mammal Assessment at http://www.iucnredlist.org/mammals/download_gis_page. These were selected because they are the best available maps for African rhinolophids. However, results should nevertheless be interpreted with caution because there are likely differences in sampling effort for each species. Differential sampling may mean that it is inaccurate to compare estimates of range size between species. Furthermore, these distribution maps are broad polygons drawn around known localities which may introduce errors of omission and commission (Gaston and Fuller 2009). The respective geographic range sizes for the 12 study species could therefore be over- or underestimated. To quantify the extent of occurrence, a 1° x 1° grid (approximately 100 km^2) was overlaid onto the distribution map of each species using ArcGIS 9.2. The number of grid cells where any part overlapped with the distribution map was counted. This follows the methods used by Blackburn (1997), Gaston et al. (1997a) and Brandle and Roland (2001).

Body Size

Body size has been shown to have a positive, negative or triangular relationship with geographic range size (Bohning-Gaese et al. 2006; Fernandez and Vrba 2005; Pyron 1999). Therefore, body size of African rhinolophids may influence geographic range size and obscure any relationship between niche breadth and range size. To test this, I used data for forearm length from Jacobs et al. (2007) to correlate body size with geographic range size. Forearm length is often used as a standard measure of body size in bats instead of body mass because the latter may be influenced by the time of day when the bat was caught, reproductive status and whether or not the animal has recently fed (Stoffberg 2007).

Diversity in microhabitat use

Microhabitat use among rhinolophids was investigated using data collected by acoustic monitoring at five sites in South Africa (Figure 3). This method has been used widely in studies of bat habitat use (Sherwin et al. 2000). Acoustic monitoring took place in areas with different degrees of clutter because rhinolophids are known to forage in cluttered environments (Arita and Fenton 1997; Neuweiler 1989; Siemers and Ivanova 2004). Monitoring took place in three zones each with different densities of clutter namely edge (zone 1), semi clutter (zone 2) and high clutter (zone 3). The relative clutter densities of each habitat zone were determined subjectively but by the same observer and kept constant as much as possible across each of the five sites. The edge habitat zone was characterized by linear landscape features such as tree lines, semi clutter was characterized by vegetation with gaps that were > 1m wide and high clutter was characterized by vegetation with gaps < 1m wide.

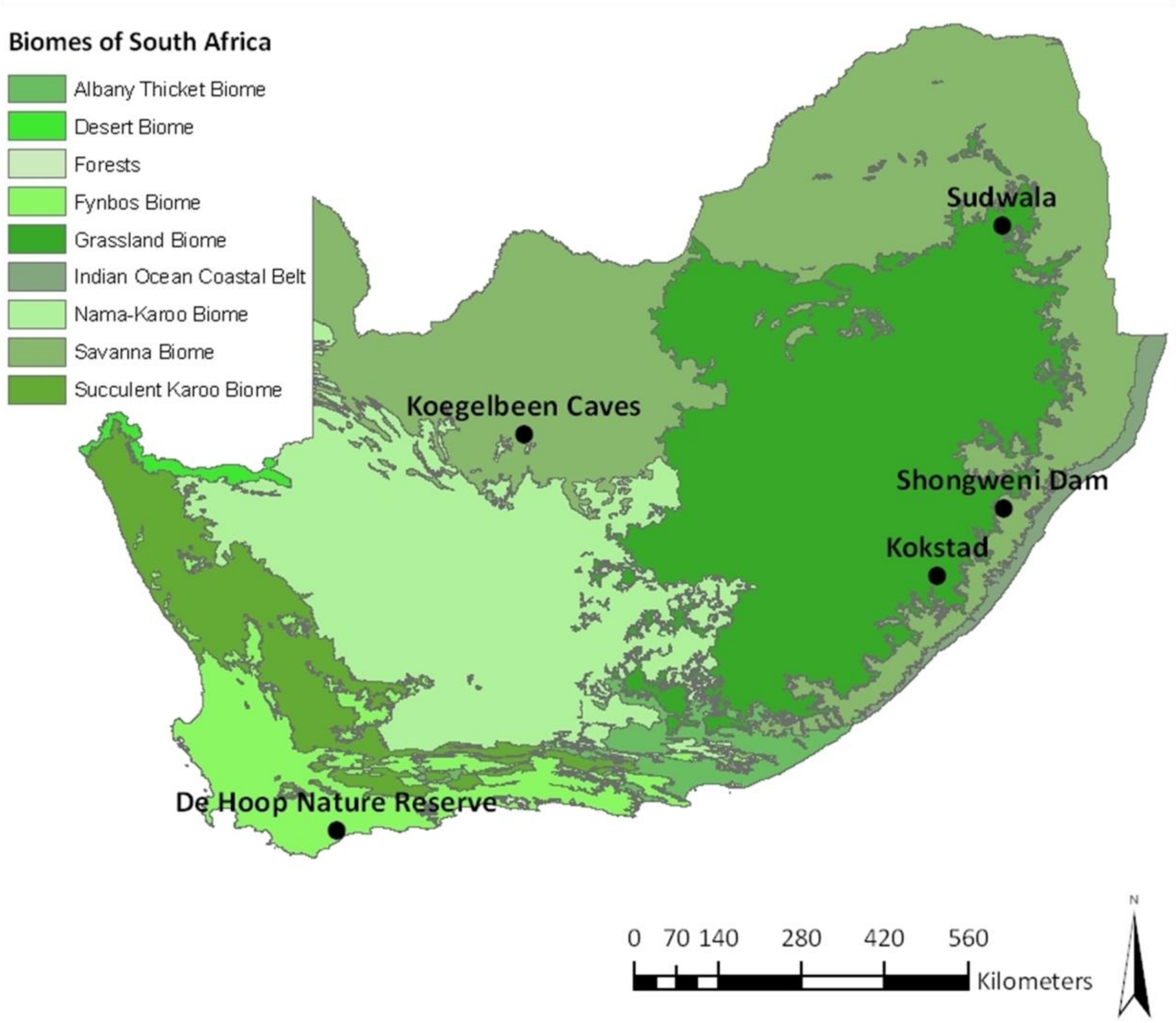


Figure 3: Map of the biomes of South Africa showing the sampling locations. The dates of sampling trips were as follows: Sudwala: 22/09/2009 – 08/10/2009; Koegelbeen Caves: 09/10/2009 – 16/10/2009; Kokstad: 13/12/2009 – 17/12/2009; Shongweni Dam: 18/12/2009 – 21/12/2009; De Hoop Nature Reserve: 13/02/2010 – 16/02/2010.

At each site and on each sampling night, three Petterson D240X bat detectors (Petterson Elektronik AB, Uppsala, Sweden) were used simultaneously for passive acoustic monitoring. At each study site the detectors were deployed beginning at sunset and left overnight in the field. One bat detector was placed in each habitat zone in such a way that they would not simultaneously record bats present in another zone. Echolocation calls were recorded onto a handheld Edirol R-09HR digital wave recorder (Roland Corporation US, Los Angeles, CA.) connected to each detector. All recordings were analyzed using BatSound Pro software (version 3.20, Petterson Elektronik AB, Uppsala, Sweden). Each species was identified from their echolocation calls using reference calls collected by D.S. Jacobs and colleagues at the University of Cape Town. During passive acoustic monitoring, I also used active monitoring at each site using a D1000X bat detector (Petterson Elektronik AB, Uppsala, Sweden) by walking transects through the three habitat zones to determine which species of rhinolophid were present.

Prior to commencing passive acoustic monitoring, each D240X bat detector was calibrated using a hand-held rhinolophid because these bats are capable of echolocating while stationary (Speakman et al. 2004). This involved moving the bat away from the detector and simultaneously adjusting the gain on the detector to determine the maximum distance at which the bat could be detected. Three different *Rhinolophus clivosus* individuals were used separately for the calibration and it was determined that these bats could be detected up to 5m away when the gain was in the HIGH position on the detector and the Trigger level was set to LOW. McDonald et al. (1990) found the same detection distance for *R. capensis* and *R. clivosus* at De Hoop Nature Reserve using a QMC Mini Bat Detector (QMC Instruments Ltd., London). This ensured that the detectors in each foraging zone all sampled the same volume of space.

In addition to the active and passive acoustic monitoring, I set mist nets in the three different habitat zones to catch bats. Mist-netting effort was restricted to one habitat zone per night. The mist nets were unfurled for approximately 5 hours each night and checked regularly. Captured bats were removed as quickly as possible. Approval and permits to capture and handle bats came from the Science Faculty Animal Ethics Committee of the University of Cape Town (Clearance # 2009/V1/JA) and the necessary authorities in the KwaZulu-Natal, Mpumalanga, Northern Cape and Western Cape provinces in South Africa.

The number of bat passes recorded and the number of bats captured in each habitat zone respectively, were combined across all sites to calculate the total number of rhinolophid occurrences in each zone for each species. These data were used to calculate the diversity in microhabitat use using the Shannon-Weiner diversity index (Shannon and Weaver 1949):

$$H = -\sum_{i=1}^{n} pi \ln pi$$

Where p_i is the proportional use of each habitat zone

Data were collected for eight species: *Rhinolophus blasii*, *R. capensis*, *R. clivosus*, *R. darlingi*, *R. denti*, *R. hildebrandti*, *R. simulator* and *R. swinnyi*. Typical echolocation calls were used to identify each species (Figure 4).

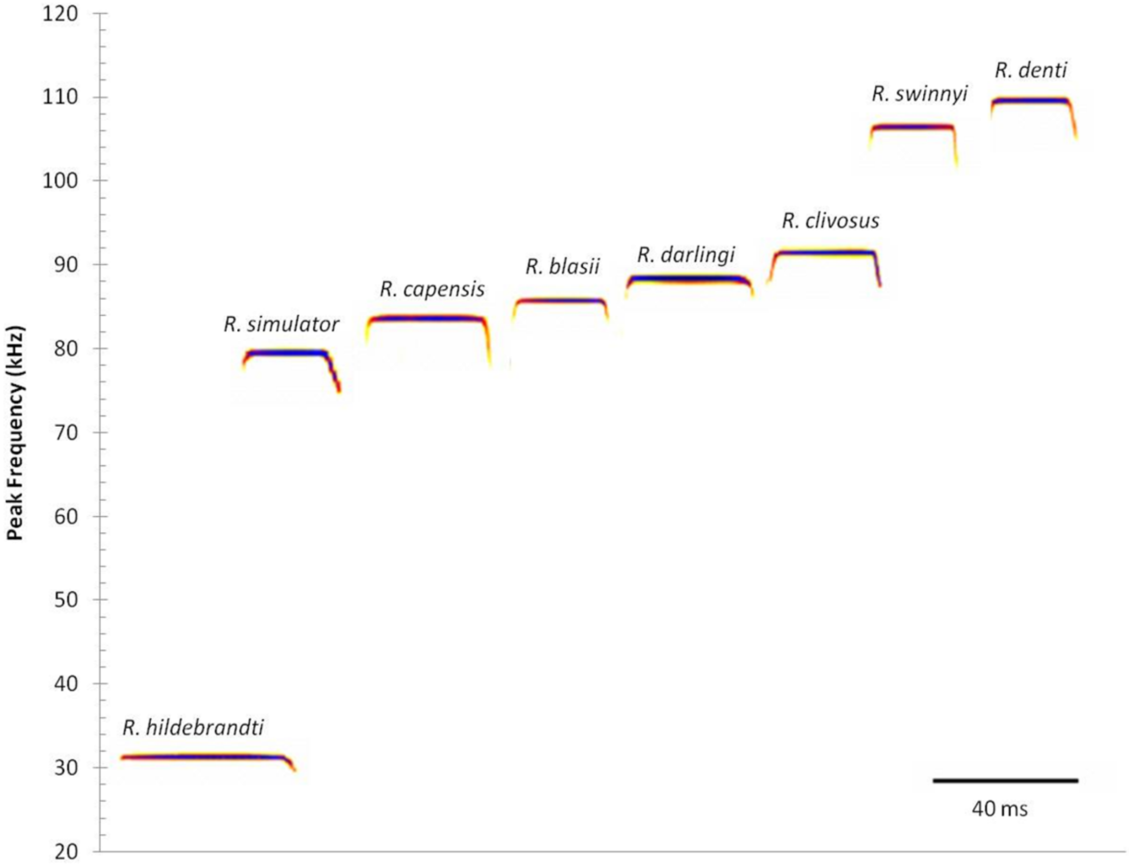


Figure 4: Typical echolocation calls showing the mean peak echolocation frequency for 8 African *Rhinolophus* species.

Dietary diversity

I assessed the diet of rhinolophids captured in mist nets or removed directly from roosts at each study site (Figure 3) to determine the composition and diversity of prey eaten by each species. Bats were kept in cotton bags for approximately one hour after capture for the collection of faeces and then released at the point of capture. If sufficient pellets were not collected during this time, bats were kept overnight. These bats were all released the following night at the point of capture.

Each pellet was teased apart under 70% ethanol and the arthropod exoskeleton fragments identified to the ordinal level using several taxonomic texts and a reference collection of insects trapped at each site (see below). The percent volume of each insect order in the pellets were determined for each species following Whitaker (1988). Rhinolophid dietary diversity was then calculated using these data. Simpson's diversity index or the Food Niche Breadth (FNB) index has been used by other authors investigating dietary diversity in insectivorous bats and was used in this study (Bowie et al. 1999; Findley and Black 1983; Jiang et al. 2008). Food Niche Breadth is described by:

$$FNB = 1/\sum_{i=1}^{n} P_i j^2$$

Where P_i is the proportion of the i^{th} prey category of species j

Insect availability at each study site was sampled using a 22W battery-operated black-light insect trap (BioQuip Products Inc., 2321 E Gladwick St., Rancho Dominguez, CA 90220 USA). Light-traps were operated during the same time period as the passive acoustic monitoring. They were placed in the vicinity of the bat detectors but at sufficient distance away (from 50m to 80m) from them to ensure that the light-traps did not affect bat activity at the detectors. The insects captured in the light-traps were used as a reference collection to identify insect fragments in faecal pellets collected from captured bats.

I collected data on diet for *R. capensis*, *R. clivosus* and *R. denti* in South Africa and combined these with additional diet data for these and other species of rhinolophids obtained from the literature. In total, data were available for 10 species and these were used to calculate Food Niche Breadth.

Diversity in roost use

Diversity in the types of roosts used by the 12 species of African rhinolophids was determined from the literature. The number of different types of roosts used by each species was used as a measure of niche breadth along the roost axis.

Ecological Niche Factor Analysis (ENFA)

The ENFA is a GIS-based technique conducted using the BIOMAPPER software version 4.0 (Hirzel et al. 2002). The study area (i.e. the continent of Africa) was represented as a raster map composed of adjacent isometric cells with a quarter degree resolution (approximately 25 km^2). In a raster map, each cell in the matrix contains a value representing information, for example elevation. Locality data for the 12 species of African rhinolophids were obtained from the Africa Chiroptera Report (2008), Csorba et al. (2003) and from several South African museums including the Transvaal Museum, the Durban Natural Science Museum, the Amathole Museum, the Iziko Museum, the McGregor Museum and the National Museum of Bloemfontein (Table 1).

To characterise the habitat in Africa available to rhinolophids, three types of environmental variables were used for the ENFA, namely climate [mean annual temperature (°C), mean annual precipitation (mm) and an index of aridity], topography [altitude (masl)] and vegetation [Whites Vegetation of Africa (1983)]. The mean annual temperature and mean annual precipitation variables are bioclimatic variables derived from monthly temperature and rainfall values (Hijmans et al. 2005). These data were taken from www.worldclim.org as ESRI grids and are for the period 1950-2000. The Aridity Index data were obtained from the CGIAR-CSI Global-Aridity and Global-PET Database (Trabucco and Zomer 2009) made available by the CGIAR Consortium for Spatial Information at http://csi.cgiar.org. The data used to derive this index were also for the period 1950-2000. The climate data were for the whole planet so the data for Africa had to be extracted using the 'Extract by Mask' tool in the Spatial Analyst toolbox using ArcGIS 9.2.

Table 1: The number of locality records used in the ENFA for 12 African *Rhinolophus* species.

Species	# of Localities points
R. alcyone	32
R. blasii	43
R. capensis	66
R. clivosus	240
R. darlingi	109
R. denti	28
R. eloquens	46
R. fumigatus	135
R. hildebrandti	116
R. landeri	190
R. simulator	147
R. swinnyi	60

The climate and topographical variables were already quantitative in nature but vegetation first had to be quantified before it could be used in the ENFA. This was done as follows. A digital version of Whites vegetation map of Africa was obtained as an ESRI shapefile from the Geo Data Portal of the United Nations Environment Programme at http://geodata.grid.unep.ch/. Whites' vegetation map consists of 19 different vegetation types classified in terms of physiognomy. Physiognomy describes the structure of vegetation and includes characters such as height, density, thorniness and deciduousness (White 1983). The 19 vegetation types vary in the size of the areas they occupy. For the ENFA, vegetation types comprising only a small part of the continent (except for the Fynbos and Succulent Semi-Desert vegetation types) were excluded. In total I quantified 12 vegetation types for use in the ENFA. To do this, each of the 12 vegetation types was converted into a separate Boolean raster map using ArcGIS 9.2 where cells in which a particular vegetation type was present were coded 1 and cells without that particular vegetation were coded 0. This generated a Boolean raster map for each vegetation type. The completed maps were then fed into the module 'Distance Analysis' module (version 1.3.1.19) in BIOMAPPER and, using the minimum distance algorithm, the distance from the focal cell to a cell in which the variable of interest was present was calculated. This resulted in new maps with cells whose values represented the distance to particular vegetation types. These maps could then be used in the ENFA as separate environmental variables. In total 16 environmental variables (Table 2) were put into the ENFA for each species, with each map containing 40555 cells. Although multinormality is theoretically required for factor extraction through the Eigen-system computation, the ENFA is robust to deviations from normality (Hirzel et al. 2002). Nonetheless, all environmental variables were first normalized using a Box-Cox Transformation in BIOMAPPER before running the models.

Table 2: Environmental variables used in the ENFA.

Altitude
Aridity
Mean Annual Temperature
Mean Annual Precipitation
Distance to Arid-fertile Savanna
Distance to Desert
Distance to Dry Forest and Thicket
Distance to Fynbos
Distance to Hydromorphic Grassland
Distance to Moist-infertile Savanna
Distance to Mopane Savanna
Distance to Mosaics of Forest
Distance to Shrubland and Grassy Semi-desert
Distance to Succulent Semi-desert
Distance to Tropical Lowland Rainforest
Distance to Unpalatable Grassland

Statistical analyses

All statistical analyses were performed using Statistica (Version 9, StatSoft. Inc. Tulsa, OK, USA). Separate polynomial regression analyses were undertaken to determine the relationship between each measure of niche breadth (and body size) and geographic range size. There were 6 different measures of niche breadth: Shannon-Weiner Diversity Index, Food-Niche Breadth, # of Roost Types Used, Marginality, Tolerance and Specialisation. In a polynomial regression, different powers of the X variable are successively added to the model to determine whether they increase the R^2 value. An *F* test is applied to determine if the increase is significant (Zar 1984). First a linear model is fitted to the data followed by a quadratic and then a cubic model. This method was used because it allows for a determination of whether a linear or a curvilinear model best describes the data.

RESULTS

Rhinolophus species range size distribution

Most of the 12 African rhinolophids have small to medium sized geographic ranges and only a few species have large geographic ranges (Figure 5). *Rhinolophus landeri* and *R. fumigatus* are the two most widely distributed horseshoe bats on the continent with geographic ranges of 111400 km^2 and 83300 km^2 respectively. *Rhinolophus clivosus* is the most widely distributed across the continent in terms of latitudinal extent but its distribution is disjunct (Figure 2) resulting in a total geographic range of 44500 km^2. *Rhinolophus blasii* also has a disjunct distribution in Africa. *Rhinolophus alcyone* and *R.*

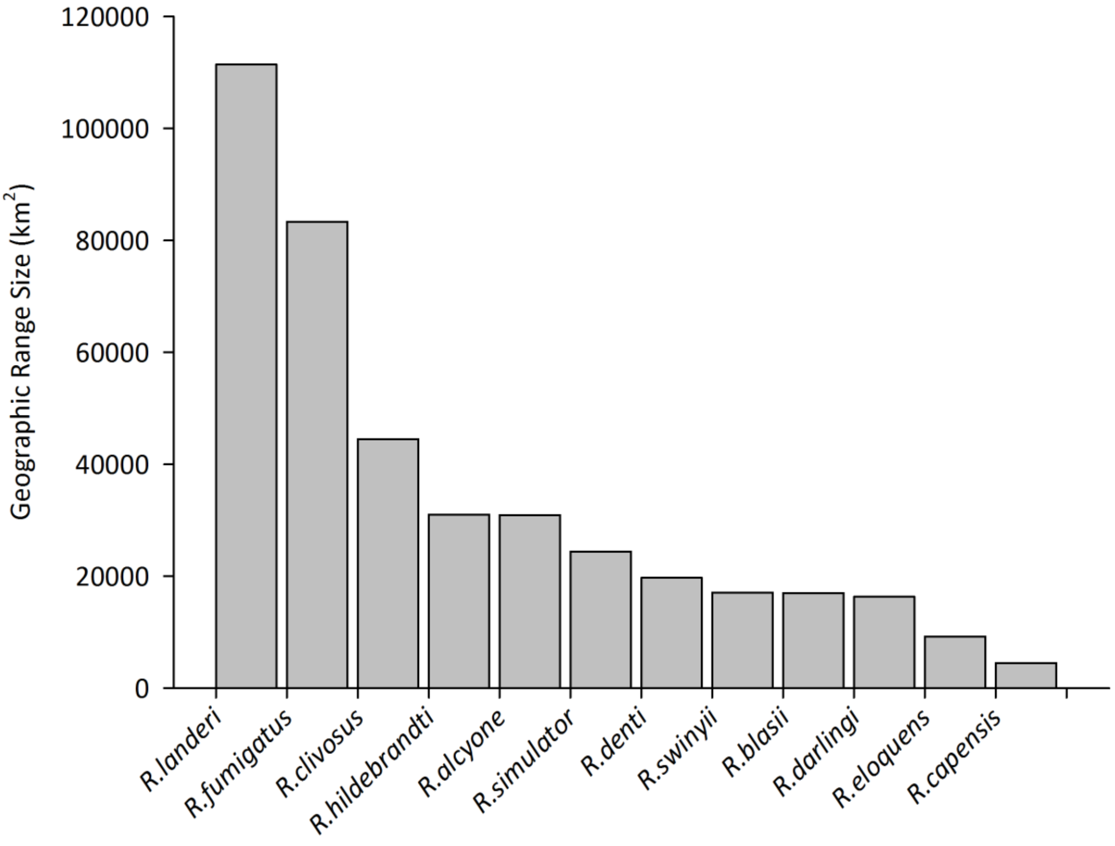


Figure 5: The geographic range sizes for 12 African *Rhinolophus* species.

hildebrandti differ in their respective geographic range sizes by only 100 km^2 as do *R. blasii* and *R. swinyii*. The two most narrowly distributed species are *R. eloquens* and *R. capensis* with geographic ranges of 9200 km^2 and 4500 km^2 respectively.

Body Size

There is no significant linear (R^2 = 0.02, d.f. = 8, p = 0.73) or polynomial (R^2 = 0.03, d.f. = 7, p = 0.90) relationship between forearm length and geographic range size in African rhinolophids (Figure 6). The increase in the R^2 value between the two models was not significant (p = 0.91).

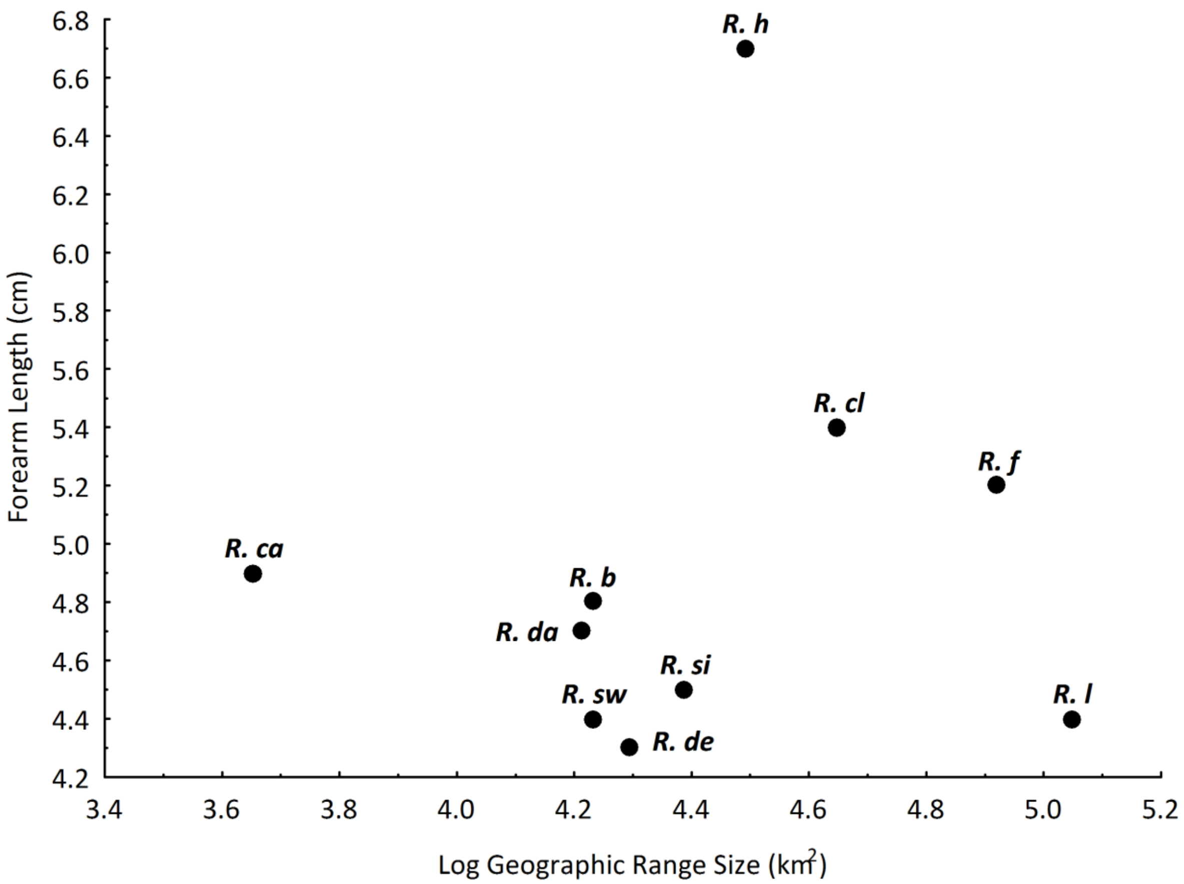


Figure 6: A plot of log geographic range size and forearm length for 10 African *Rhinolophus* species. The following abbreviations are used for the species: *Rhinolophus blasii* (*R.b*), *R.* capensis (*R.ca*), *R. clivosus* (*R.cl*), *R. darlingi* (*R.da*), *R. denti* (*R.de*), *R. fumigatus* (*R.f*), *R. hildebrandti* (*R.h*), *R. landeri* (*R.l*), *R. simulator* (*R.si*), *R. swinnyi* (*R.sw*).

Diversity in microhabitat use

In total, 172 passes were recorded at five study sites in all three habitat zones during passive acoustic monitoring. The majority of passes (101) were recorded in the high clutter habitat zone and all rhinolophids were detected at least once in this zone. In the semi clutter habitat zone, 65 passes were detected and in the edge habitat zone 6 passes were detected (Table 3). No rhinolophids were recorded during active acoustic monitoring transects. Thirty two rhinolophids were caught in mist nets at the five sites and in all three habitat zones. Twenty were caught in the high clutter habitat zone, three in the semi clutter habitat zone and nine in the edge habitat zone (Table 3).

Table 3: Summary of the number of rhinolophid bat passes recorded and mist-net captures in each habitat zone at each study site.

Species	Site	Habitat Zone	# of passes	# of captures
R. blasii	Sudwala	High-Clutter	1	0
R. capensis	De Hoop	High-Clutter	0	1
		Semi-Clutter	1	0
		Edge	3	9
R. clivosus	Koegelbeen	High-Clutter	0	7
		Semi-Clutter	0	1
	Sudwala	High-Clutter	28	1
		Semi-Clutter	55	2
		Edge	1	0
R. darlingi	Koegelbeen	High-Clutter	8	0
		Edge	1	0
	Sudwala	High-Clutter	2	1
		Semi-Clutter	1	0
R. denti	Koegelbeen	High-Clutter	8	9
		Semi-Clutter	1	0
R. hildebrandti	Sudwala	High-Clutter	16	0
		Semi-Clutter	4	0
		Edge	1	0
R. simulator	Shongweni	High-Clutter	5	0
	Sudwala	High-Clutter	32	1
		Semi-Clutter	3	0
R. swinnyi	Kokstad	High-Clutter	1	0

Rhinolophus clivosus was the most diverse species in terms of microhabitat use (Table 4). This species was recorded predominantly in semi clutter (58 records) and high clutter (36 records) with only one pass detected in the edge habitat zone (Table 3). *Rhinolophus hildebrandti* and *R. capensis* were also diverse in their microhabitat use (Table 4). Both these species were detected in all three habitat zones but *R. hildebrandti* was detected predominantly in high clutter whereas most records for *R. capensis* were in the edge habitat zone (Table 3). *Rhinolophus darlingi* was present in all three microhabitats but the majority of records were in high clutter giving this species a relatively low H' value (Table 4). *Rhinolophus simulator* and *R. denti* also showed low microhabitat diversity (Table 4). Neither species was detected in the edge habitat zone. The least diverse species in terms of microhabitat use were *R. blasii* and *R. swinnyi* which were only recorded in high clutter. Shannon-Weiner H' values could therefore not be calculated for these two species (Table 4). Overall I found no significant relationship between geographic range size and diversity in microhabitat use with either a linear ($R^2 = 0.09$, d.f. = 4, $p = 0.57$) or a quadratic ($R^2 = 0.55$, d.f. = 3, $p = 0.30$) model (Figure 7). The large increase in the R^2 value between the two models was not significant ($p = 0.19$). However, the two most widely distributed species, *R. clivosus* and *R. hildebrandti* did have the highest H' values (Table 4).

Table 4: Habitat use by rhinolophid species based on acoustic monitoring and mist-netting in each habitat zone. H' is the Shannon-Weiner diversity index for each species.

Species	High-Clutter	Semi-Clutter	Edge	H'
R. blasii	1	0	0	-
R. capensis	2	1	12	0.63
R. clivosus	36	58	1	0.72
R. darlingi	11	1	1	0.49
R. denti	17	1	0	0.22
R. hildebrandti	16	4	1	0.67
R. simulator	38	3	0	0.26
R. swinnyi	1	0	0	-
TOTAL	**122**	**68**	**15**	

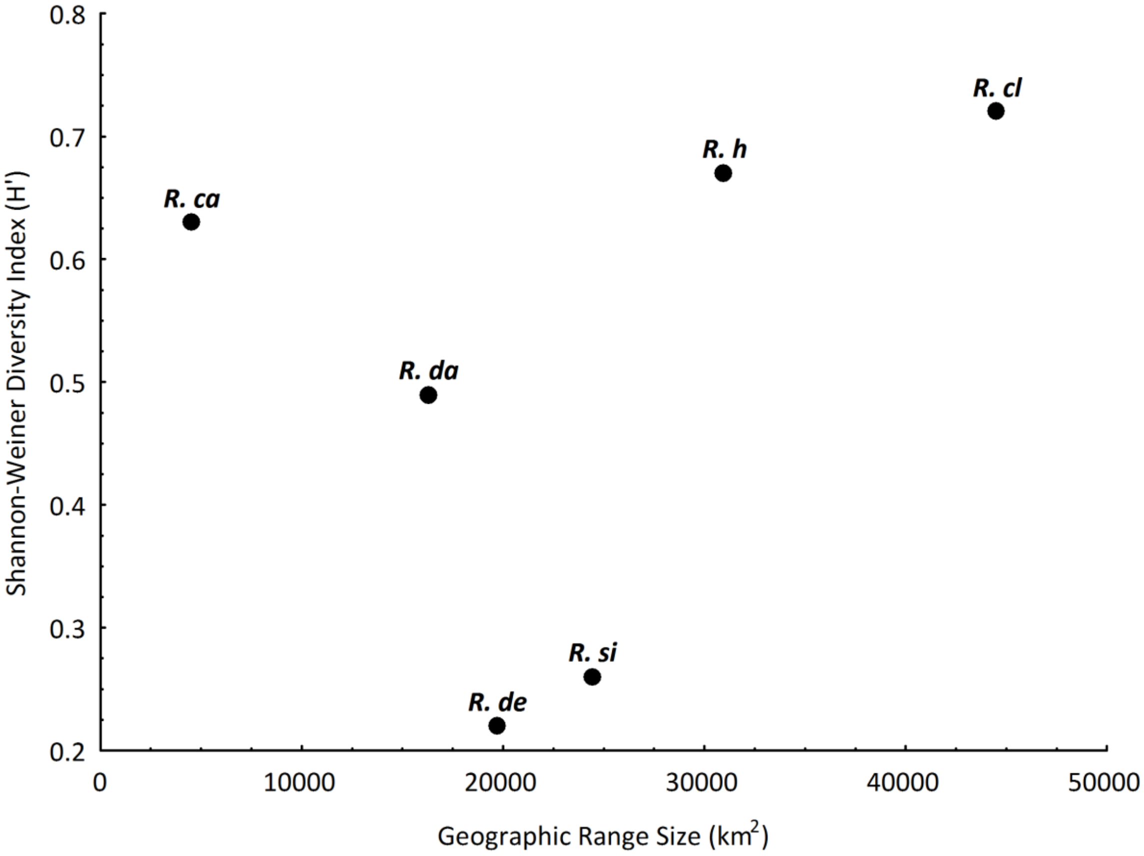


Figure 7: A plot of geographic range size and the Shannon-Weiner Diversity Index (H') for 6 African *Rhinolophus* species. The abbreviations are the same as those used in Figure 6.

Dietary diversity

Although prey included at least 11 different insect orders in total, the diets of most rhinolophids are dominated by Coleoptera and Lepidoptera (Table 5). On average, these two orders make up approximately 80% of the diet. The relative proportions of the two orders varied between species (Table 5). *Rhinolophus fumigatus* consumed fewer moths than cogenerics; its diet consists mainly of Coleoptera and Hemiptera. *Rhinolophus blasii* and *R. landeri* consume fewer beetles than cogenerics and preyed heavily on moths.

Table 5: Mean, SD and range of percentage by volume of prey categories in the diets of 10 African *Rhinolophus* species. The numbers in superscript represent the data sources for each species.

	R. blasii [1, 4, 10]			*R. capensis* [8, 9, 10, 12]			*R. clivosus* [3, 7, 8, 10, 12]			*R. darlingi* [8, 11]			*R. denti* [11, 12]		
Prey Category	mean	SD	Range	mean	SD	Range	mean	SD	Range	mean	SD	Range	mean	SD	Range
Coleoptera	2.3	3.8	0.0 - 6.7	22.8	20.7	3.0- 72.0	48.0	20.6	0.0 - 74.0	28.3	26.6	0.0 - 100	16.5	20.6	0.0 - 60.0
Lepidoptera	91.8	8.4	82.1 - 96.9	64.8	32.0	7.0 - 97.0	41.3	25.7	2.0 - 100	56.3	27.5	0.0 - 100	73.5	21.9	30.0 - 95.0
Diptera	0.4	0.4	0.0 - 0.7	2.3	5.9	0.0 - 19.0	2.0	6.9	0.0 - 24.0				2.9	3.9	0.0 - 10.0
Ephemeroptera															
Hemiptera	1.7	2.9	0.0 - 5.0	7.3	19.7	0.0 - 63.0	6.7	11.8	0.0 - 35.0	11.9	17.3	0.0 - 60.0	2.1	5.7	0.0 - 15.0
Hymenoptera	0.1	0.2	0.0 - 0.3	0.2	0.5	0.0 - 1.6	0.2	0.4	0.0 - 1.4						
Isoptera	1.6	1.4	0.0 - 2.5												
Mantodea															
Neuroptera	0.8	1.4	0.0 - 2.5	1.1	3.5	0.0 - 11.0	1.1	3.1	0.0 - 11.0						
Orthoptera				0.1	0.3	0.0 - 0.9	0.004	0.01	0.0 - 0.1						
Trichoptera				0.5	1.7	0.0 - 5.3									
Unknown	1.3	2.1	0.0 - 3.8	0.9	1.8	0.0 - 5.0	0.8	1.6	0.0 - 4.6	3.5	5.6	0.0 - 20.0	5.0	7.6	0.0 - 20.0

	R. fumigatus [5, 11]			*R. hildebrandti* [3, 5, 10]			*R. landeri* [2, 3, 11]			*R. simulator* [1, 4, 6, 10]			*R. swinyii* [1, 4, 9]		
Prey Category	mean	SD	Range	mean	SD	Range	mean	SD	Range	mean	SD	Range	mean	SD	Range
Coleoptera	27.1	24.9	3.3 - 53.0	43.7	9.3	33.0 - 50.1	4.2	5.0	0.0 - 10.0	11.3	6.0	4.2 - 18.3	20.0	10.5	5.6 - 29.0
Lepidoptera	5.0	8.7	0.0 - 15.0	48.5	6.9	42.4 - 56.0	85.6	17.6	60.0 - 100	69.5	8.5	57.6 - 77.4	67.1	16.1	55.2 - 89.3
Diptera	5.7	9.8	0.0 -17.0	1.7	2.9	0.0 - 5.0	2.5	5.0	0.0 - 10.0	2.6	1.8	0.3 - 4.5	7.1	8.1	2.3 - 18.1
Ephemeroptera										2	4.0	0.0 - 7.9			
Hemiptera	39.3	34.6	0.0 - 65				3.3	6.7	0.0 - 13.0	1.6	3.1	0.0 - 6.2	0.2	0.2	0.0 - 0.4
Hymenoptera	5.7	9.8	0.0 - 17.0							0.4	0.8	0.0 - 1.5	1.6	3.1	0 - 6.2
Isoptera										7.8	8.4	0.0 - 19.4	2.7	3.2	0.0 - 6.3
Mantodea										0.05	0.1	0.0 - 0.2			
Neuroptera	1	1.7	0.0 - 3.0							0.2	0.5	0.0 - 0.9			
Orthoptera				1.07	1.8	0.0 - 3.2	1.9	3.8	0.0 - 7.6	2.4	2.7	0.0 - 4.9	0.7	0.8	0.0 - 1.5
Trichoptera										0.8	1.7	0.0 - 3.3			
Unknown	16.67	14.2	7.0 - 33.0	5.1	5.5	0.0 - 11	2.5	5.0	0.0 - 10.0	1.35	1.6	0.4 - 3.8	1.8	1.3	0.0 - 2.8

[1] Whitaker and Black 1976

[2] Fenton 1975

[3] Fenton et al. 1977

[4] Findley and Black 1983

[5] Aldridge and Rautenbach 1987

[6] Jacobs 2000

[7] Schoeman and Jacobs 2003

[8] Jacobs et al. 2007

[9] Kelly 2008

[10] Schoeman and Jacobs 2010

[11] D.S. Jacobs unpublished data

[12] This study

Rhinolophus fumigatus had the greatest FNB followed by *R. clivosus* (Table 6). The least diverse species in terms of diet was *R. blasii*. Both the linear (R^2 = 0.07, d.f. = 8, p = 0.46) and quadratic (R^2 = 0.08, d.f. = 7, p = 0.76) models indicated no significant relationship between dietary diversity and log geographic range size (Figure 8). The increase in the p-value between the two models was also not significant (p = 0.97).

Table 6: Food niche breadth (FNB) indices for 10 African *Rhinolophus* species.

Species	FNB
R. blasii	1.18
R. capensis	2.06
R. clivosus	2.46
R. darlingi	2.42
R. denti	1.75
R. fumigatus	3.77
R. hildebrandti	2.33
R. landeri	1.36
R. simulator	1.98
R. swinnyi	2.01

Diversity in roost use

Horseshoe bats use a variety of daytime roost sites but prefer sheltered environments such as caves or mine adits (Csorba et al. 2003; Skinner and Chimimba 2005). All 12 African rhinolophids I studied have been recorded to use such roosts. Several species (*R. blasii*, *R. darlingi*, *R. fumigatus*, *R. hildebrandti* and *R. landeri*) have also been recorded roosting in piles of boulders (Skinner and Chimimba 2005). Three species, *R. clivosus*, *R. darlingi* and *R. denti* will roost in crevices or fissures in rocks (Skinner and Chimimba 2005). *Rhinolophus fumigatus* and *R. hildebrandti* have been recorded roosting in rock cavities (Skinner and Chimimba 2005). *Rhinolophus darlingi* and *R. landeri* have been recorded from rocky outcrops or koppies (Maree and Grant 1997; Skinner and Chimimba 2005).

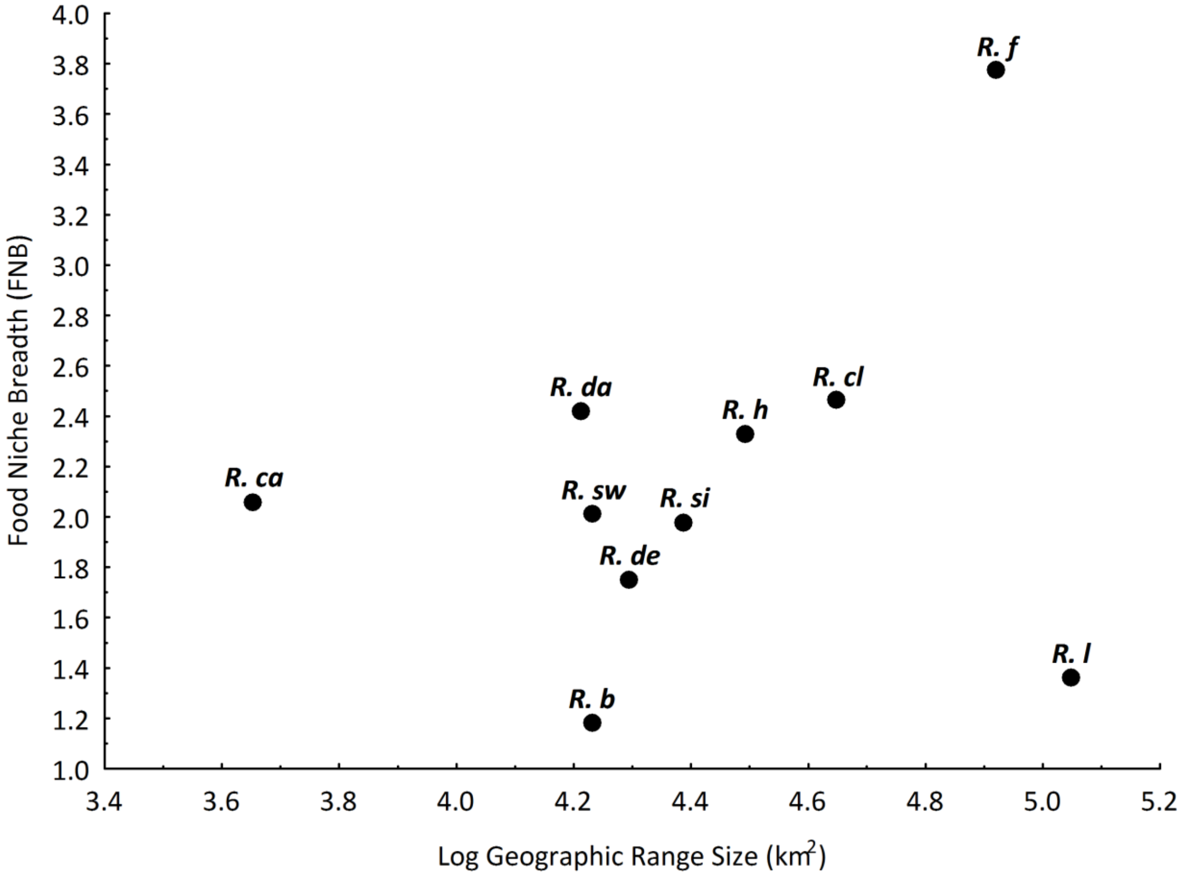


Figure 8: A plot of log geographic range size and Food Niche Breadth (FNB) for 10 African *Rhinolophus* species. The abbreviations are the same as those used in Figure 6.

Some species of horseshoe bat will roost in man-made structures other than mines. *Rhinolophus clivosus* and *R. simulator* have been recorded roosting in tunnels and *R. clivosus*, *R. darlingi* and *R. hildebrandti* have been found roosting in road culverts (D.S. Jacobs, unpublished data). Disused buildings have also been used as roosts by *R. clivosus*, *R. darlingi*, *R. hildebrandti* and *R. landeri* (Benda et al. 2008; Pienaar 1964; Skinner and Chimimba 2005). *Rhinolophus fumigatus*, *R. hildebrandti*, *R. landeri*, *R. alcyone* and *R. denti* have been recorded in roofs, the latter two species roosting under the roofs of thatched houses (Csorba et al. 2003; Skinner and Chimimba 2005). There are also specific cases of *R. landeri* roosting in wells and a steeple (Brown and Dunlop 1997; Skinner and Chimimba 2005), of *R. clivosus* roosting in store houses (Benda et al. 2008) and of *R. darlingi* roosting in stables (Skinner and Chimimba 2005).

Horseshoe bats also use more natural roosts such as old burrows of ant bears (*Orycteropus afer*) in which *R. hildebrandti* has been recorded. *Rhinolophus alcyone* has been recorded roosting in hollow trees (Csorba et al. 2003) and *R. hildebrandti* and *R. landeri* have been recorded roosting in hollow Baobab trees (*Adansonia digitata*; Brown and Dunlop 1997; Fenton and Rautenbach 1986).

Overall, I found a positive, linear relationship between diversity in roost use and log geographic range size (Figure 9). There was a significant relationship when the data were fitted with a linear model (R^2 = 0.39, d.f = 10; p = 0.03) but not with a quadratic model (R^2 = 0.39, d.f = 9; p = 0.11). The increase in the R^2 between the two models was not significant (p = 0.99).

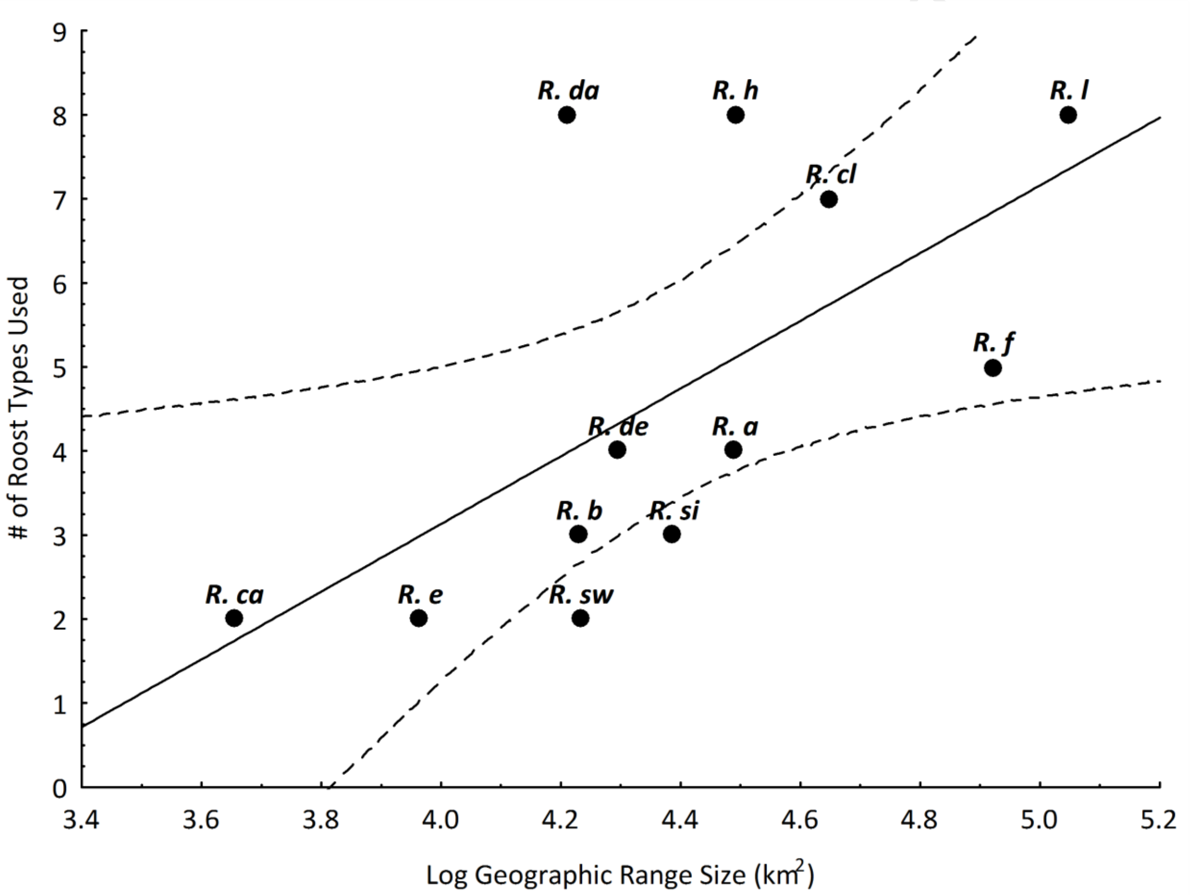


Figure 9: A plot of log geographic range size and the number of different roost types used for 12 African *Rhinolophus* species. The solid line represents the best fit where # of Roost Types Used = 12.976 – 4.0272*Geographic Range Size, the dashed line represents the 95% confidence interval. The following abbreviations are used for the species: *Rhinolophus alcyone* (*R.a*), *R. blasii* (*R.b*), *R. capensis* (*R.ca*), *R. clivosus* (*R.cl*), *R. darlingi* (*R.da*), *R. denti* (*R.de*), *R. eloquens* (*R.e*), *R. fumigatus* (*R.f*), *R. hildebrandti* (*R.h*), *R. landeri* (*R.l*), *R. simulator* (*R.si*), *R. swinyii* (*R.sw*).

Ecological Niche Factor Analysis (ENFA)

All 12 *Rhinolophus* species had overall marginality values higher than 1 meaning that they all occupy particular habitats (i.e. their niches show departure from the average available habitat). This suggests that horseshoe bats in Africa occupy a relatively narrow range of habitats. The species with the highest Marginality was *R. capensis* and the lowest was *R. fumigatus*. I found a significant negative linear relationship between Marginality and log geographic range size (Figure 10). Although the quadratic relationship ($R^2 = 0.52$; d.f = 9; p = 0.04) had a higher R^2 than the linear relationship ($R^2 = 0.51$, d.f = 10; p = 0.009), the difference was not significant (p = 0.92). On the basis of its lower p-value, the linear model better describes the relationship between Marginality and log geographic range size.

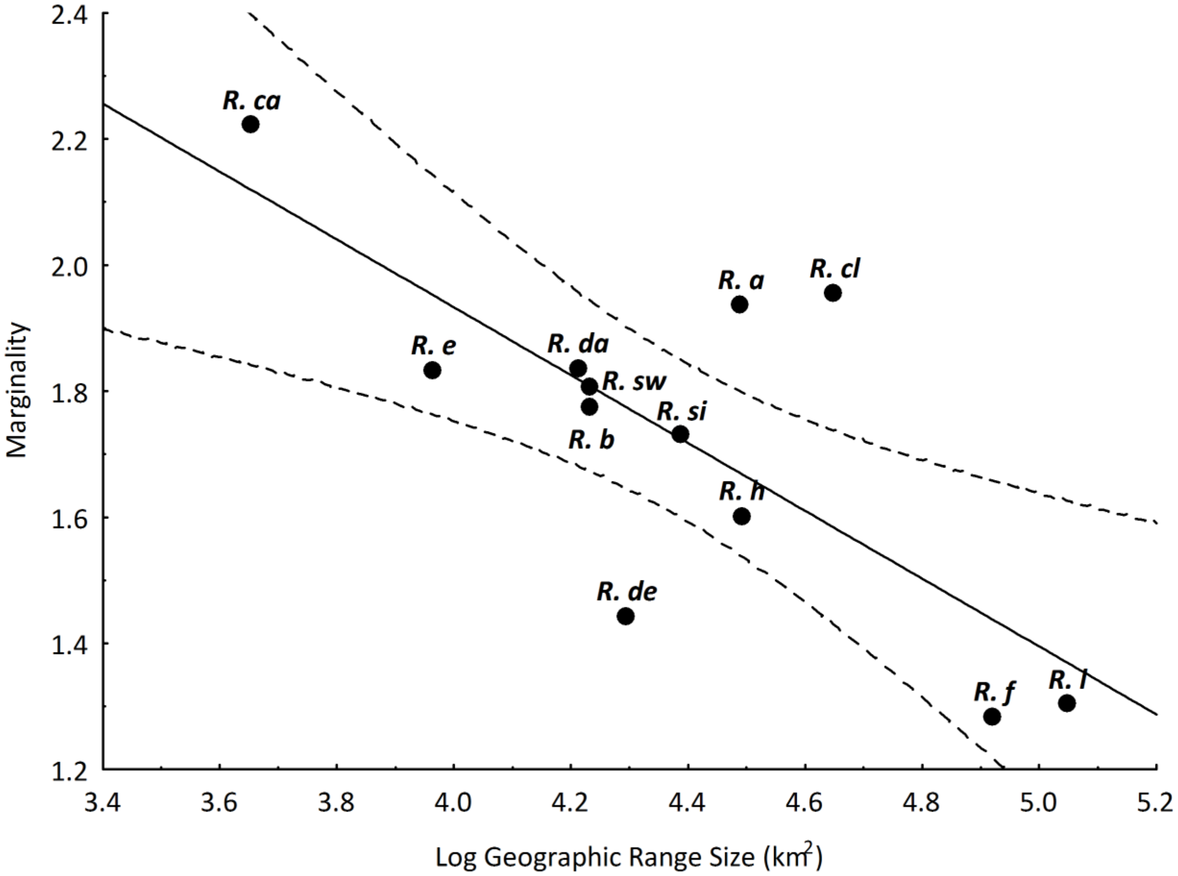


Figure 10: The regression of log Geographic Range Size and Marginality for 12 African *Rhinolophus* species. The solid line represents the best fit where Marginality = 4.0845-0.5379*Geographic Range Size, the dashed line represents the 95% confidence interval. The abbreviations are the same as those used in Figure 9.

Rhinolophus landeri and *R. fumigatus* were the two most tolerant species and *Rhinolophus capensis* was the least tolerant. Tolerance had both a significant linear (R^2 = 0.62; d.f = 10; p = 0.002) and quadratic (R^2 = 0.69; d.f = 9; p = 0.005) relationship with Geographic Range Size. There was a significant increase in the R^2 from a linear model to a quadratic (p = 0.17), therefore Tolerance is best described as having a polynomial relationship with Geographic Range Size (Figure 11).

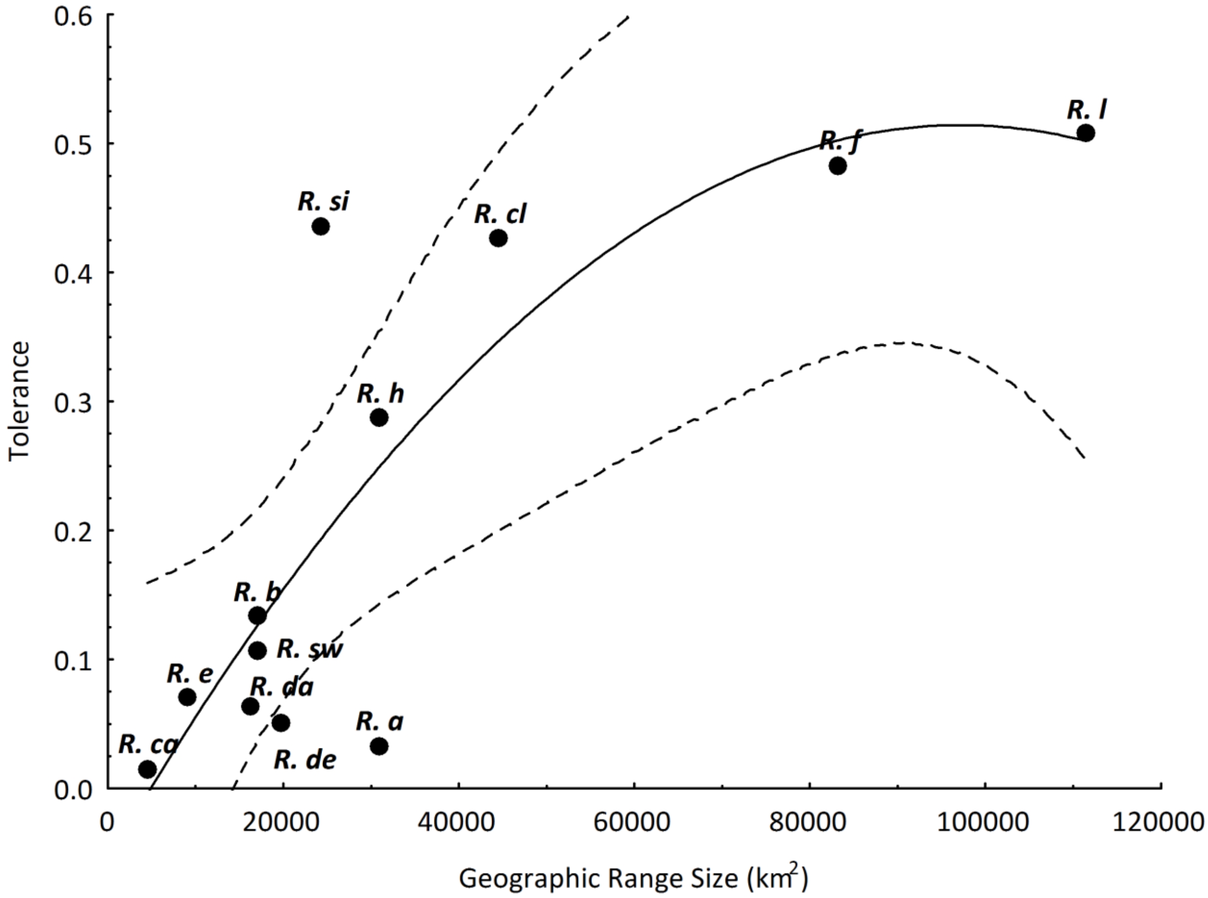


Figure 11: The regression of geographic range size and tolerance for 12 African *Rhinolophus* species. The solid line represents the best fit where Tolerance = 0.1954*Geographic Range Size^2 - 1.3042 *Geographic Range Size + 2.1546, the dashed line represents the 95% confidence interval. The abbreviations are the same as those used in Figure 9.

Overall specialisation values ranged from 1.97 for *R. landeri* to 64.84 for *R. capensis*. Specialisation had both a significant linear ($R^2 = 0.49$; d.f = 10; p = 0.01) and quadratic ($R^2 = 0.69$; d.f = 9; p = 0.01) relationship with log Geographic Range Size. There was a significant increase in the R^2 from a linear model to a quadratic (p = 0.03), therefore Specialisation is best described as having a polynomial relationship with log Geographic Range Size (Figure 12).

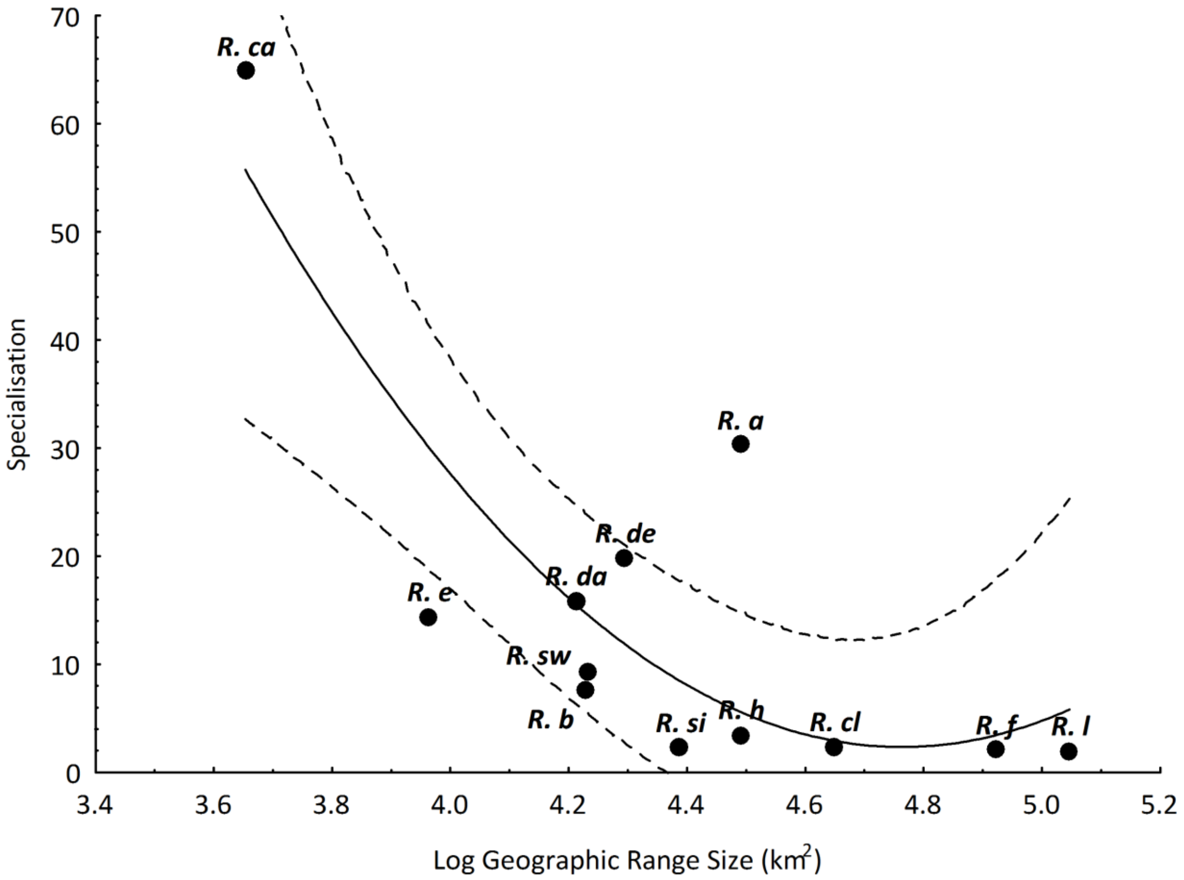


Figure 12: The regression of log geographic range size and specialisation for 12 African *Rhinolophus* species. The solid line represents the best fit where Specialisation = 43.307*Geographic Range Size^2 – 421.61*Geographic Range Size + 985.12, the dashed line represents the 95% confidence interval. The abbreviations are the same as those used in Figure 9.

DISCUSSION

I found that niche breadth assessed using environmental variables correlated with geographic range size in African Horseshoe bats supporting Brown's hypothesis (Brown 1984). Marginality and Specialisation were negatively correlated with geographic range size, and Tolerance was positively correlated with geographic range size. However, support for Brown's hypothesis was more ambiguous when niche breadth was assessed using specific biological variables. With the exception of diversity in roost use, biological variables did not explain variation in geographic range size in African Horseshoe bats. Diversity in microhabitat use and diet were not correlated with geographic range size, contradicting Brown's hypothesis but diversity in roost use was positively correlated with geographic range size consistent with Brown's hypothesis.

The ENFA characterized the niche of each of the 12 rhinolophids using climate, topography and vegetation as niche dimensions. In terms of these environmental variables, rhinolophids in general had high Marginality (Figure 10) which means that they only occupy certain habitats in Africa, or are present at a site only under certain environmental conditions. Marginality is a measure of the departure of a species' niche from the average available habitat or conditions. A specialist will exhibit more departure from the average available habitat, selecting a smaller subset of the available habitats, than a generalist and will have higher Marginality values (Entling et al. 2007). For example, the ENFA showed that *R. eloquens* was highly marginal in terms of altitude. The mean altitude in the locations where this species has been recorded (±1480 masl) is much higher than the mean altitude in Africa (±740 masl). In other words, *R. eloquens* prefers areas in Africa with higher than average elevation. Contrast this with *R. landeri* which showed almost no marginality in terms of altitude and occurs at a mean altitude of ±790 masl, much closer to the average altitude in Africa.

Widespread species such as *R. fumigatus* and *R. landeri* had the lowest Marginality values (Figure 10), did not show as much deviation from the mean conditions available in Africa as the other rhinolophids, and can be considered generalists. *Rhinolophus capensis,* the most restricted species, had the highest Marginality and is therefore classified as a specialist. This species was particularly marginal in terms of vegetation and mean annual temperature. It prefers Fynbos and succulent semi-desert and lower than average temperatures relative to the African mean. Thus the association displayed by these species between range size and whether they are generalists or specialists supports Brown's hypothesis.

Some species deviated from the relationship between Marginality and geographic range size, falling outside the 95% confidence interval. *Rhinolophus alcyone* should have a lower Marginality for its range size (Figure 10). In other words, this species is a specialist despite being fairly widespread relative to other rhinolophids. The ENFA showed that *R. alcyone* was marginal in terms of vegetation. This species exhibited a strong preference for tropical lowland rainforest and mosaics of forest and its niche was also characterised by high humidity and high mean annual precipitation which explains its restriction to tropical Africa (Figure 2). *Rhinolophus clivosus* also had a higher Marginality than would be predicted based on its range size. This indicates that this species does select particular conditions which could explain why it has a disjunct distribution (Figure 2). *Rhinolophus clivosus* expressed highest marginality in terms of mean annual temperature suggesting that temperature is an important factor determining where it occurs. It also showed preferences for certain vegetation types particularly Fynbos, succulent semi-desert and unpalatable grassland. Finally, *R. denti* had a lower marginality than predicted suggesting that it is a generalist. However, this species has a disjunct distribution occurring in West and southern Africa (Figure 2). The latitudinal extent of this species' distribution is thus fairly large but its extent of occurrence is still smaller that most African rhinolophids. In West Africa *R. denti* occurs in moist-infertile savanna and mosaics of forest but in southern Africa the species is associated with arid regions occurring predominantly in arid-fertile savanna and shrubland and grassy semi-desert. According to Csorba et al. (2003), there are two recognised subspecies of *R. denti*; *R. d. knorri* which occurs in West Africa is slightly smaller, darker in colour with heavier dentition than *R. d. denti* which occurs in southern Africa. Given this, and the different habitats used by *R. denti* across the continent, these two subspecies could well be cryptic species. If this is true, the two forms of *R. denti* will show higher marginality which could bring these species in line with the general trend between Marginality and geographic range size shown by most members of the genus (Figure 10).

Despite these exceptions, it appears that Marginality is a good predictor of geographic range size supporting Brown's hypothesis. Similar to Marginality, all the African rhinolophids had Tolerance values lower than 1 which indicates at least some form of specialisation (Hirzel et al. 2002). This means that, in addition to selecting marginal habitats, rhinolophids as a whole also tend to live in a narrow range of conditions showing restricted niches in terms of climate, topography and vegetation. They are also not tolerant toward deviations from their niches.

Rhinolophids that are widespread showed greater environmental tolerance than the more restricted species and there was a positive correlation with geographic range size as predicted by Browns hypothesis (Figure 11). Widespread species such as *R. fumigatus* and *R. landeri* had the highest Tolerance values indicating that they are more generalist than other rhinolophids. Although they had a narrow niche, it was relatively wider than other rhinolophids. Restricted species such as *R. capensis* and *R. eloquens* had low Tolerance values indicating that they are specialists with narrow niches. However, the relationship between the two variables was not linear. Tolerance reached a maximum when geographic range size became large and the relationship between the two was curvilinear, being best described by a polynomial equation. Brown's hypothesis does not explicitly predict linear relationships between niche breadth and range size as opposed to simply positive ones. In similar studies on hawkmoths (Beck and Kitching 2007), African primates (Eeley and Foley 1999) and European tree species (Köckemann et al. 2009), the respective authors report positive relationships between their measure of niche breadth and range size but failed to test specifically whether the relationship was linear. Nonetheless, their data do look linear and it is therefore interesting to find a non-linear relationship between niche breadth and geographic range size for rhinolophid bats. However, Essl et al. (2009) showed that in Austria, niche breadth of endemic plant taxa measured as a species' altitudinal range and as the number of habitats colonized had a curvilinear relationship with range size. These authors found that a logarithmic function best explained their data and not the polynomial one I found.

The non-linear relationship does make sense for rhinolophids from an adaptation perspective. As geographic range size increases, the range of conditions that a species can use (i.e. its Tolerance) increases too (Figure 11). Eventually, as range size continues to increase, the range of conditions that the species can use stops increasing. Both the Marginality and Tolerance indices showed that rhinolophids occupy a relatively narrow range of particular habitats and conditions. They are also adapted to use particular microhabitats namely clutter (Neuweiler 1989; Norberg and Rayner 1987; Schnitzler and Denzinger 2010; Schnitzler et al. 2003) and tend to avoid open areas, typically flying within vegetation cover and commuting between roosts and foraging areas along linear landscape features such as tree lines (Stone et al. 2009). Therefore, as range size increases fewer habitats for which they are adapted will be available to rhinolophids and hence Tolerance stops increasing. For example, *R. capensis* appears to be restricted to Fynbos and as geographic area in Africa increases beyond Fynbos and starts to incorporate other habitats and conditions the range of conditions that can be tolerated by this species does not increase linearly. A linear relationship would imply that rhinolophids are adapted to an infinite range of habitats and that there is no limit to their niche breadth.

Several species, e.g. *R. simulator* and *R. alcyone*, deviate from the general relationship between Tolerance and geographic range size. *Rhinolophus simulator* had a higher Tolerance than would be predicted from the size of its geographic range (Figure 11) and it is therefore a generalist with a restricted distribution. An alternative hypothesis to Brown's is that range size is determined largely by the availability of suitable habitat as opposed to being determined by niche breadth. This is called the Resource Availability hypothesis (Gaston et al. 1997b; Venier and Fahrig 1996) and it predicts that specialists using widespread resources can be widespread and that generalists using restricted resources can be restricted. This hypothesis is often tested by determining a species' niche position which is an indirect measure of habitat availability or of how typical the conditions used by a species are relative to the overall conditions (Gregory and Gaston 2000; Kolb et al. 2006; Seagle and McCracken 1986).

Several studies have found support for the Resource Availability hypothesis (Entling et al. 2007; Gregory and Gaston 2000; Rannap et al. 2009; Seagle and McCracken 1986) and it appears that niche position is a more important factor than niche breath for *R. simulator.* The ENFA showed that this species was a generalist occurring in a wide range of vegetation types such as mosaics of forest, unpalatable grassland and mopane savanna. However, these vegetation types have relatively small geographic extents in Africa which could explain why *R. simulator* also has a relatively small geographic distribution despite being a generalist. Its distribution could therefore be constrained by its preference for resources not widely distributed. Similarly, *R. alcyone* has a lower Tolerance than would be predicted from the size of its distribution. This species has a relatively large geographic distribution despite being a specialist. This too can be explained by the Resource Availability hypothesis because the vegetation types *R. alcyone* tends to occur in (especially mosaics of forest and tropical lowland rainforest) are relatively widespread across central Africa, congruent with the distribution of this species (Figure 2).

In fact the negative relationship I found between Marginality and geographic range size (Figure 10) also supports the Resource Availability hypothesis. Some studies have used the outlying mean index (OMI) analysis to measure niche breadth and niche position (Dolédec et al. 2000; Heino 2005). This analysis uses a similar technique to the ENFA in that it measures the distance between the mean habitat conditions used by a species and the mean habitat conditions across the study area. This provides a measure of the marginality of a species or its niche position. High values of OMI mean the species has a marginal niche and low values mean non-marginal niches. Therefore the Marginality index derived from the ENFA also describes the niche position of the 12 African rhinolophids modelled in this study. As in this study, Heino (2005) found that the niche position of stream insects in Finland was negatively correlated with distribution and that niche breadth was positively correlated. The negative relationship between niche position (i.e. Marginality) and geographic range size for African rhinolophids therefore supports the Resource Availability hypothesis. This means that in addition to niche breadth, niche position (i.e. the availability of suitable habitats or environmental conditions) is also important for African rhinolophids.

Similar to the Tolerance indices, the Specialisation indices indicate that all 12 rhinolophids exhibit at least some specialisation. This is expected because Tolerance is the inverse of Specialisation. *Rhinolophus capensis* showed the most specialisation meaning it has the narrowest niche in terms of climate, topography and vegetation. This species was significantly more specialized than the other species (Figure 12). Overall, widespread species had low specialisation and restricted species had high specialisation as predicted by Brown's hypothesis. There was a negative, curvilinear relationship between Specialisation and geographic range size (Figure 12). Specialisation decreased as geographic range size increased but eventually Specialisation reached a minimum suggesting there are limits to how much of a generalist rhinolophids can be. This limit is likely imposed by adaptations which restrict these bats to using a narrow range of resources e.g. cluttered habitats (Neuweiler 1989; Norberg and Rayner 1987; Schnitzler et al. 2003).

Niche breadth characterized by diversity in microhabitat use showed no relationship with geographic range size, contrary to Brown's hypothesis (Figure 7). Rhinolophid species that are more diverse in their microhabitat use are not more widely distributed than species that are less diverse. Microhabitat use among rhinolophids is clearly centered in highly cluttered environments and most seem to be high-clutter specialists showing low diversity in microhabitat use (Table 4). The vast majority of occurrences were in the high-clutter foraging zone and all species were detected at least once in this zone. Two species, *R. blasii* and *R. swinnyi*, were only detected in high-clutter. Overall occurrences declined as clutter density declined which is expected because rhinolophids are adapted for cluttered habitats (Arita and Fenton 1997; Neuweiler 1989; Norberg and Rayner 1987; Schnitzler et al. 2003; Siemers and Ivanova 2004). Occurrences in semi-clutter were dominated by *Rhinolophus clivosus*. Other rhinolophids were only rarely encountered in this type of habitat suggesting that *R. clivosus* can tolerate semi-cluttered environments more so than cogenerics. *Rhinolophus clivosus* was also more common in semi-clutter compared to high-clutter. Four species were present in the edge foraging zone but overall occurrences were low in this habitat except for *R. capensis*. This species used edge habitat significantly more than other rhinolophids in this study and was also more common in edge habitat compared to high-clutter and semi-clutter combined. Some rhinolophids prefer foraging in edge habitat, for example *R. euryale* (Goiti et al. 2008), so the presence of *R. capensis* in edge habitat is not anomalous. *Rhinolophus capensis*, with a relatively high Shannon-Weiner H' value is a generalist in terms of microhabitat use. This is contrary to Brown's hypothesis because it has a very restricted geographic range (Figure 2).

The lack of a relationship between the Shannon-Weiner Index and geographic range size (Figure 7) seems to be driven by the higher than expected value for *R. capensis*. When *R. capensis* is removed from the analysis, there is a significant positive relationship between diversity in microhabitat use and geographic range size. Most rhinolophids seem to conform to Brown's predictions but *R. capensis* has a wider niche breadth in terms of microhabitat use than expected for its range size. *Rhinolophus capensis* is syntopic across its range with just one other rhinolophid, *R. clivosus*. In contrast, the distributions of other rhinolophid species overlap (Figure 2). For example, at Sudwala (Figure 3) several rhinolophids co-occur and it appears that these species are competing because I found three species in the same habitat together (pers. obs.). Similarly, Kingston et al. (2000) suggested that competition has resulted in niche differentiation in a guild of 15 rhinolophoid bats in Malaysia. Schuchmann and Siemers (2010) also proposed that niche differentiation is likely in a community of five European horseshoe bats through variation in echolocation call intensities and prey detection distances. These studies suggest that where many rhinolophids are syntopic, competition could occur between species. Therefore, the absence of cogenerics at De Hoop could allow *R. capensis* to use a wide range of microhabitats.

The lack of a correlation between microhabitat use and geographic range size is surprising because habitat breadth is a good predictor of geographic range size in numerous studies (Eeley and Foley 1999; Fernandez and Vrba 2005; Pyron 1999; Verberk et al. 2010). However, rhinolophids use cluttered habitats and it is likely that this type of microhabitat will be available at a wide range of sites and therefore unlikely to prevent a rhinolophid from occurring there. For example, *R. denti* occurs in arid habitats in southern Africa which tend to be more open and have sparser vegetation than mesic areas. This might suggest that there will be a lack of cluttered microhabitats at sites in such areas making them unsuitable for rhinolophids. However, at Koegelbeen Cave, which is in an arid region in South Africa (Figure 3), *R. denti* was observed foraging close to the available vegetation, low to the ground and is therefore likely still perceiving the environment as cluttered (Schnitzler et al. 2003). In this way, microhabitat use among rhinolophids is unlikely to influence large-scale distribution patterns because suitable microhabitat is not a limiting factor for these bats. Using a greater diversity of microhabitats would therefore not result in an increase in range size in rhinolophids.

All the rhinolophids I studied had low food niche breadth with most feeding predominantly albeit to varying degrees on just two insect orders, Coleoptera and Lepidoptera (Table 6). This pattern is similar to other rhinolophids for example the eastern horseshoe bat, *Rhinolophus megaphyllus* in Australia (Pavey and Burwell 2004) and the Mediterranean horseshoe bat, *Rhinolophus euryale* (Goiti 2004; Goiti et al. 2008). Most species in the genus feed mainly on moths and beetles (Jones 1992). Despite low overall dietary breadth, there were differences in the degree to which different species were specialised and there is evidence that some African rhinolophids are more specialised in terms of diet than others. For example, *R. blasii* and *R. landeri* appear to be moth specialists while *R. fumigatus* appears to be a dietary generalist. However, dietary breadth failed to predict geographic range size in African rhinolophids overall. Species that have a greater dietary breadth are not more widely distributed than species with lower dietary breadth.

The lack of a relationship between dietary niche breadth and geographic range size (Figure 8) overall is possibly because of the low dietary niche breadth of *R. landeri* and the higher than expected dietary niche breadth of *R. capensis.* Similar to diversity in microhabitat use, most rhinolophids seem to conform to Browns predictions about dietary niche breadth and range size. For example, *R. blasii* had the lowest food-niche breadth showing definite preferences for moths. Whitaker and Black (1976) found that the stomach contents of several individuals contained only moths. Moth specialisation by *R. blasii* is therefore likely and ecomorphological evidence supports this as well. Freeman (1979) found a relationship between skull morphology and diet in insectivorous bats. Species with robust skulls consume more hard-bodied prey (e.g. beetles) while species with gracile skulls prefer soft-bodied prey (e.g. moths). Freeman (1981), Jacobs (1996), Bogdanowicz et al. (1999) and Jacobs (2000) have all published data consistent with this relationship. Freeman (1981) showed that *R. blasii* has a gracile skull and suggested that consequently this species should be specialized to feed on soft bodied prey, particularly moths. The high degree of specialisation for moths supports Brown's hypothesis because *R. blasii* has a fairly small geographic range size in Africa, although this species also occurs in southern Europe and in the middle east (Csorba et al. 2003).

Brown's hypothesis predicts that *R. capensis*, which is the most restricted African rhinolophid, should have low dietary niche breadth. In contrast, I found that *R. capensis* has a relatively high FNB for its range size. *Rhinolophus capensis* does not exhibit as much specialisation in terms of diet as do *R. blasii* or *R. landeri* for example despite having a much smaller geographic range. The estimate for food niche breath for *R. capensis* was based on multiple studies some of which, for example Jacobs et al. (2007), took place over several months encompassing more than one season. Bat diets often vary seasonally (Schoeman and Jacobs 2010; Whitaker and Black 1976) therefore estimates of dietary diversity will be influenced by the timing and duration of the study. Longer studies such as Jacobs et al. (2007) should therefore characterize dietary preferences of bats more accurately. Thus, it is unlikely that the high dietary niche breadth of *R. capensis* is a sampling artefact. On the other hand, *Rhinolophus landeri* was predicted to have a high dietary niche breadth but I found that it has a low dietary niche breadth despite being the most widespread rhinolophid in Africa. Unlike *R. capensis*, published dietary data for *R. landeri* are sparse and the estimate for food niche breath for this species was based on just two short term studies (approximately one month respectively); Fenton (1975) and Fenton et al. (1977). Therefore, the low dietary niche breadth of *R. landeri* is potentially a sampling artefact.

The high dietary niche breadth of *R. capensis* is anomalous for such a restricted species and as noted, likely not a sampling artefact. This species was captured primarily in the edge habitat zone and showed high diversity in microhabitat use overall (Table 4). Edge habitats are characterized by linear landscape features such as tree lines and hedgerows.

Linear landscape elements are often associated with high species diversity in many taxa including invertebrates such as insects (Forman and Baudry 1984; Verboom and Huitema 1997). Therefore, the use of edge habitat by *R. capensis* and the fact that it has a high diversity in terms of microhabitat use could give it access to a greater diversity of insect prey which could explain the high dietary niche breadth. Similar studies have shown geographically rare species to be diet generalists. For example microhylid frogs from the genus *Cophixalus* in Australia (Williams et al. 2006). These authors argue that this is a product of extinction filtering because geographically rare (i.e. narrowly distributed) species, which are extinction prone, are more likely to persist if they are diet generalists. Similarly, the small range size of *R. capensis* increases its extinction probability but the high diversity in both diet and microhabitat use could help this species reduce its extinction risk.

The fact that rhinolophid dietary diversity failed to correlate with geographic range size is also surprising because studies have shown that dietary breadth is an important predictor of range size and that diet is therefore one of the more important niche axes (Beck and Kitching 2007; Eeley and Foley 1999; Garcia-Barros and Benito 2010). However, rhinolophids are insectivorous bats and insects are the most abundant macroscopic organisms in most terrestrial habitats (Picker et al. 2002). Coleoptera and Lepidoptera, which are consumed by most rhinolophids, are among the most diverse insect orders (Gullan and Cranston 2010). Furthermore, Schoeman and Jacobs (2010) sampled insects during summer and winter using black-light traps at 6 sites across South Africa and found that moths were the most abundant medium and large sized prey. It is therefore likely that rhinolophids will find suitable insect prey at a wide range of sites and that their distributions will not be limited by the lack of available prey. It is also likely that the measure of dietary niche breadth failed to capture the true variation in the diets of the 12 species across their respective distributions. There are not many rhinolophid diet data for African species and the data that does exist is better for some than others. This inconsistency means that it is difficult to validly determine if rhinolophid dietary niche breadth can influence geographic range size without correcting for spatial and temporal variation in diet.

In terms of roost diversity, the slope of the regression line was significantly different from zero but the R^2 value was low (< 0.5) suggesting that there is only a weak relationship between the diversity of roosts used and geographic range size. One species, *R. darlingi*, seems to be responsible for the overall weak relationship as it has much higher roost diversity than other species with similar geographic range sizes (Figure 9). However, *R. darlingi* might be a species complex (D.S. Jacobs, unpublished data) so the true estimate for diversity in roost use could be lower for these 'species'. When *R. darlingi* is removed from the analysis, the linear regression is even more significant and the R^2 value much higher (> 0.5) resulting in an overall stronger relationship between diversity in roost use and geographic range size. *Rhinolophus hildebrandti* also deviated from the genus trend (Figure 9) but similarly, the taxonomic status of this species is uncertain with evidence suggesting that there may be more than one species of *R. hildebrandti* in southern Africa (Monadjem et al. 2010a; Monadjem et al. 2010b).

This result confirms that roosts are limiting factors in bat distributions as has been demonstrated previously (Churchill 1991; Kunz and Lumsden 2003; Maree and Grant 1997). The generalist species in terms of roost diversity are *R. clivosus*, *R. fumigatus*, *R. hildebrandti* and *R. landeri* which are the four most widely distributed species. In contrast, *R. capensis* and *R. eloquens*, which have restricted distributions, occupy a narrow range of roosts and are thus specialists. These two species have only been recorded roosting in caves and mines (Skinner and Chimimba 2005; Swanepoel et al. 2007). Diversity in roost use therefore explains variation in geographic range size in Horseshoe bats; species that use a greater variety of roosts also tend to be widely distributed, consistent with Brown's hypothesis

The reason why diversity in roost use was the only biological factor to correlate with geographic range size could be because roosts are a more significant limiting factor for bats because they are crucial to both survival and reproduction (Bell et al. 1986; Kunz 1982). Relative to cluttered microhabitats and insects, suitable roosts are not as widespread and readily available. For example, in savanna habitats, which extend widely across Africa, trees are scarce and the availability of suitable roosts sites is likely low (Aguirre et al. 2003). Rhinolophids that have a narrow tolerance for different roosts, preferring caves for example, can only expand into areas with suitable caves. A species that has a wide tolerance for different roosts can move into new areas where such roosts exist and if these roosts are associated with human activities (e.g. buildings, mines, tunnels) this is likely to result in an increase in the geographic range size of that species. It seems that the probability of a bat occurring at a site is highly dependent on the availability of suitable roosts and that roosts are more important in influencing their geographic distributions than microhabitat use and diet. A bat is more likely to find suitable microhabitat and prey at a particular site than it is to find suitable roosts.

Environmental factors appear to have more influence on the distribution patterns of rhinolophids across Africa than biological factors. Andrews and O'Brien (2000) have shown previously that small mammal species richness and distributions across southern Africa are strongly related to climate and vegetation. Cumming (2002) showed that for African ticks, biotic variables may be important predictors of distribution at smaller scales but that they play a subordinate role to climate in limiting the ranges of ticks at broad spatial scales. Similarly, the distribution of rhinolophids at smaller scales may be determined by microhabitat use and diet but at larger scales, their distributions seem largely determined by environmental factors. Perhaps diversity in microhabitat use and diet in rhinolophids might correlate with range size measured at smaller spatial scales such as at the landscape level or at the level of individual home ranges.

The size of a species' geographic range can be determined by a large number of factors (Bohning-Gaese et al. 2006; Calosi et al. 2010) which often act in combination rather than separately (Bohning-Gaese et al. 2006; Heino 2005). This is evidenced by the importance of both niche breadth and niche position in shaping the distributions of rhinolophids in Africa. Other current species-specific traits that could influence geographic range size such as dispersal ability and body size should not hold for this group of bats. There is no correlation between body size and range size in African rhinolophids (Figure 6) despite the existence of positive relationships between body size and geographic range size in many other taxa (Pyron 1999). Similarly, Arita (1993) found no significant relationship between body mass and area of distribution in neotropical bats.

One other factor that could influence the geographic range size of species' is the influence of human activity (Gaston 2008). If, as I suggest, habitat or resource availability is important for African rhinolophids, any human activity that reduces the amount of habitat available to a species could result in the reduction of the geographic range size of that species. Although most are listed as Least Concern, the major threats to some African rhinolophids according to the IUCN Red List of Threatened Species^{TM} include habitat loss in at least some parts of their range resulting from logging, conversion of land to agriculture and mining operations. Some species are also threatened via destruction and disturbance of roost sites. One other anthropogenic impact that could be relevant to bats is light pollution which has been proposed as an emerging threat to biodiversity (Hölker et al. 2010). In an experimental study testing the effects of light pollution on lesser horseshoe bats, *R. hipposideros*; Stone et al. (2009) found that bat activity was reduced and the onset of commuting behaviour was delayed by artificial lighting. Their results suggest that light pollution may fragment commuting routes causing bats to alter their commuting behaviour. Because rhinolophids use linear habitat features for commuting they are especially vulnerable to fragmentation which could have conservation consequences (Stone et al. 2009). To assess variation in geographic range size it is important to consider these effects.

Finally, history can have a dramatic effect on current day distributions of species (Brown et al. 1996). There is evidence that species distributions reflect a long history of responses to habitat or environmental changes produced by geological activity over the past several million years (Riddle 1996). This is referred to as the history of place and it has influenced past colonization, speciation and extinction events that may affect current day distributions (Brown et al. 1996). Current day distributions can also be affected by phylogenetic constraints imposed by a species' history of lineage (Brown et al. 1996). This refers to the changes in the intrinsic characteristics of a species inherited from their ancestors. Past environments have acted as selective agents to influence environmental requirements and tolerances of contemporary species which in turn affects their geographic range. For example, Flanders et al. (2010) combined an ecological niche model with phylogeographical analyses to test the prediction that the greater horseshoe bat *R. ferrumequinum* did not undergo dramatic range contractions in Central/East China and

Japan at the time of the Last Glacial Maximum (LGM). They argue that populations of *R. ferrumequinum* were able to persist in multiple refugia over time and that during the peak of the LGM there would have been a relatively small southerly shift in this species' range. Their results suggest that the current and past distributions of *R. ferrumequinum* are not dramatically different. Although this study demonstrated that current species specific traits such as niche breadth and niche position correlate well with geographic range size, the current distributions of African rhinolophids also need to be considered in the context of their evolutionary history.

There have been relatively few attempts to evaluate Brown's hypothesis (Gaston and Spicer 2001). In part this is because it is based on Hutchinson's *n*-dimensional niche concept which is difficult to make fully operational (Colwell and Futuyma 1971; Gaston et al. 1997b; Thompson et al. 1999). However, the ENFA is based directly on Hutchinson's idea and is therefore a useful tool for quantifying niche breadth. I argue that this method allowed for a reliable test of Brown's hypothesis which seems to be supported by my study. For closely related, ecologically similar organisms such as horseshoe bats, generalists tend to be widespread and specialists tend to be narrowly distributed. This is the first study to test Brown's hypothesis using bats and it adds to the diversity of taxa for which positive relationships have previously been found suggesting some generality to Brown's idea. However, Brown originally developed his hypothesis to explain the often observed positive relationship between abundance and distribution (Brown 1984; Gaston et al. 1997b) making no predictions about the shape of the relationship between niche breath and range size. Most tests of this hypothesis report linear trends but I found that the shape of the relationship between niche breadth and range size was curvilinear. This could exist because rhinolophid bats are adapted to use a narrow range of habitats and niche breadth is therefore restricted; as range size increases, niche breadth stops increasing. Future tests of Brown's hypothesis should also consider the shape of the curve and it would be interesting if other organisms similarly adapted to a narrow range of niches also displayed the same curvilinear relationship that I found in African rhinolophids. In conclusion, I found that range size appears to be influenced mainly by abiotic factors such as climate, topography and vegetation as opposed to biotic factors. However, as for African rhinolophids, biotic variables can also have an important influence on geographic range size for some taxa.

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