THE RELATIVE INFLUENCE OF COMPETITION AND COEVOLUTION ON THE COMMUNITY STRUCTURE OF INSECTIVOROUS BATS IN SOUTHERN AFRICA

M. Corrie Schoeman

University of Cape Town
February 2006

Supervisor: A/Prof David. S. Jacobs

A thesis submitted to the University of Cape Town in
candidacy for the degree of Doctor of Philosophy

DECLARATION

This thesis is the result of my own research and includes nothing which is the outcome of work done in collaboration except where specifically indicated in the text. The text does not exceed 80,000 words and no part has been submitted to any other university in application for a higher degree or diploma.

signature removed

M. Corrie Schoeman

ABSTRACT

Biotic filters rather than abiotic filters should influence the community structure of animals such as insectivorous bats with life histories characterized by low fecundity, low predation risk, long life expectancy, and stable populations. I investigated the relative influence of biotic filters on various parameters that define bat community structure, based on predictions from competition and coevolution hypotheses. Each of the competing hypotheses was considered from a number of different perspectives to provide multiple opportunities from which to uncover the mechanism that could result in non-random patterns of community structure. I used a battery of null model and multivariate analyses to test the deterministic or non-deterministic nature of phenotypic, trophic, and species composition patterns of insectivorous bat communities - which I called ensembles. I obtained data for these analyses by sampling the local and regional species richness of insectivorous bats of southern Africa between 2001 and 2004. Rarefaction and species richness estimators indicated that species inventories of the fynbos, forest, and savanna ensembles, and the Cape Floristic Kingdom regional pool, were complete. As hypothesised, competition and coevolution filters strongly influenced parameters that define bat community structure. My results show that the phenotypic and trophic community structure of insectivorous bats at a local scale exhibit non-random patterns consistent with competition and coevolution hypotheses. Except for an even body size distribution, non-random patterns are not ubiquitous across ensembles. This is linked to multiple causations of competition and coevolution filters operating at a local scale. There was evidence that competition influenced body size distribution across ensembles, and echolocation and dietary patterns in ensembles with high species richness or abundance. At the same time, coevolution filters - mediated by prey defence - strongly influence dietary niche patterns, and to a lesser degree, echolocation patterns. Thus, the non-random phenotypic and trophic patterns of ensembles across southern Africa reflect competition and coevolution filters operating in tandem, or separately, at a local scale. Moreover, abiotic filters such as geographic distribution ranges of small and large-bodied species, extinction risk, and the physics of flight and sound probably also interacted at local and/or regional scales to influence the structure of coexisting bats at a local scale.

ACKNOWLEDGEMENTS

First, and foremost, I express my gratitude to my supervisor, A/Prof David Jacobs, who played an instrumental role during my studies at UCT. It was the trust he placed in this project, and willingness to debate it with passion and intelligence, that made me want to succeed – hopefully to his high standards.

I thank my UCT colleagues, Daniel Robeiro, Samantha Stoffberg, and Dr. Geeta Eick, for their time and invaluable help in the field. These were adventures, I will never forget. Many people assisted in fieldwork, but a special thanks to Ernest Seaman, Mark Kratzman, and Pieter Malan. I also owe a special thanks to Dr. Geeta Eick and Samantha Stoffberg for the genetic analyses, and explanations of them, that significantly strengthened the statistical analyses of Chapters 5 and 6.

In addition, I am grateful to Prof. Robert Barclay, who during his sabbatical at UCT listened with patience and wisdom to my (often wild) ideas, and always managed to separate clarity from clutter.

I especially thank Tania Nash for her assistance, skill and patience when designing the final manuscript, and most importantly, for pacifying the cranky author during many of his darkest hours. Her generosity will not be forgotten.

This work was supported by grants from the National Research Foundation, K. W. Johnston Bequest Scholarship, Department of Zoology Merit Scholarship, and University of Cape Town Research Associateship Award

Finally, I am obliged to my family members, who each played unique but important roles during the years of my studies.

CONTENTS

Chapter 5 Phenotypic niche patterns support competition and coevolution hypotheses

Chapter 6 Trophic niche patterns support competition and coevolution hypotheses

Chapter 7 Patterns of species composition do not support competition hypotheses

"What is it like to be a bat? ....what is it like for a bat to be a bat?"

Thomas Nagel *Philosophical Review LXXXIII* (p. 436, 1974)

Chapter 1

COMMUNITY ECOLOGY AND INSECTIVOROUS BATS

INTRODUCTION

> "Throw up a handful of feathers, and all must fall to the ground according to certain laws: but how simple is this problem compared to the action and reaction of the innumerable plants and animals which have determined, in the course of centuries, the proportional numbers and kind of trees now growing on the old Indian ruins!"
>
> (Darwin 1859, p. 59)

Community ecology is one of the most challenging and most difficult of all sciences due to its innate complexity, multi-dimensionality, extensive scale in space and time, multiple causality, and empirical difficulties of data collection and analyses (Lawton 2000). However, the study of community ecology is also one of the most promising, important, and urgent of scientific pursuits (Gotelli & Graves 1996, Gaston & Blackburn 2000, Lawton 2000, Webb *et al.* 2002, Gotelli 2004). There are many reasons, moral, and aesthetic, why we should be alarmed by the rapid destruction of the earth's pristine systems (for a full discussion see Kunin & Lawton 1996). In particular, many complex communities of pristine natural systems are vanishing rapidly before we can understand how they are organized or how they behave, and influence other communities, within the larger system (Lawton & May 1995). These insights would be a reliable guide to practical management plans to conserve complex natural systems "in the face of the human onslaught" (Wilson 1992).

The taxonomic and ecological diversity of insectivorous bats may render them as ideal study animals for community organization studies (Findley 1993, Patterson, Willig & Stevens 2004). Tropical bat communities may comprise more than 50 species (Findley 1993, Kingston *et al.* 2000). Indeed, no other group of mammals is known to approach such high degrees of alpha diversity (Patterson, Willig & Stevens 2004). This leads to the question whether their species-rich communities are structured in any way, specifically by competition to partition available resources (Kingston *et al.* 2000, Patterson, Willig & Stevens 2004). However, one of the main assumptions underlying many testable theories of community organization is that the community members perceive the environment as relatively stable and the system has reached an ecological and evolutionary equilibrium (Gotelli & Graves 1996). Otherwise, the organization of communities will change through time, and the observed "patterns" of community structure may be more apparent than real (Wiens 1981). The biology, life history and population structure of bats suggest that they perceive their habitat as relatively stable and predictable (Findley 1993).

THE BIOLOGY OF INSECTIVOROUS BATS

TAXONOMY AND TROPHIC DIVERSITY

Bats belong to the order Chiroptera and constitute approximately one-quarter of living species of mammal. Chiroptera includes 18 families and 202 genera (c.a. 1100 species), traditionally divided into two suborders, Microchiroptera and Macrochiroptera (Honeycutt & Adkins 1993, McKenna & Bell 1997, Simmons & Geisler 1998, Simmons 1998, 2003, Simmons & Conway 2004). Recent molecular evidence suggests that the Microchiroptera are paraphyletic, however (Teeling *et al.* 2000, 2002, Hutcheon & Kirsch 2004, Van Den Bussche & Hoofer 2004, Eick, Jacobs & Matthee 2005). The microchiropteran superfamily, the Rhinolophoidea (Rhinolophidae, Hipposideridae, Megadermatidae and Rhinopomatidae) now appear to be more closely related to the Pteropodidae, traditionally the only family in the Macrochiroptera, than to other Microchiroptera. I thus follow the division of chiropterans into the two suborders proposed by Hutcheon & Kirsch (2004) and Eick, Jacobs & Matthee (2005), 'Pteropodiformes' (representing the Pteropodidae, Rhinolophidae, Hipposideridae, Megadermatidae and Rhinopomatidae) and 'Vespertilioniformes' (representing the remaining microchiropteran families).

Bats are the only mammals capable of true flight, and exhibit the highest trophic diversity among mammals (Kunz & Pierson 1994, Hutson, Mickleburgh & Racey 2001, Simmons 2003). Bat diets can be classified broadly into herbivory and animalivory (Patterson, Willig & Stevens 2004). Roughly, a third of bats (families Phyllostomidae and Pteropodidae) visit plants exclusively or opportunistically for fruit, nectar, or pollen (Fleming 1993). Herbivorous bats are common in the tropics (Fleming 1993) where they play important roles as seed dispersers and pollinators in local ecosystems (Dumont 2004). However, most bats are insectivorous (>70%), which are distributed worldwide (Jones & Rydell 2004), and dominant in all temperate and most tropical bat assemblages (Francis 1990, Heller & Volleth 1995, Simmons & Voss 1998, Patterson, Willig & Stevens 2004). The enormous adaptive radiation of insectivorous bats is principally attributed to adaptations of flight and echolocation enabling them to capture nocturnal flying insect prey in a diversity of habitats (Fenton 1984, Neuweiler 1990, 2003, Fenton *et al.* 1995, Arita & Fenton 1997, Teeling *et al.* 2002, Simmons & Conway 2004).

The oldest known fossil bat, *Icaronycteris index*, dates back at least 53 million years, and already exhibits flight and echolocation capabilities of modern day insectivorous bats (Simmons & Geisler 1998). Echolocation has evolved in the bat suborder Vespertilioniformes, in the bat families Rhinolophidae and Hipposideridae (Pteropodiformes), and in the bat genus *Rousettus* (Pteropodiformes). Echolocation also evolved in dolphins and in certain bird species (*Staetornis caripensis* and *Collocalia* and *Aerodrama* spp). By comparison, most other animals that hunt prey at night use vision as their sensory mechanism (Neuweiler 2000).

Moreover, the remarkably high local and regional diversity that insectivorous bats achieve can be linked to flight and echolocation adaptations enabling bats to occupy a high diversity of niches (Patterson, Willig & Stevens 2004). The ability of bats to move quickly and efficiently over large distances in search of food, roosts, and mates probably permits an extensive and refined partitioning of resources (Patterson, Willig & Stevens 2004). Conversely, non-volant mammals must operate within a smaller spatial scale, which leads to less specialized patterns of resource utilization (Patterson, Willig & Stevens 2004). In addition, resource partitioning is frequently linked to the sensory abilities of coexisting bats. For example, echolocation signals reflected niche differentiation in five sympatric congeneric low duty-cycle echolocating bat species (Siemers & Schnitzler 2004). Thus, the sensory ecology of bats probably plays an important role in the structuring of their communities (Siemers & Schnitzler 2004).

THE ROLE OF ECHOLOCATION AND FLIGHT IN COMMUNITY STRUCTURE

Echolocation involves the emission of sound pulses and analysis of the returning echoes to detect, characterize, and localize objects that reflect the impinging pulse as an echo (Fenton 1990, Neuweiler 2000, Schnitzler & Kalko 2001). Two different echolocation systems evolved independently in the Chiroptera: high and low duty-cycle echolocation (Eick, Jacobs & Matthee 2005).

High duty and low duty-cycle echolocating bats

Quality of information extracted from the spectral and temporal parameters of echoes depends on the physical structure of the emitted echolocation call and the performance of the bat's auditory system. Species using low duty-cycle echolocation emit narrowband or broadband pulses separated by inter-pulse intervals that are much longer than the duration of the emitted pulses. Such species thus separate the emitted pulse from the returning echo in time (Fenton 1990).

In contrast to narrowband CF and QCF low duty-cycle echolocation signals, broadband frequency modulated (FM) low duty-cycle echolocation signals typically sweep downward through as much as an octave for a short duration of time (Fenton 1990, Neuweiler 2000, Schnitzler & Kalko 2001), with concomitant increased accuracy in range and position of the target in space (Simmons & Stein 1980). FM signals sweep rapidly through the corresponding neuronal filters, and are therefore reliable time markers to determine the range of a target (Moss & Schnitzler 1995). In addition, many neuronal filters are activated across the broad frequency range of the echo, increasing reliability of the monaural and binaural cues to localize prey in space (Schnitzler & Kalko 1998, 2001). However, low duty-cycle FM signals are less suited for the detection of weak echoes since neuronal filters are activated for only a short time. Such signals are therefore not as good for increasing the distance at which objects are detected (Schnitzler & Kalko 1998, 2001).

Low duty-cycle narrowband signals composed of constant frequency (CF) or shallow-modulated frequency (QCF) components are well suited for detection because they activate the neuronal filters to the corresponding frequency band during the entire echo (Schnitzler & Kalko 1998, 2001). In addition, if these signals are of long duration, amplitude and frequency modulations in the echoes resulting from target movement assist classification of target (Schnitzler and Kalko 1998, 2001). An acoustic 'glint', a short prominent amplitude peak in the echo, is created when a fluttering insect's wing is perpendicular to the incoming sound wave. Glints can be 20 to 30 dB stronger than an echo from the body from the insect, increasing likelihood of detection (Kober & Schnitzler 1980, Moss & Zagneski 1994). Narrow band signals are therefore better at increasing the distance at which objects are detected. Inter-pulse intervals of the CF signals used by rhinolophids, hipposiderids, and the mormoopid, *Pteronotus parnelii*, are shorter than the duration of the call and these bats are consequently known as high duty-cycle echolocators (Fenton 1990). The long CF signals often overlap with the returning echo but the overlap does not produce masking effects because Doppler-shift compensation keeps the target echo in the range of the neurons of the acoustic fovea (Neuweiler 1990). The acoustic fovea is a group of neurons that are sharply tuned to a very narrow frequency band, a few kHz higher than the peak frequency of the emitted signal. Hence, the emitted pulse is separated from the returning echo in frequency rather than time (Fenton 1990). In contrast to low duty-cycle signals, high duty-cycle signals are well suited for the detection of weak echoes, but less suited for localization of the target (Schnitzler & Kalko 1998, 2001). On the other hand, Doppler-shift compensation combined with a specialized auditory system, enable high duty cycle echolocating bats to detect and classify fluttering prey in cluttered habitats by listening to the unique acoustic glints imprinted by the fluttering wings of different insects onto the echoes of their CF calls (Schnitzler 1987, von der Emde & Menne 1989, von der Emde & Schnitzler 1990).

Echolocation is ineffective over long ranges (Kick 1982), and therefore sets spatial limits on where bats can forage. Geometric and atmospheric attenuation severely reduce the intensity of echolocation echoes with increasing target distance (Pye 1980, Lawrence & Simmons 1982). Furthermore, the intensity of the target echo depends on the size and the form of the target (Barclay 1985, Barclay & Brigham 1991, Waters, Rydell & Jones 1995). Consequently, the flight style, wing shape, and echolocation systems of bats are adapted specifically for the habitat structure in which they forage (Aldridge & Rautenbach 1987, Norberg & Rayner 1987, Fenton 1990, Schnitzler & Kalko 1998, 2001, Neuweiler 2000). Based on these adaptations, coexisting insectivorous bats of communities can be sub-classified into three broad functional feeding groups (Crome & Richards 1988, Fullard *et al.* 1991, Schnitzler & Kalko 1998, 2001).

Functional groups: open-air, clutter-edge, and clutter feeders

Comparative studies show that the most important ecological constraint on foraging insectivorous bats is clutter i.e. the number of obstacles a bat has to detect and avoid. Clutter in this context, poses perceptual as well as mechanical problems for bats (Fenton 1990). Perceptually, bats are constrained by the capabilities of their sensory mechanism (e.g. echolocation, vision, olfaction, hearing) to detect, classify, and localize potential prey near clutter. Mechanically, bats are constrained by the capabilities of their motor mechanism, in particular flying ability (Norberg & Rayner 1987). Wing morphology and echolocation signals are therefore part of the same adaptive complex (Arita & Fenton 1997). For example, a wing shape that allows fast flight would be useless if coupled with echolocation calls that only permit short detection distances. Such a bat would not be able to detect prey soon enough to capture them. Conversely, wing morphology adapted for slow manoeuvrable flight in clutter needs to be coupled with echolocation signals suitable for distinguishing between prey and clutter echoes.

Clutter echoes and obstacles pose no problems for the open-air functional group of bats that feed on volant prey high above the ground and far from vegetation. Masking problems are not likely to affect echolocation signals as long as the emitted signal does not overlap with the returning echo. Nevertheless, open-air bats must find relatively small prey in a big space. Hence, echolocation signals are optimized for detection, and wing morphology geared for speed and agility (Norberg & Rayner 1987, Schnitzler & Kalko 1998, 2001).

The clutter-edge functional group comprises bats that hunt for insects near the edges of clutter such as forest edges and gaps, and therefore experience perceptual and mechanical constraints at the same time. They must distinguish insect echoes from edge clutter echoes, and navigate along these edges avoiding collision. Clutter-edge bats solve these problems by using mixed signals (Schnitzler & Kalko 1998, 2001). Typically, search phase echolocation consists of QCF signals alternated with FM signals. QCF signals increase detection distance and the FM signals facilitate the localization and classification of clutter echoes from insect echoes (Schnitzler & Kalko 1998, 2001). Wing morphology is variable but most species have average wingspans and wing areas. Consequently, some bats are very flexible in their foraging and echolocation behaviour and often switch between open-air and clutter-edge space (Fenton 1990).

The clutter functional group comprise bats that search and capture insects in highly cluttered space close to the vegetation or ground, and therefore experience more perceptual and mechanical constraints than clutter-edge foragers. Clutter bats must distinguish insect echoes buried in clutter echoes, and at the same time know their exact spatial position to navigate and avoid collision with the clutter. Two different sensory strategies have evolved to solve these problems (Schnitzler & Kalko 1998, 2001). The first strategy is used by high duty-cycle echolocating bats use overlap insensitive CF signals of long duration to hunt fluttering insects. The second strategy evolved in bats that use low duty-cycle echolocation to glean prey from surfaces. These bats solve the perceptual problems by using overlap sensitive uni- or multi harmonic FM signals of short duration at low intensities (< 100 dB). Short duration and low intensity of emitted signals may prevent overloading the sensory system with clutter echoes (Schnitzler & Kalko 1998, 2001). In addition, many of these bats have large ears used for prey generated acoustic cues such as calls of crickets and frogs (Tuttle & Ryan 1981, Bell 1982, Fenton, Gaudet & Leonard 1983). Despite two different echolocation mechanisms, all clutter foraging bats have similar short and broad wings associated with slow manoeuvrable flight necessary for clutter habitats (Norberg & Rayner 1987).

To conclude, coexisting bats within communities exhibit highly diversified morphologies and corresponding echolocation strategies that allow them to hunt for their insect prey in particular habitats. Most insectivorous bat communities probably exhibit this basic functional feeding group structure (McKenzie & Rolfe 1986, Crome & Richards 1988, Fullard *et al.* 1991, Schnitzler & Kalko 1998, 2001, Patterson, Willig & Stevens 2004). In addition to habitat use, ecological and evolutionary factors associated with flight and echolocation adaptations also severely constrain the body size of insectivorous bat species (Arita & Fenton 1997). Body size is an important phenotypic trait that defines community structure at the levels of morphology, physiology, behaviour, and ecology (Barclay & Harder 2004, Simmons & Conway 2004, Speakman & Thomas 2004, Swartz, Freeman & Stockwell 2004, Willig, Patterson & Stevens 2004).

THE BODY SIZE OF BATS

Body sizes of bats are small compared to other flying vertebrates (Simmons & Conway 2004). Weighing between 1.5 - 2 g, the bumblebee bat, *Craseonycteris thonglonglyai*, is the smallest extant mammal (Jones 1996). In contrast, the largest extant bat, *Pteropus vampyrus*, has a mean body mass of 1.2 kg (Koopman 1994). By comparison, birds can weigh as little as the bumblebee bat, but wandering albatrosses, *Diomedea exulans*, have body masses of over 11 kg (Maclean 1985). In addition, body sizes of insectivorous and carnivorous bats are significantly smaller than body sizes of frugivorous and nectarivorous bats. For instance, Jones (1996) calculated a mean body mass > 200 g for 55 species of pteropodids, but the largest non-pteropodid, *Cheiromeles torquatus*, weighed 160 g. Indeed, more than 70% of insectivorous species have a mean body mass < 20 g, and almost 40% weigh less than 10 g (Jones 1996, Jones & McLarnun 2001).

The mechanics and metabolic requirements for sustained flapping flight are the main factors limiting upper body size in bats (Speakman & Thomas 2004). Large birds glide and soar for much of their flight, relative inexpensive strategies in terms of metabolic requirements. However, the nocturnal habits of bats preclude them from thermal soaring since convective air currents are absent at night (Speakman & Thomas 2004). In addition, gliding is not possible due to limits on the length and design (e.g. slits for drag reduction - provided by primary feathers of birds) of bat wings (Speakman & Thomas 2004). Furthermore, the mammalian metabolic system may not be able to provide sufficient power for animals larger than 1.5 kg to fly (Speakman & Thomas 2004). Combined, these factors account for the tenfold smaller body sizes of bats compared to birds.

The physics of flight and sound combined with the size of available prey may put further limits on the body size of echolocating bats. Most available aerial prey are relatively small (Black 1974, Jones & Rydell 2004). The mechanics of prey capture in flight coupled with the small effective range of echolocation selects for a small body size capable of the maneuverability and agility necessary to hunt small prey at short range (Norberg & Rayner 1987, Barclay and Brigham 1991, Jones 1996, Norberg 1998). Furthermore, the coupling of flight and echolocation mechanisms puts a lower limit on echolocation frequencies, and therefore an upper limit to body size, necessary to detect small flying prey (Jones 1994, 1996). To summarize, the body sizes of insectivorous bats are severely constrained by the mechanics of flight coupled with the efficiency and energetic cost of echolocation necessary to capture abundant small volant prey. However, the life history traits of bats are usually associated with large-bodied mammals.

LIFE HISTORIES AND POPULATION STRUCTURE

Though small, bats in general exhibit low fecundity coupled with long lifespan. These life history traits are relatively invariable among species, despite the high taxonomic and ecological diversity of the order (Barclay & Harder 2004). Low reproductive rate in bats is probably compensated by low mortality from predation, allowing an extended life span (Racey & Entswistle 2000, Barclay & Harder 2004). Furthermore, the reproductive biology of bats suggests that they rely on a stable population structure (Findley 1993, Racey & Entswistle 2000, 2004).

Life in the slow lane

Bats are remarkably long-lived. Average longevity of bats, based on 41 longevity records, is 14.6 years (Tuttle & Stevenson 1982). Records show Greater horseshoe bats (Rhinolophidae) live up to 30 years in the wild (Corbet & Harris 1991), and a little brown bat, *Myotis lucifugus*

(Vespertilionidae), lived for at least 34 years (Davis & Hitchcock 1965). Longevity is coupled with low fecundity. On average, female bats produce one young per year (Barclay & Harder 2004). Although litters of two or more young occur in 43% of vespertilionid species, females of the most speciose genus, *Myotis*, bear only one, except *M. austroriparius* (Barclay & Harder 2004). In addition, period of infant dependency is relatively long (Barclay & Harder 2004), and sexual maturity comes at a relatively advanced age (Corbet & Harris 1991, Racey & Entwistle 2000). By comparison female shrews live 10 times shorter, produce an additional litter per year each numbering 3.7 times more offspring, lactate for a 2.4 times shorter period, and wean litters three times heavier than similar sized female insectivorous bats (Barclay & Harder 2004).

Factors causing low fecundity

Four different factors might account for life in the slow lane: flight, food resources, monotocous reproduction, and low risk of predation (Barclay & Harder 2004). Flight is energetically more costly than terrestrial locomotion per unit time (Thomas 1987), and pregnancy caries an additional cost for volant females (Myers 1978). However, there is little evidence that high energetic costs of flight constrain life history options for bats (Barclay & Harder 2004). For example, pregnant and lactating female *Myotis yumanensis* differed significantly in wing loading but foraged in the same habitat (Brigham, Aldridge & Mackay 1992). Furthermore, males and females add so much body fat before hibernation that they weigh more than pregnant females (Kunz, Wrazen & Burnett 1998). In general, female bats do not carry a significantly lower litter mass than other similarly sized female mammals (Kurta & Kunz 1987).

If there is a high energetic cost to weaning large sized young, the number a female bat could raise at once may be limited (Barclay 1994, 1995). In tropical environments, energy content of resources limit reproductive output less for bat species that consume plant material than bat species that hunt animals (Barclay & Harder 2004). However, female bats that produce one young per litter encompass the dietary diversity, duration of reproductive season, and body size exhibited by Chiroptera as a whole, therefore it is unlikely that energetic content of food resources limits their reproductive output (Barclay & Harder 2004). Alternatively, calcium content of diet rather than its energy content, might limit reproductive output by bats (Barclay 1994, 1995). The hypothesis is based on the assumptions (Barclay & Harder 2004) that calcium demands increase during pregnancy (Keeler & Studier 1992), and calcium content of insects, fruit, and pollen is relatively low (Studier & Sevick 1992). Despite some support, the calcium hypothesis requires further investigation, in particular assessment of calcium demands during reproduction, and calcium content in diet and available prey (Barclay & Harder 2004).

Most bats may be evolutionary constrained to life in the slow lane by their monotocous reproductive system, i.e. only one egg per cycle matures and is released for fertilization (Neuweiler 2000, Barclay & Harder 2004). Production of more than one young per litter could potentially open up a greater range of life-history options to these bats (Barclay & Harder 2004). For example, in climates where food resources are unpredictable, it may be adaptive to fertilize multiple eggs (e.g. female *Eptesicus fuscus* have up to seven implanted embryos), and reabsorb the excess embryos if food resources are low (Neuweiler 2000). At least two families, Pteropodidae and Vespertilionidae, include polytocous members (Neuweiler 2000, Barclay & Harder 2004). However, polytocous bats still produce significantly fewer young than similar sized nonvolant mammals (Barclay & Harder 2004). Thus, the low number of eggs available for fertilization only partly explains the evolution of low fecundity in bats (Barclay & Harder 2004).

If mortality risk faced by bats from predators is sufficiently low, there may be no selection for high fecundity (Barclay & Harder 2004). Reports of predation on bats are mostly anecdotal and few studies test related hypotheses (Findley 1993, Fenton 1995). Predation hypotheses require age-specific mortality data that is seldom obtainable for bats (Barclay & Harder 2004). Predators, such as owls, hawks, and snakes, are known to attack bats as they leave their roosts usually at dusk (Findley 1993, Fenton *et al.* 1994, Fenton 1995). However, bats have several behaviours that make them less susceptible to predation. For example, a delayed time of emergence may decrease encounter rates with predators, but also with potential prey, in particular flying insects that are most abundant at dusk (Fenton 1995). Burst-emergences often accompanied by shrill cries by bats from roosts may therefore represent anti-predator behaviour (Fenton *et al.* 1994, Fenton 1995).

Longevity data for bats versus other mammals lend strong support for high adult survival (Findley 1993, Barclay & Harder 2004). Highest risk of mortality for bats is in their first year (Ransome 1995, Cummings & Bernard 1997). Thereafter, mortality rates drop significantly. Flight is associated with a reduced risk of predation since volant animals face a lower diversity of predators, and escape from them more easily compared to terrestrial prey (Pomeroy 1990, Holmes & Austad 1994). Furthermore, nocturnal habits of bats decrease susceptibility to detection and capture by predators that rely on visual acuity (Fenton 1995, Speakman 1995). Indeed, life history options associated with high mortality risks are rarely exhibited by bats (Barclay & Harder 2004). For example, migration is far less common in bats than birds. Conversely, hibernation further reduces risk of mortality and is common in bats (Barclay & Harder 2004).

Stable population structure

If evolutionary life history options for bats depend primarily on low mortality from predation (Barclay & Harder 2004), then population structure and abundance of species are probably stable and close to the carrying capacity of the environment (Findley 1993). Genetic analyses investigating population structure have revealed that certain bat colonies are socially closed and stable units even in the absence of dispersal barriers (Racey & Entswistle 2004). For example, Miller-Butterworth, Jacobs & Harley (2003) combined nuclear and mtDNA with morphological analyses to examine patterns of diversity within southern African populations of *Miniopterus natalensis*. Genetic diversity between populations was correlated with local biomes and differentiation in wing morphology suggesting restricted gene flow and philopatry. In addition, long-term population studies suggest that many bats maintain stable populations that seldom fluctuate in densities (Gaisler 1979, Findley 1993). For example, a 9-year study of *Carollia perspicillata* on Costa Rica showed relatively constant population densities (Fleming 1988). Conversely, studies investigating long-term changes of bat populations in Europe suggest that some species (e.g. *Rhinolophus* spp) are declining (Racey & Entswistle 2004). However, the principle cause for declines is the dramatic alteration of the environment by man, a relatively recent evolutionary event (Racey & Entswistle 2004). Since bats did not evolve the "buffer" of high fecundity, they cannot recover from sudden loss of habitat and disturbance of population structure (Racey & Entswistle 2004).

In conclusion, bat life histories are characterized by high longevity, low fecundity and mortality, and stable population structure. Thus, bats likely perceive their habitat as relatively stable and predictable (Findley 1993). If so, niche space of coexisting bats are probably near or completely filled, and communities therefore saturated (Findley 1993, Lawton 2000). In saturated communities, biotic processes such as competition and coevolution are more likely to influence local species composition than abiotic processes such as tolerance to temperature fluctuations (Cornell and Lawton 1992).

SOUTHERN AFRICA AND ITS BAT FAUNA AS A MODEL SYSTEM FOR COMMUNITY ECOLOGY

The southern African region is defined here as comprising all land mass south of 20° latitude on the African continent and includes the countries South Africa, Lesotho, and Swaziland, and parts of Mozambique, Zimbabwe, Botswana, and Namibia (Fig. 3.1). Within these boundaries, between 47 and 59 insectivorous bat species are known (Skinner & Smithers 1990, Taylor 2000, Friedman & Daily 2004).

There are three main reasons for the southern African insectivorous bat fauna being an ideal model for the study of factors structuring communities. First, the boundaries of the geographic region can be clearly defined, and except for the northern 20° latitude border line, are natural in that they represent a real discontinuity in habitat for African bats: the eastern border of the region's landmass is defined by the Atlantic Ocean, and the western border by the Indian Ocean, down to the southernmost point of the continent where the two oceans meet. Although not a closed system in that bats can move in and out from above the 20° latitude border line, it is a reasonably readily circumscribed one. The existence of powerful biogeographical forces separating the southern region from the rest of the continent is well documented (Fernándes & Vrba 2005), and exemplified by, for example, endemic insectivorous bats found nowhere else (e.g. *Cistugo leseueri* and *Rhinolophus capensis*, Stadelmann *et al.* 2004, Csorba, Uyhelyi & Thomas 2004).

Second, although situated at the southern tip of continental Africa, the southern African flora displays higher plant richness and endemism than tropical African flora (Cowling & Hilton-Taylor 1997). The rich and varying assemblage of habitats and biotas is correlated with a longitudinal gradient in aridity that ranges from wet sub-tropical savannas in the east, to arid Succulent Karoo and Namib desert in the west, and winter-rainfall regime of the Cape Floristic Kingdom in the south and south-west. Influence of such variation on diversity of resources and importance of biotic factors in community structure can therefore be examined (Gaston & Blackburn 2000).

Third, differences in the biogeographical histories of the Old and New Worlds means they differ not only in the systematics of local bat faunas, but also in the degree to which abiotic and/or biotic factors structure these communities (Willig, Patterson & Stevens 2004). More comparisons between these continental regions are necessary to establish the ubiquity of particular factors operating on insectivorous bat communities (Heller & Volleth 1995, Willig, Patterson & Stevens 2004). In particular, the importance of size, flight and echolocation in the community ecology of insectivorous bats, and the life history characteristics of bats, suggest that biotic processes rather than abiotic processes influence patterns of species composition at a local scale.

Chapter 2

THE INFLUENCE OF BIOTIC FILTERS ON BAT COMMUNITIES

INTRODUCTION

One of the principal questions of community ecology is whether local communities have "limited membership" (Elton 1927) or are they mere assemblages of species that happen to co-occur (Roughgarden 1983). Processes that may influence community organization or structure can be investigated on two broad scales: a local scale and a macroecological scale. However, there are inherent problems with focussing on a local scale only.

SPECIES COMPOSITION ON A LOCAL SCALE IS UNPREDICTABLE

Studies of community ecology over the past few decades have compiled detailed information on patterns of species organization on relatively limited geographic and temporal scales (i.e. local scale) to infer the processes that determine species composition of communities (Gaston & Blackburn 2000, Lawton 2000). The main conclusion from these studies is that the important processes that influence local species composition differ, often markedly, from system to system (Lawton 2000). The kind of processes identified as operating on a local scale is largely dependent upon the organisms and environments examined (Lawton 2000). In other words, there are no "universal rules" on a local scale (May 1986, Lawton 1999). To complicate matters more, long term studies of coexisting species on a local scale suggest that species composition changes with increasing environmental change over time (Williamson 1987). It is hypothesized that increased environmental change causes increased population variability and therefore decreased predictability of local species composition and the processes structuring them (Williamson 1987, Maurer 1999, Lawton 2000). This is based on the reasonable assumption (Bengtsson, Baillie & Lawton 1997), supported by evidence from field studies (Böhning-Gaese, Taper & Brown 1994, Taper, Böhning-Gaese & Brown 1995, Brown, Valone & Curtin 1997, Lawton 2000), that coexisting species respond to environmental change in different ways. Hence hard won insights from studies of species composition on a local scale are essentially ephemeral (Lawton 2000). It therefore remains impossible to predict which processes will be important in which types of local systems at any particular time and place (Lawton 2000).

GENERAL RULES APPEAR ON A MACROECOLOGICAL SCALE

Useful rules and generalizations (May 1986) only emerge when a "macroscopic" view is taken (Brown 1995, Gaston & Blackburn 1999, 2000, Maurer 1999, Lawton 2000); for example, when different local communities or guilds are compared across large spatial scales, using simple parameters such as species richness or body size. Here, focus is less on the properties of single species and more on the emergent properties of community organisation (Maurer 1999). This larger theatre is formally known as "macroecology", and incorporates elements of biogeography, evolutionary biology, and community ecology (Brown & Maurer 1989, Morin 1999, Gaston & Blackburn 2000, Lawton 2000).

Some of the important macroecological patterns that have been identified thus far include the almost universal positive correlation between local population abundance and the size of species geographic ranges (Hanski, Kouki & Halkka 1993, Gaston, Blackburn & Lawton 1997). There are also usually strong relationships between local species composition and the species composition of larger surrounding regional areas (MacArthur & Wilson 1967, Brown 1975, 1987, Abele 1984, Ricklefs 1987, Maurer 1999, Morin 1999, Gaston & Blackburn 2000, Lawton 2000), suggesting that regional species pools influence local species composition. However, local species compositions are not simply reflections of regional species pools, suggesting that factors in the environment play a major role in which of the species from the regional species pool become established locally. These factors are known as environmental filters.

ENVIRONMENTAL FILTERS

Within a macroecological framework, species composition on a local scale is viewed as a multi-stage, multi-layered process (Morin 1999) that starts at the top with a regional species pool that extends over a much larger spatial scale than the local species community. Species originate from this pool and pass through a series of environmental filters, both abiotic (e.g. tolerance to extreme temperatures) and biotic (e.g. interspecific competition) before establishing themselves as members of the local community (Morin 1999, Lawton 2000). These filters work on different spatial and temporal scales, and may overlap (Angermeier & Winston 1998).

Environmental filters can take many forms. Species first have to reach a local site before they can assemble viable populations (Maurer 1999, Lawton 2000). This depends for the most part on the species' geographic distribution range and its ability to cover the distance to the local site (e.g. species from a mainland coastal area are more likely to colonise nearby islands than distant ones). The next immediate requirement is the ability to adjust to the abiotic conditions of the particular area. Species are filtered out if they cannot tolerate the climatic patterns of temperature, light, rainfall, and wind, as well as altitude, soil texture, water salinity and depth, and availability or non-availability of inorganic and organic nutrients. These filters are assumed to be independent of species interactions or densities hence abiotic by definition.

There are more subtle abiotic filters between the regional pool and the local community on a landscape scale (Holt 1993). These include density dependent processes such as species-area relationships and the shape and spatial arrangement of habitat patches (Holt 1993, Wiens *et al.* 1993, Hanski

1998). For example, a consistent macroecological pattern is the positive correlation between the local species abundance and the regional distribution of that species (Gaston & Blackburn 2000, Lawton 2000). If geographic ranges of species expand (e.g. because prey resources become more available), local populations in the original range will increase in abundance. However, if their geographic ranges contract (e.g. because of climate change, habitat loss, or other unfavourable changes in birth and death rates) surviving local populations will decline even in areas untouched by these problems (Lawton 2000). These filters are assumed to be independent of species interactions hence abiotic by definition.

When species make it through these non-interactive abiotic filters, they still have to survive interactions with other organisms before joining the local community. Biotic filters most often cited as restricting community membership include competition, predation, and coevolution (Giller 1984, Morin 1999, Lawton 2000). However, predation as a biotic filter is unlikely to have a strong influence on bat communities (Chapter 1). Traditional ecological theories frequently assumed that biotic filters, particularly competitive interactions, ultimately determine local species composition (Darwin 1859, Hutchinson 1957, MacArthur & Levins 1967, Dayan & Simberloff 1998, Bruno, Stachowicz & Bertness 2003). However, fierce debate on the relative roles of abiotic and biotic filters in community ecology has continued for almost three decades with no consensus in sight (Dayan & Simberloff 1998, Morin 1999, Lawton 2000).

RELATIVE INFLUENCE OF ABIOTIC AND BIOTIC FILTERS

Community ecologists have no *a priori* way of knowing if abiotic or biotic filters structure local communities (Lawton 2000). Two types of bivariate relationships might mark the ends of a continuum between regional species richness (the source pool) and local species richness (Cornell & Lawton 1992, Srivastrava 1999, Lawton 2000, but see Loreau 2000, Hellebrand & Blenckner 2002, Arita & Rodriguez 2004). In unsaturated communities, local species richness is directly proportional to species richness in the regional source pool. According to this model, biotic filters play no role in species composition of local ensembles. Conversely, biotic filters exert much influence in saturated communities and local species richness increases at a slower rate relative to increasingly species rich regional source pools. Although a majority of ecological systems, covering a wide range of plant and animal taxa, appear to be unsaturated (Cornell 1999, Srivastrava 1999, Lawton 2000), there are many examples of saturated communities (Abele 1984, Ricklefs 1987, Kelt *et al.* 1997, Angermeier & Winston 1998). Indeed, biotic filters in the form of competitive interactions have influenced local species composition of many different animal systems. Among vertebrates, these include fish (Jackson, Peres-Neto & Olden 2001), lizards (Losos 1990), birds (Moulton & Pimm 1986, 1987, Diamond *et al.* 1989, Wiens 1989, Gotelli & Graves 1990), rodents (Brown 1987, Fox & Brown 1993), mustelids (Dayan & Simberloff 1994), cats (Dayan *et al.* 1990), and bats (Heller & von Helversen 1989, Kingston *et al.* 2000).

Despite not knowing *a priori* if abiotic or biotic filters predominate in communities, two general predictions can be made. First, biotic filters are more likely to structure communities in stable systems than those in unstable systems (Giller 1984, Begon, Harper & Townsend 1990, Lawton 2000, Jackson, Peres-Neto & Olden 2001). In particular, biotic filters rather than abiotic filters should structure species composition of animals such as bats with life histories characterized by low fecundity, low predation risk, long life expectancy, and stable populations (Findley 1993, Chapter 1). Secondly, influences of biotic filters on communities are probably more species specific than the influences of abiotic filters. For example, species richness in most volant and non-volant mammal communities decreases with increasing latitude due mainly to lower temperatures (Gaston & Blackburn 2000). Conversely, predation by carnivores should influence communities of small non-volant mammals such as rodents more significantly than small volant mammals (i.e. bats) because of the latter's lower risk of predation (Pomeroy 1990, Holmes & Austad 1994).

INFLUENCE OF COMPETITION ON BAT COMMUNITY STRUCTURE

HISTORY OF COMPETITION AND NICHE THEORY

The idea that two species with identical ecological resource requirements cannot survive simultaneously in the same place was implicit in Darwin's writings (Hardin 1960). Between 1920 and 1940 mathematical equations and controlled laboratory experiments combined to provide strong support for competitive exclusion of a species in the formation of a two species population equilibrium (Volterra 1926, Lotka 1925). Consequently, competition theory gained huge popularity. In particular, the principle of competitive exclusion stated as: 'complete competitors cannot coexist indefinitely', became one of the central tenets of theoretical ecology (Hutchinson 1957, Hutchinson & MacArthur 1957, Giller 1984). A corollary to this central tenet is that there must be some ecological difference between two coexisting species, and therefore each must have a unique niche (Giller 1984).

Hutchinson (1957) was the first to formally define and quantify the concept of the niche within the context of a community (Giller 1984, Pulliam 2000). The niche of a species is defined as the total range of environmental variables (abiotic and biotic) to which the species must be adapted to successfully live and reproduce within a particular habitat. Each environmental gradient represents a dimension in space. If there are *n* dimensions, then the niche is described in terms of an *n*-dimensional space. Within a community context, the position of a species and its response to factors of the total community's niche space defines its niche (Giller 1984). However, the distribution and abundance of the species is ultimately determined by its tolerance to the extremes of the physical conditions and biotic essentials of habitat, hosts etc. (the fundamental niche), and then further limited in range of habitats and population size by biotic interactions with other organisms (the realized niche) (Giller 1984). When communities are organized by such biotic interactions, the manner and degree of organization will be reflected in differences in size and shape of the realized and fundamental niches (Giller 1984). These differences can thus be used to infer the extent to which biotic interactions have structured these communities.

Both intraspecific and interspecific competition can influence the niche of a species. Intraspecific competition causes niche expansion, and pushes the realized niche towards the fundamental niche (Van Valen 1965, Bolnick 2001). On the other hand, interspecific competition counteracts this expansion, increasing the difference between the fundamental and realized niches, ultimately regulating species composition of communities. If species are very similar in niche requirements, competitive exclusion of one or more species can occur (MacArthur & Levins 1967, Grant 1972, Connell 1983, Schoener 1983). Alternatively, exclusion can be avoided by reducing overlap, and size and/or position of niches through niche shift or character displacement (Brown & Wilson 1956, Levins & Brown 1956, Hutchinson 1957, 1959). Thus, according to niche theory, species coexisting within a community must partition the resources of their environment - if the environment is assumed to be stable and its resources limited - until interspecific competition becomes, overall, less significant than intraspecific competition (Giller 1984).

Measuring the intensity of interspecific competition based on differences in niches amongst coexisting species is not only difficult, but controversial (Gotelli & Graves 1996). However, this controversy has resulted in marked improvements in rigor when designing field experiments to test predictions of competition theory (Simberloff 1982, Connell 1983, Schoener 1983). Moreover, advances in the development of analytical tools such as null models (Chapter 3) enable researchers today to better distinguish between patterns observed and patterns expected from chance when testing complex predictions from competition theory (Conner & Simberloff 1979, Strong, Szyska & Simberloff 1979, Harvey *et al.* 1983, Gotelli & Graves 1996).

Niche axes (dimensions) most likely to be partitioned by competing species are time, habitat, and food (Schoener 1974, 1986). Due to lack of consistent evidence, however, temporal partitioning of resources by bats appears unlikely (Saunders & Barclay 1992, Hickey, Acharya & Pennington 1996, Patterson, Willig & Stevens 2004). On the other hand, divergence in habitat use and diet may be principle avenues of resource partitioning (Findley 1993, Patterson, Willig & Stevens 2004) in insectivorous bats.

INFLUENCE OF COMPETITION ON THE TROPHIC NICHE

Evidence that competition drives the divergence in the diets of coexisting bats is conflicting. After reviewing evidence for resource partitioning, Fenton (1982) concluded that dietary specialization was rare in bats, and most were generalists. Several studies showed that insectivorous bats foraging in similar habitats consume the same types of prey (Fenton & Morris 1976, Aldridge & Rautenbach 1987). However, Black (1974) and Warner (1985) were able to group coexisting insectivorous bats species of the New World into moth and beetle specialists. Similarly, Findley & Black (1983) noted dietary specializations based on volant or non-volant prey types in an African insectivorous bat community. Even studies involving morphologically similar species (Saunders & Barclay 1992, Arlettaz 1999) have indicated differences in the dietary composition amongst coexisting bats, attributed to differences in micro-habitat selection by these bats.

Since closely related species are usually morphologically and ecologically similar, one would predict strong competition between them if their distributions overlapped (Findley & Black 1983, Findley 1993). Some studies seem to provide some evidence of competition for food between closely related sympatric bats. For example, at a site where the gleaning insectivores *Myotis auriculus* and *M. evotis* coexisted, one favoured beetles while the other specialised in moths (Husar 1976). Where the two occurred allopatrically, these differences disappeared. In addition, males and females of each species had different diets in allopatry, but in sympatry these differences disappeared. Thus, intraspecific diet niche width decreased in the presence of a congener. However, these two species occupy geographically distinct ranges with a minute zone of overlap, and should therefore be considered as competitive parapatric species instead of sympatric species (Arlettaz, Perrin & Hausser 1997). A detailed niche displacement study comparing the diets of sympatric gleaning insectivores across Europe, found strong evidence for resource partitioning between the sibling species *Myotis myotis* and *M. blythi* (Arlettaz, Perrin & Hausser 1997). However, the authors found no evidence for niche expansion under allopatric conditions, and therefore concluded that active interspecific competition is not the underlying mechanism responsible for food partitioning currently observed between the two species. Nevertheless, competition may have played a role in the past establishing niche segregation (Arlettaz, Perrin & Hausser 1997). Thus, there is some evidence that competition may have influenced the trophic structure of two closely related insectivorous bats.

A consideration of the niche overlap between all species making up a community, however, may be more rigorous than two-species comparisons. In particular, the hypothesis of diffuse competition predicts that niche utilization of a species in a community will be affected by many competing species (MacArthur 1972, Pianka 1974). For example, dietary and morphological similarity were positively correlated amongst nine species of coexisting insectivorous bats in Zambia, central Africa (Findley & Black 1983). In addition, species markedly distinct from others in morphology or diet, tended also to be relatively more variable in those two attributes. In this model, closely related species occupy narrow niches near the community centroid and are restricted in resource use because of competitive interactions with near neighbours (Findley 1976, Findley & Black 1983). In contrast, species occupying broad niches on the periphery of the community centroid are taxonomically and ecologically very different from neighbours and therefore released from competitive interactions. However, the degree to which the trophic or phenotypic structure of bat communities is the product of competition, or any other biotic filter, remains largely unresolved

(Patterson, Willig & Stevens 2004).

INFLUENCE OF COMPETITION ON THE PHENOTYPIC NICHE

There are many statistical and ecological benefits to using size, morphological, or echolocation attributes for inferring resource utilization and ecological relationships amongst bats (for a full discussion see Stevens & Willig 1999, Patterson, Willig & Stevens 2004). Consequently, many researchers have used the phenotypic structure of bat communities to investigate the influence of biotic filters (Fenton 1972, Findley 1976, O'Shea & Vaughan 1980, Findley & Black 1983, Schum 1984, McKenzie & Rolfe 1986, Willig 1986, Aldridge & Rautenbach 1987, Norberg & Rayner 1987, Crome & Richards 1988, Pavey & Burwell 1998, Stevens & Willig 1999, 2000, Jacobs 2000, Kingston *et al.* 2000, Schoeman and Jacobs 2003).

Although a number of studies have described phenotypic patterns in bat community structure indicative of resource partitioning (e.g. O'Shea & Vaughan 1980, Aldridge & Rautenbach 1987, Crome & Richards 1988), only a few have tested the deterministic nature of such patterns using, for example, null models (Kingston *et al.* 2000, Patterson, Willig & Stevens 2004). However, there is little consensus regarding the influence of competition on the phenotypic structure of bat communities. For example, patterns of skull morphology in the bat assemblages of Caatinga and Cerrado habitats of northeastern Brazil (Willig & Moulton 1989) and the state of Yucatan in Mexico (Arita 1997), were no different than expected from chance. This suggests that competition played a minor role, if any, in the phenotypic structure of these bat communities. However, 12 of the 15 bat assemblages spanning 50° latitude in the New World, exhibited non-random morphological patterns of skull morphology that suggest the influence of competition (Stevens & Willig 1999). Among the five trophic guilds investigated, evidence for competition was particularly consistent amongst aerial insectivores (Stevens & Willig 1999). Similarly, echolocation and flight morphology in a single insectivorous bat community in the Malaysian tropics consisting of high duty-cycle echolocating bats was more regularly spaced than would be expected from chance (Heller & v. Helversen 1989, Kingston *et al.* 2000). These patterns were interpreted as evidence of niche differentiation in response to competition. Because body size, echolocation, and flight are fundamental to the ecology of bats, they are also important indicators of community organization of insectivorous bats (Chapter 1). These phenotypic parameters are particularly instrumental in habitat and resource utilization, and are therefore the most likely phenotypic characters to exhibit non-random patterns that indicate resource partitioning caused by competition. However, competition is not the only biotic filter that can structure the phenotypic or trophic niches of coexisting bats.

INFLUENCE OF COEVOLUTION ON BAT COMMUNITY STRUCTURE

Coevolution between a community of predators with its prey could influence the trophic structure and therefore also the phenotypic structure of the community of predators. Selection pressure exerted by prey defences on the predators could cause evolutionary responses in the predator that results in phenotypic and dietary patterns different from those predicted under a hypothesis of interspecific competition. For example, if coevolution between predators and prey is the predominant and pervasive force structuring communities, it can be predicted that the phenotypic traits of species within a guild should be more similar than expected from chance (Willig & Moulton 1989).

The interaction between bats and moths is one of the most cited examples of a coevolutionary arms race (Rydell, Jones & Waters 1995, Waters 2003). Moths have auditory systems adapted to hear the echolocation calls of bats that prey on them, and the bats in response may have adapted their echolocation calls and /or foraging behaviour to overcome these moth defences. Although there is no doubt that the auditory system of moths evolved in response to predation pressure from bats, the evolutionary response of bats to moths is more ambiguous (Waters 2003, Jones & Rydell 2004). The strict version of coevolution (Janzen 1980) requires specificity (i.e. the evolution of a trait in one species is a consequence of the evolution of trait in the other species) and reciprocity (i.e. both traits evolve) (Futuyma & Slatkin 1983). On the other hand, reciprocal evolutionary change between many interacting species may differ across a geographical landscape where a number of species may display a broad range of adaptations in response to prey defences or predator stealth, and some may not show any adaptive traits at all (Thompson 1994, Waters 2003). If populations of moths evolved hearing-based defences to counteract predation from populations of bats, but specific and reciprocal responses from bats are less certain, the interaction between bats and moths might be more accurately defined as an example of guild or diffuse coevolution (Futuyma & Slatkin 1983). If counter-adaptive responses by bats are completely absent, coevolution has not occurred.

EVOLUTION OF MOTHS EARS IN RESPONSE TO BAT PREDATION

Echolocation has the obvious drawback of being used by prey as an early warning system provided the prey could evolve the necessary capacity to do so. At least seven insect orders, including moths, lacewings, beetles and praying mantises appear to have evolved ears independently as a defensive mechanism against bat predation (Roeder 1967, Miller 1983, Fullard 1987, Surlykke 1988, Miller & Surlykke 2001). Bats and insects have coexisted for at least 50 million years (Jones & Rydell 2004), and insectivorous bats from the Eocene already used echolocation to locate their insect prey (Simmons & Geisler 1998). Before insectivorous bats evolved, nocturnal flying insects may have been relatively unexploited by predators (Jones & Rydell 2004). The radiation of bats during the early Tertiary period probably resulted in strong selective pressure favouring insects that can detect the echolocation calls of bats and take evasive action (Jones & Rydell 2004). Insects evolve faster than bats because they have shorter generation times and possess a diverse range of morphological, behavioural and physiological defences against bats (Jones & Rydell 2004).

Ultrasonic hearing organs evolved independently at least once in each of the seven superfamilies of Lepidoptera (Scoble 1995, Hoy & Robert 1996, Fullard & Yack 2003). Tympanate ears of moths, located on different parts of the body, were adapted from specialized mechanoreceptors called chordotonal organs (Scoble 1995). Morphology of tympanic ears varies among different families, but all possess a thin membrane covering an air-filled sack to which a small number of sensory cells are attached that send messages to the central nervous system. In contrast, hearing organs in the hawkmoths (Family: Sphingidae) evolved from modified mouthparts independently in two subfamilies, the Sphinginae and Macroglossinae (Göphert & Wasserthal 1999). With some unusual exceptions (Conner 1999, Waters 2003), moth ears have no function other than to detect approaching bats (Roeder 1975, Fullard & Yack 1993), and therefore probably evolved in that context (Spangler 1988).

White (1877) was the first to suggest that moth ears were for detecting bats (Roeder 1967, Waters 2003), long before the discovery by Griffin & Galambos (1941) of the ultrasonic echolocation used by bats. However, the link between moth ears and bats only became clear from the 1950s (Treat 1955, Roeder and Treat 1957, Roeder 1967). Three facts strongly support the hypothesis that moths ears evolved in response to bat predation. First, ears of moths have best frequencies between 20 and 60 kHz, coinciding with the peak-frequency range of most echolocating bats (Fenton & Fullard 1979, Fullard & Thomas 1981, Fullard 1987, Rydell, Jones & Waters 1995, Fenton *et al.* 1998b). The reason that peak echolocation frequencies of bats fall within this frequency range probably lies in the frequency dependent effects of atmospheric attenuation and target strength (Jones & Rydell 2004). Second, range of best moth hearing coincides with the range of echolocation frequencies used by the most common sympatric bats. Moths sampled at sites with high bat diversity and density have a significantly wider range of best frequencies, particularly pronounced at both low (< 25 kHz) and high (> 80 kHz) frequencies, than moths at sites with low bat diversity and density (Fullard 1982, 1987). Third, day-flying moths, no longer subjected to bat-predation, display advanced auditory degeneration (Fullard 1994, Fullard *et al.* 1997, Surlykke *et al.* 1998).

Moreover, tympanate ears of larger moths have lower best frequencies and are more sensitive than ears of smaller moths (Surlykke *et al.* 1999, Norman & Jones 2000). One possible explanation for this is that allometric scaling of moth size affects the tuning and sensitivity structures of their ears. However, tympanum size increases less with body size than other non-auditory features (Surlykke *et al.* 1999). An alternative and more likely explanation, therefore, is that larger moths need more sensitive ears because they are easier to detect by echolocating bats. Echoes from large moths are more intense than echoes from small moths (Pye 1993) and this is compounded by the fact that fast flying bats foraging in the open use low frequency echolocation calls that increase the range at which bats detect prey, particularly if the prey are large (Waters, Rydell & Jones 1995). Selection may therefore have favoured increased auditory sensitivity in the otherwise more vulnerable larger moths (Surlykke *et al.* 1999, Waters 2003).

Hearing combined with a complex suit of evasive flight manoeuvres (Roeder 1967) render tympanate moths 40% more successful at evading bats than non-tympanate moths (Roeder 1967, Rydell 1992, Acharya & Fenton 1999). Among larger moths (Macrolepidoptera and Pyrilidae), the vast majority (c.a. 94%) have ears (Rydell & Lancaster 2000), illustrating the importance and efficacy of hearing-based defenses in these insects (Jones & Rydell 2004). Thus hearing moths may exert considerable selection pressure on insectivorous bats favouring adaptations that enable bats to overcome these prey defences.

EVOLUTION OF ECHOLOCATION AND BEHAVIOUR IN RESPONSE TO MOTH HEARING

Although tympanate ears are effective - some moths can hear a bat echolocating up to 30 m away (Roeder 1967) - sensitivity falls off slowly to frequencies above 60 kHz and sharply below 20 kHz (Fullard 1987, Surlykke 1988). One possible counter-adaptation employed by bats may thus be to exploit the frequencies above or below the moth's optimum hearing range (Novick 1977, Fenton & Fullard 1979). Fullard (1987) called these frequencies 'allotonic frequencies'. There is evidence supporting this. For example, the Large-eared free-tailed bat *Otomops martiensseni* emits echolocation calls with the most energy between 7 and 16 kHz and appears to feed heavily on moths (Fenton *et al.* 2004). At the other end of the spectrum, the hipposiderid *Cloeotis percivali* uses echolocation frequencies as high as 212 kHz and feeds almost exclusively on moths (Whitaker & Black 1976, Jacobs 2000).

Alternative to high or low peak echolocation frequencies, bats may use passive listening and low intensity echolocation calls combined with gleaning to hunt moths. For example, low intensity calls allow the long-eared bat, *Plecotus auritus*, to approach tympanate moths more closely before being detected (Waters & Jones 1995, 1996). The combination of low intensity and short duration calls of the gleaning bat, *Myotis evotis*, also appear relatively inaudible to moths (Faure, Fullard & Barclay 1990). Nonetheless, low intensity calls may not be an adaptation *per se* to avoid detection by moths, but simply a feature of the gleaning habit (Waters 2003). This is likely the case with short duration calls, necessary to avoid pulse-echo overlap in cluttered habitats (Schnitzler & Kalko 2001).

In conclusion, bats may use allotonic frequencies, quiet calls, or short duration calls to overcome hearing-based defensive systems. These echolocation designs may allow bats to prey upon tympanate moths, but evidence that they are adapted specifically for this remains scant. In contrast, there is little doubt that moth hearing evolved in response to bat echolocation (Waters 2003, Jones & Rydell 2004). There would be little benefit for moths as prey to evolve a hearing-based defence sensitive to only a few bat species. On the other hand, there would be much benefit for some bats as predators to evolve a single strategy to avoid detection from most moths as long as the rest of the bat community remained diverse in terms of prey selection and echolocation structure (Waters 2003).

THE ALLOTONIC FREQUENCY HYPOTHESIS

The allotonic frequency hypothesis (AFH) predicts that the incidence of eared insects should be highest in the diet of coexisting bats whose peak echolocation frequencies fall outside the 20 to 60 kHz range (Fenton & Fullard 1979, Fullard 1982, 1987). Thus, across bat species with calls dominated by frequencies < 20 kHz or > 60 kHz the incidence of tympanate insects in their diet should increase. This seems to be the case whether the focus of the study is global, incorporating a number of families of bats (Jones 1992, Bogdanowicz, Fenton & Daleszczyk 1999), or local focusing on a single community of bats (Pavey & Burwell 1998, Jacobs 2000, Schoeman & Jacobs 2003).

Jones (1992) compared published echolocation and dietary data from around the world on bats belonging to the families Hipposideridae and Rhinolophidae. These bats use high duty-cycle echolocation calls dominated by a single constant frequency (CF). As predicted by the AFH, a positive relationship was found between peak echolocation frequency and the proportion of moths in the diets. Bogdanowicz, Fenton & Daleszczyk (1999) extended this study to include species that use low duty-cycle echolocation (i.e. families Vespertilionidae and Molossidae that use calls dominated by a frequency modulated (FM) component). Support for the AFH was found in the shape of a parabolic relationship between moth consumption and echolocation call frequency for bats whose echolocation calls are dominated by frequencies < 100 kHz. Thus as echolocation frequency increased above about 20 kHz so too did the proportion of moths in the diets of the bats. Below 20 kHz the proportion of moths in the diets of the bats increased as the echolocation frequency decreased. However, this relationship was not significant for bat species using echolocation calls dominated by sounds > 100 kHz, suggesting that for these species morphological characteristics rather than call frequency may limit the range of potential prey items (Bogdanowicz, Fenton & Daleszczyk 1999).

Jacobs (2000) argued that although the approach used by Jones (1992) and Bogdanowicz, Fenton & Daleszczyk (1999) has strong statistical validity, their data were collected in a number of different ways and at different times. Their dietary and echolocation data were not therefore collected at the same time or in the same place for each species in the analyses. Three studies tested the predictions of the AFH using echolocation and dietary data collected at the same time: Pavey & Burwell (1998) on three sympatric bat species with CF calls, Jacobs (2000) on a single insectivorous bat community dominated by high duty-cycle echolocating bats, and Schoeman & Jacobs (2003) on a single insectivorous bat community dominated by low duty-cycle echolocating bats. As predicted by the AFH, echolocation frequency was positively related to the proportion of moths in the diets of the bats. In addition, echolocation frequency was a better predictor of diet than wing loading, suggesting that selection pressure exerted by moth hearing might have acted directly on echolocation frequency and secondarily on body size or wing parameters (Jacobs 2000, Schoeman & Jacobs 2003). However, the ubiquity of the AFH remains to be tested on a variety of communities.

RESEARCH QUESTIONS

THE RELATIVE INFLUENCE OF COMPETITION AND COEVOLUTION ON THE COMMUNITY STRUCTURE OF INSECTIVOROUS BATS IN SOUTHERN AFRICA

This study investigates the relative influence of competition and coevolution on various parameters that define bat community structure, viz. species composition and patterns of ecomorphology (body size, wing morphology, and echolocation) and diet. If interspecific competition influences bat communities, competitive exclusion or extinction of one or more species that are too similar can occur. Alternatively, exclusion can be avoided by reducing niche or overlap, and and/or niche occupancy through niche shift or character displacement. Either way, differentiation between niches of coexisting bat species should be larger than expected by chance. Similarly, the differences between niches of coexisting bat species should be less variable than expected by chance, because of the exclusion or displacement of species that exceed the limit of similarity with other resident species (Patterson, Willig & Stevens 2004). This raises the following questions:

1. Do phenotypic niche patterns support competition as the factor driving bat community structure? If so, I predict that there should be a limit to the similarity of phenotypic traits (body size, wing morphology, and echolocation) among coexisting bats. The differences in traits between coexisting species should be less variable than expected by chance (Chapter 5).
2. Do trophic niche patterns support a competition hypothesis? If so, I predict that there should be a limit to the degree of dietary overlap between coexisting bats, and the differences in overlap between coexisting species should be less variable than expected by chance (Chapter 6).
3. Do patterns of species composition support a competition hypothesis? If competition influenced species combinations of communities, I predict that there should be a smaller number of unique species combinations in communities, and a larger number of species combinations that never occur in communities, than expected by chance. In addition, if competition influenced the niches of species in communities, variance of species richness among communities should be smaller than predicted by chance (Chapter 7).

If coevolution influences bat community structure, on the other hand, selection pressure exerted by prey defences on the predators could cause evolutionary responses in the predator that results in phenotypic and dietary patterns different from those predicted under a hypothesis of interspecific competition. I tested the coevolution hypothesis by asking the following questions:

1. Do phenotypic patterns support a coevolution hypothesis? If coevolution influenced the phenotypic structure, the ecomorphological traits of coexisting species should be more similar than expected by chance (Chapter 5).
2. Do trophic patterns support the Allotonic Frequency Hypothesis? According to this hypothesis, the peak echolocation call frequencies used by bats should be significantly correlated with the proportion of moths in the diets of insectivorous bat species within each community, and should be the best overall predictor of diet (Chapter 6).

To answer these questions, I use a battery of null models and multivariate analyses to test the deterministic or non-deterministic nature of phenotypic, trophic, and species composition patterns of insectivorous bat communities at a local and regional scale. I obtained data for these analyses by sampling the bat fauna of southern Africa at a local and regional scale between 2001 and 2004 (Chapters 3 and 4).

Chapter 3

RESEARCH APPROACH AND METHODS

INTRODUCTION

Much of the confusion and controversy in community ecology today can be ascribed to the multi-dimensionality of processes, and the failure of ecologists to separate observed pattern from process when testing complex predictions generated by theoretical ecology (Peters 1991, Gotelli & Graves 1996). I use a battery of null models and multivariate analyses to test the deterministic or non-deterministic nature of phenotypic, trophic, and species composition patterns in insectivorous bat communities, which I call ensembles.

ENSEMBLES AND FUNCTIONAL GROUPS

ENSEMBLE VERSUS COMMUNITY

In its most expansive sense, community ecology deals with patterns and processes linked to coexisting species that interact, or have the potential to interact, with one another (Strong *et al.* 1984). Hence, a "community" must include both autotrophs and heterotrophs (Fauth *et al.* 1996, Lawton 2000, Patterson, Willig & Stevens 2004), and is therefore too costly, time consuming, and taxonomically challenging to study even in the simplest systems. Most community ecology studies therefore involve subsets of communities based on, for example, taxonomy i.e. assemblages (e.g. bats) or guild structure (e.g. insectivores). Cross-classified groupings, e.g. frugivorous birds or insectivorous bats, are termed "ensembles" (Fauth *et al.* 1996). Grouping of very different entities such as assemblages, guilds, or ensembles under the umbrella term "community" may inhibit progress in understanding the dynamics of these complex ecological systems (Giller & Gee 1987, Patterson, Willig & Stevens 2004). My use of the term "ensemble" emphasizes that coexisting insectivorous bats constitute an ensemble rather than a community, and is a terminological reminder that other non-bat insectivores may exert important impacts on these bats (Patterson, Willig & Stevens 2004). For example, prey resources may be exploited jointly by insectivorous bats and birds (Speakman *et al.* 2001), or bat roosts may be occupied by birds (Sedgeley & O'Donnell 1999).

FUNCTIONAL GROUP MEMBERS

I classified the individual bat members of an ensemble into three functional groups to avoid a "dilution effect" of patterns in the data (Diamond & Gilpin 1982). This happens when species with little potential to interact are included in, for example, null model analyses, obfuscating observed and expected patterns of community structure (Gotelli & Graves 1996). Specifically, wing morphology and echolocation characteristics related to habitat associations clearly define the niche and foraging behaviour of sympatric bats to three functional groups, open-air, clutter-edge, and clutter feeders (Norberg & Rayner 1987, Fenton 1990, 1995, Arita & Fenton 1997, Schnitzler & Kalko 1999, 2001, Racey & Entwistle 2004). Thus, member species of each functional group may be more likely to interact with each other than with member species of other functional groups.

I identified functional group members of ensembles principally on taxonomy, but also from their flight and echolocation characteristics (Chapter 5), and observation of habitat use in the field (e.g. Jacobs, Barclay & Schoeman 2005). *Open-air* bat species represented the families Molossidae and Emballonuridae. These bat species were characterised by long and narrow wings coupled with narrowband echolocation calls of low frequencies (< 30 kHz) and long duration (> 8 ms). *Clutter-edge* feeders represented bat species from the families Vespertilionidae and Miniopteridae. In general, these bat species were characterised by average wingspans and wing areas coupled with echolocation calls of intermediate frequencies (30 – 70 kHz) that range from broadband (> 60 kHz) to narrowband signals (30 – 60 kHz) of intermediate duration (3 – 8 ms). *Clutter* bat species included high duty-cycle echolocating bats of the families Hipposideridae and Rhinolophidae that emit CF signals of long duration (10 – 100 ms), and medium to high peak frequency (> 30 kHz), and low duty-cycle echolocating bats of the family Nycteridae that use FM signals of short duration (1 – 3 ms) at low intensities (< 100 dB). Despite having very different echolocation systems, wings of all clutter feeders were relatively short and broad.

STUDY BIOMES, ENSEMBLES AND ADDITIONAL SAMPLING SITES

I sampled the insectivorous bat faunas of ensembles located in four biomes of southern Africa (Rutherford 1997). Intensive studies of single ensembles do not consider the temporal or spatial heterogeneity of the environment (Stevens & Willig 1999, Lawton 2000). Biogeographic landscapes usually exhibit substantial temporal and spatial heterogeneity (Brown 1995) that, coupled with latitudinal and elevational gradients, likely mediate the degree to which biotic and abiotic filters operate (Stevens & Willig 1999, Gaston & Blackburn 2000, Patterson, Willig & Stevens 2004).

BIOMES

The four biomes where ensembles were located included the fynbos, forest, savanna, and Nama-Karoo biomes (Fig. 3.1). Biomes are broad ecological units that represent major life zones over large natural areas (Rutherford 1997). Gelderblom *et al.* (1995) investigated the relationship between biomes and species richness of different mammalian orders, including bats, in South Africa. The savanna, followed by the grassland, were the most important biomes in terms of percentage of museum records, number of species, and number of endemics in the Chiroptera, Carnivora, and Insectivora. However, after controlling for the geographic size of the biomes, the fynbos followed by the Succulent-Karoo became the most important biomes in terms of species density and endemics. Bats and insectivores displayed strong biome specificity. Indeed, the relatively unique faunas of these mammals in the fynbos, Nama- and Succulent-Karoo biomes warrant them defined as distinctive zoogeographic zones (Rutherford & Westfall 1986).

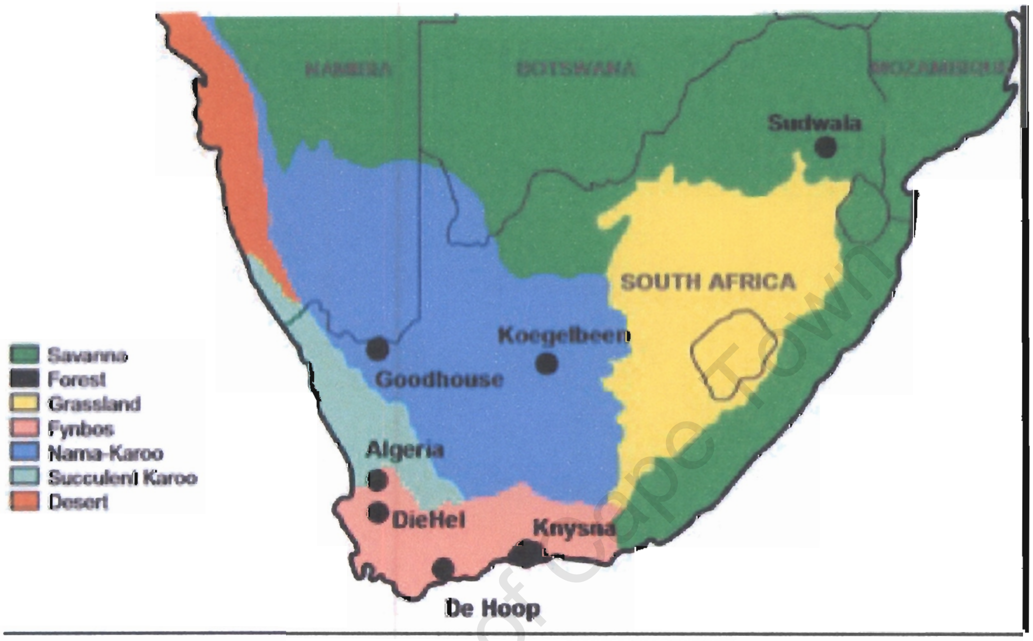

Fig. 3.1 Shows distribution of biomes and political boundaries in southern Africa (Biomes after Rutherford 1997). Locations of the seven insectivorous bat ensembles are indicated with black markers.

Sampling in the biomes

Because of the unusual diversity of flora and variable rainfall in the fynbos biome (see below), I sampled the local bat faunas of three ensembles, Algeria, Die Hel, and De Hoop. The fynbos ensembles differed in their dominant type of fynbos vegetation, elevation, and mean annual rainfall. The ensemble of the forest biome was located in the indigenous Knysna Forest, the southernmost montane forest on the African continent (Midgley *et al.* 1997). The savanna ensemble was located 60 km west of Kruger National Park, in the vicinity of Sudwala caves, Mpumalanga. I sampled two bat ensembles in the large Nama-Karoo biome. The two ensembles were far apart and differed in availability of permanent water sources. They were Goodhouse on the banks of the Orange River, and Koegelbeen cave near Kimberley, Northern Cape province.

ENSEMBLES

Defining the ensembles

I defined the insectivorous bat ensembles on three principles suggested by Stevens & Willig (1999, 2000). Firstly, an ensemble covered a delimited area where local bats had the potential to interact. Sampling took place at various trapping sites within a 10 km radius of the GPS coordinates taken at each of the fynbos, savanna, and Nama-Karoo ensembles (see below). Sampling in the Knysna ensemble took place in or near pockets of remaining forest at a variety of sites from Rondevlei Nature Reserve in the west to Keurboomstrand in the east, a distance of c.a. 80 km. Secondly, I sampled all ensembles, with the exception of the Goodhouse ensemble, during wet and dry seasons. Thirdly, I standardized sampling effort and assessed the completeness of ensemble inventories with statistical rarefaction and species richness estimators (Chapter 4). In addition, I selected sites for which published records on the bat fauna of the local area were available. The following sections provide a short summary of the biotic and abiotic characteristics of the ensembles.

Fynbos ensembles: Algeria, Die Hel, and De Hoop

The Cape Floral Kingdom (CFK) is the smallest of the six Floral Kingdoms in the world (90 000 km^2), and the only Kingdom contained within a single country (Cowling, Richardson & Mustard 1997). The CFK covers the extreme southwestern and southern parts of southern Africa, where the climate is Mediterranean characterized by a winter rainfall season (Schultze 1997). Annual rainfall is extremely variable, ranging from a low of 300 mm to a high of 3000 mm in other parts (Schultze 1997). The fynbos biome is considered by many to be synonymous with the CFK. However, the fynbos biome refers to the two key vegetation groups, fynbos and renosterveld, within the CFK region, whereas CFK refers to the general geographical area and includes vegetation types typically associated with the Forest, Nama-Karoo, Succulent Karoo and Thicket biomes (Cowling & Holmes 1992, Cowling, Richardson & Mustard 1997).

Fynbos ("fine bush") dominates the CFK and consists of hard-leafed, evergreen, and fire-prone shrubs that thrive on the region's rocky or sandy nutrient-poor soils (Cowling, Richardson & Mustard 1997). The vegetation is structurally characterized by restioids, a high cover of ericoid shrubs, and an over-storey of proteoid shrubs (Cowling and Holmes 1992, Cowling, Richardson & Mustard 1997). Renosterveld ("rhinoceros veld," a reference to the black rhinoceros, *Diceros bicornis*, now extinct in the region) covers some 20 000 km^2 and comprises a low shrub layer dominated by the renosterbos (*Elytropappus rhinocerotis*), with a ground layer of grasses and seasonally active geophytes (Cowling, Richardson & Mustard 1997). The fynbos biome includes more than 7300 plant species, of which 80 % are endemic and most of which belong to the Ericaceae, Restionaceae, Rutaceae, Thymelaceae, Rosaceae, and Lobeliaceae families (Cowling, Richardson & Mustard 1997).

Algeria Forestry Station ('Algeria') (32°22'S, 19°03'E) forms part of the Cederberg Wilderness Area that occupies 71 000 hectares of the Cederberg mountain range. The site reminded a French nobleman, Count de Regne, of the Atlas mountain range in Algeria, hence the name. Bats were caught at altitudes between 600 – 750 meters above sea level. The area experiences an average rainfall of 647 mm per year, most of which falls between April and September. In winter, minimum temperatures can drop below freezing point, while in summer temperatures regularly exceed 40° C. Vegetation is predominantly mountain fynbos, with small pockets of *Widdringtonia cedarbergensis* on the mountain slopes at altitudes > 1000 m above sea level. Capture records indicate the presence of at least 10 insectivorous bat species in the area (Rautenbach 1978, Jacobs & Fenton 2001, Schoeman & Jacobs 2003, Jacobs, Schoeman & Barclay 2005). I surveyed Algeria's bat fauna during summer and winter months in 2001 (see Schoeman and Jacobs 2003 for details), 2002 (November 6 - 13), and 2004 (November 22 - 28)

Groot Wintershoek Wilderness Area ('Die Hel') extends over 19 220 ha and lies within the mountain range of the same name. The landscape is rugged and mountainous, with an average altitude of 1 500 m above sea-level. Die Hel (The Hell) is reference to the central sampling site (33°05'S, 19°05'E) where the river falls into a deep pool surrounded by caves that are occupied by hundreds of fruit bats (*Rousettus egyptiacus*) and insectivorous bats throughout the year. Eighty percent of the average annual rainfall of 1200 mm occurs in winter between April and September, when snow is common. Vegetation is predominantly mountain fynbos. Rare and threatened fynbos species, such as *Sorocephalus scabridus* (Family: Protaeceae), occur only here. Capture records list four insectivorous bat species (Herselman & Norton 1985, Miller-Butterworth, Jacobs & Harley 2003). I surveyed Die Hel's bat fauna during late summer (April 5-11) and early spring (29 September - 4 October) in 2002.

De Hoop Nature Reserve ('De Hoop') (34°26'S, 20°25'E) covers a 50 km narrow strip of coastline and stretches 5 km out to sea, and is the most southerly of the protected areas that have been selected to represent the CFK as World Heritage Sites. One of 16 wetlands in South Africa that are recognised by the Ramsar Convention as being of international importance occurs within the reserve. The area receives about 380 mm rainfall annually, with August being the wettest month. Vegetation consists largely of limestone fynbos, closely associated with the limestone outcrops that stretch from Gansbaai in the west to Gouritz River in the east. In addition, unique plants (many of which are endemic) have adapted to the acidic soil pockets that are surrounded by limestone. Previous surveys at De Hoop indicated the presence of at least five insectivorous bat species (Herselman & Norton 1985, McDonald, Rautenbach & Nell 1990, Jacobs 1999).I surveyed De Hoop's bat fauna during summer and winter months in 2002 (January 27 - 31, March 15 - 20 and July 1 - 8), 2003 (January 25 - February 3), and 2004 (January 28 - February 4, and April 4 - 6).

Forest ensemble: Knysna

The Knysna Forest ('Knysna') (33°57'S, 23°10'E) consists of relatively small areas of indigenous forest in the southeastern parts of the CFK, covering an area of 558 km^2 along the southern coast from Mossel Bay to the Krom River and inland to the Outeniqua and Titsikamma Mountains. Knysna forests thrive at low altitudes of 50 m above sea level in contrast to montane forests in the tropics that occur above elevations of 2000 m (Midgley *et al.* 1997). One reason is the proximity to the sea, which ensures that the annual rainfall (between 1000 - 1500 mm) occurs throughout the year (Midgley *et al.* 1997). The forest has a closed canopy at an average height of 20 m. The tree composition of the forest varies depending on various factors including the height above sea level, rainfall, type of soil, and slope (Midgley et al. 1997). Tree types include Yellowwood *(Podocarpus folius)*, hard pear *(Olinia ventosa)*, Stinkwood *(Ocotea bullata)*, and Cherrywood *(Pterocelastrus tricuspidatus)*. A previous survey of the bat fauna at the Knysna forests suggested the presence of at least five insectivorous bat species (Herselman & Norton 1985).I surveyed Knysna's bat fauna during early spring (September 28 - October 9) in 2003 and late summer (March 16 - 30) in 2004.

Savanna ensemble: Sudwala

The savanna biome dominates the African continent (Rutherford 1997) and covers 54 % of southern Africa (Scholes 1997). Common to savannas around the world are climate (a hot wet season of four to eight months and a mild dry season for the rest of the year), and frequent grass-layer fires (Scholes 1997). In southern Africa, annual rainfall in the savanna biome is around 750 – 1000 mm and occurs in the summer between October and April (Scholes 1997, Schulze 1997). Vegetation can be varied but consists mainly of open woodland with mopane, *Colophospermum mopane,* and *Acacia* trees, good grass cover, and various shrub species (Scholes 1997). Sudwala cave (25°22'S, 30°42'E) is located 60 km from Nelspruit, Mpumalanga at an altitude of 660 m above sea level. In addition to the above vegetation, the area is known for its stinkwood trees, *Ocotea bullata,* and abundance of the rare aloe, *Aloe alooïdes.* Capture records at Sudwala suggested the presence of at least five insectivorous bat species (Jacobs 2000). I surveyed Sudwala's bat fauna during summer in 2002 (December 16 - 28) and 2002 (April 23 - 28), and during winter (August 9 - 16) in 2002.

Nama-Karoo ensembles: Goodhouse and Koegelbeen

The Nama-Karoo biome occurs on the central plateau of the western half of South Africa, at altitudes between 500 and 2000 m, with most of the biome failing between 1000 and 1400 m (Rutherford 1997). It covers a large area, including the greater part of central and western Botswana and Namibia, and is the second-largest biome in the southern African region (Rutherford 1997). The Goodhouse ensemble included the insectivorous bats sampled at Gougap Nature Reserve (29°31'S, 18°00'E) and Goodhouse (28°56'S, 18°07'E) during the summer month of November (10-16), 2002. Most trapping nights were at Goodhouse (71%). Vegetation at Goodhouse is a combination of arid grassland and dwarf scrubland (Palmer & Hoffman 1997). Dominant shrubs include *Eriocephalus* spp., *Filicia* spp., and *Pteronia* spp. Capture records near Goodhouse suggested the presence of at least nine insectivorous bats (Roberts 1951, Rautenbach *et al.* 1993), including the rare species *Cistugo seabrai* (Stadelmann *et al.* 2004), seldom captured anywhere else.

The Koegelbeen cave (28°39'S, 23°20'E) is found within a sinkhole 25 km from Griekwastad near Kimberly. Vegetation is classified as grassy dwarf scrubland (Palmer & Hoffman 1997). Grass species include *Aristida diffusa* and *Digitaria eriantha*. Annual rainfall is variable, occurs in summer, and ranges between 60 – 200 mm (Schultze 1997). Temperature in the summer averages 31° C, but can drop below freezing point during winter nights. Capture records at Koegelbeen indicated the presence of at least four insectivorous bat species (Miller-Butterworth, Jacobs & Harley 2003, D.S. Jacobs pers. comm.). I surveyed Koegelbeen's bat fauna during the winter in 2004 (July 20-22), and A/Prof D.S. Jacobs surveyed the site during the summer (December 24-26) in 1998.

Table 3.1 Additional locations in southern Africa where insectivorous bats were surveyed between 2001 and 2004.

Biome	Site	Code	GPS	Date of survey
Savanna	Pafuri, Mpumalanga	Sp	22°43'S, 31°19'E	30.7.02 - 5.08.02
Savanna	Kanaan, Mpumalanga	Sk	25°04'S, 31°06'E	20.12.02 - 23.12.02
Savanna	Skukuza, Mpumalanga	Ss	25°01'S, 31°35'E	17.02.04 - 21.02.04
Savanna	St Lucia, Kwazulu Natal	Sl	28°22'S, 32°25'E	30.04.03 - 5.05.03
Savanna	Mkuzi, Kwazulu Natal	Sm	27°24'S, 32°39'E	26.07.02-27.07.02
Savanna	Durban, Kwazulu Natal	Sd	29°52'S, 31°01'E	6.05.03
Savanna	Choma, Zambia *	Sz1	18°37'S, 27°00'E	28.10.03 - 30.10.03
Savanna	Lusaka, Zambia *	Sz2	15°30'S, 28°15'E	18.10.03 - 25.10.03
Savanna	Kitwe, Zambia *	Sz3	12°56'S, 28°16'E	15.10.03 - 17.10.03
Savanna	Mutare, Zimbabwe	Sz4	19°51'S, 32°19'E	10.01.01 - 16.01.01
Savanna	Maputo, Mozambique	Sm1	25°58'S, 32°35'E	26.12.02 - 29.12.02
Savanna	Bazaruto, Mozambique	Sm2	21°48'S, 35°33'E	3.01.01 - 6.01.01
Grassland	Fourways, Gauteng	Gj	25°42'S, 28°11'E	2.01.03 - 6.01.03
Grassland	Kokstad, Eastern Cape	Gk	29°36'S, 31°01'E	22.7.04 - 23.7.04
Fynbos	Attakwas, Western Cape	Fa	33°52''S, 21°54'E	9.10.03
Fynbos	Zeekoevlei, Western Cape	Fc	34°11'S, 18°22'E	29.02.02 - 30.02.02
Fynbos	Wellington, Western Cape	Fw	33°34''S, 19°02'E	29.10.02 - 3.11.02
Thicket/Forest	Pirie Forest, Eastern Cape	Tp	32°41'S, 27°42'E	25.7.04

Surveys performed by Prof. David S. Jacobs

ADDITIONAL SAMPLING SITES IN SOUTHERN AFRICA

In addition to the seven locations described above, bat faunas of 16 additional sites were surveyed to collect data from insectivorous species across southern Africa. This data was necessary to evaluate sampling efficiency at the CFK and savanna biomes (Chapter 4), and generate large regional source pools (that included bat species not captured in ensembles) for null modeling the phenotypic niche patterns of coexisting bats (Chapter 5). Most of the sites were located in the species rich savanna biome (Table 3.1).

ANALYTICAL NULL MODEL ANALYSES

Null modelling first achieved notoriety during the late 1970s and 1980s when results of null model simulations directly contradicted predictions of orthodox competition theory (Connor & Simberloff 1979, Strong, Szyska & Simberloff 1979, Connell 1980). Proponents of null models (e.g. Strong, Szyska & Simberloff 1979) suggested that pattern must be established before process can be investigated, while opponents (e.g. Roughgarden 1983) maintained that processes such as competition can be studied productively before establishment of pattern (Gotelli & Graves 1996). However, much of the controversy surrounding null models principally involved personal styles and preferences of research and philosophy that cannot be judged right or wrong (Gotelli & Graves 1996). Despite strong initial opposition, null models have proven pervasive and instrumental in the development of ecological theory, and have become one of the most important tools for describing and analyzing patterns of ecological and biogeographical data (Gotelli & Graves 1996, Colwell & Lees 2000, Gotelli 2001, 2004).

WHY USE NULL MODELS?

Traditional empirical tools used in community ecology to collect data include laboratory, field, and "natural" experimental techniques (Connell 1975, Diamond 1986, Wiens 1989). Each of these tools has distinct advantages, but each is limited by its ability to separate pattern from process (for a full discussion see Gotelli & Graves 1996). Furthermore, the biology of bats largely rule out techniques such as "removal experiments" (Abramsky & Sellah 1982) to test predictions of ecological theory (Findley 1993, Patterson, Willig & Stevens 2004). Null models, on the other hand, are not true experiments but thought-experiments that allow researchers to explore possible patterns in isolation of certain ecological or evolutionary processes.

Null models do not portray the world as entirely random or having no structure (Roughgarden 1983). Rather, the null hypothesis is that community structure is random with respect to the filter or process being investigated (Connor & Simberloff 1986, Gotelli & Graves 1996, Gotelli 2001). This allows one not only to separate pattern from process (Gotelli & Graves 1996), but to also distinguish between the observed patterns and alternative processes that may have produced them (Rathcke 1984). Furthermore, null models are often superior to natural experiments because stochastic environmental effects are incorporated. In addition, various possible outcomes are allowed, including one of "no effect" (Gotelli & Graves 1996).

Moreover, the randomization or random sampling techniques of null models that produce random or chance patterns, are a well-established protocol in conventional statistics, such as the chi-squared distribution or *F-ratio*, for constructing null hypotheses (Manly 1991). Indeed, the Monte Carlo simulation techniques of null models may be preferable to conventional statistical tests such as chi-squared distribution or ANOVAs, because they are not burdened by assumptions of normality and equal variances (Gotelli & Graves 1996, Peres-Neto & Olden 2001, Gotelli & Entsminger 2004). Furthermore, many of the technical flaws pointed out by critics have been solved (Connor & Simberloff 1983, Wilson 1987, Stone and Roberts 1990, 1992, Manly 1991, Gotelli & Graves 1996, Gotelli *et al.* 1997, Gotelli 2000), and solutions have been made accessible to researchers through computer software packages (e.g. Colwell 2004, Gotelli & Entsminger 2004).

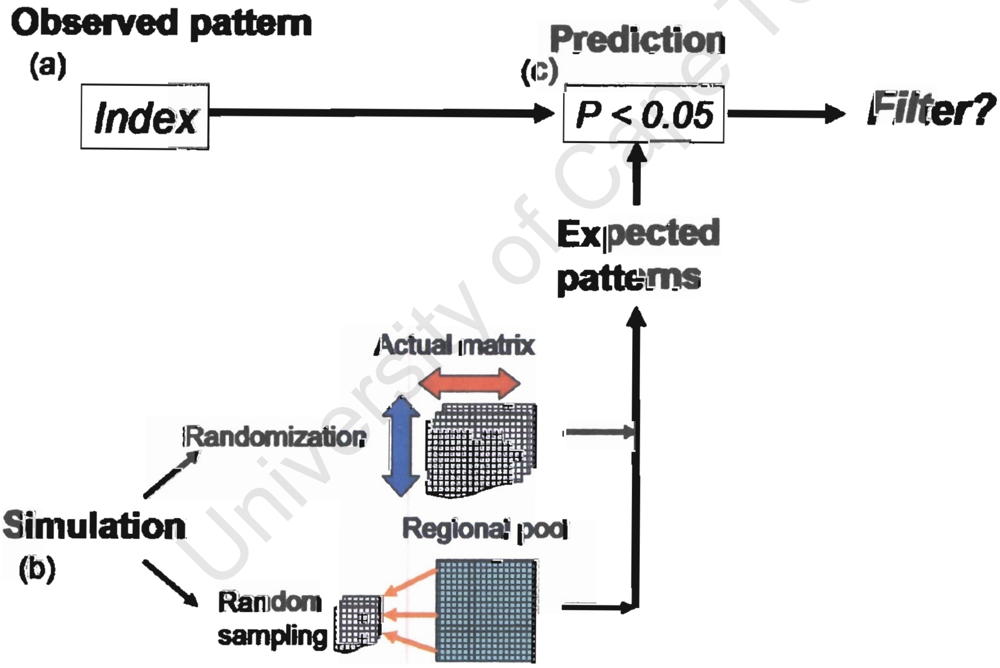

Fig. 3.2 Shows the general null modeling procedures used to test predictions from competition and coevolution hypotheses. Observed patterns of community parameters, quantified by different indices, were statistically compared with the distribution of expected patterns, produced by randomizing columns (red arrows) and/or rows (blue arrows) of actual matrices, or random sampling from known or imagined regional source pools (see Table 3.2 for more info. on a, b, and c). If the observed pattern deviated from more than 95% of the expected patterns, observed patterns were considered non-random and deterministic in relation to the predictions of the particular hypothesis of the biotic filter tested.

APPLICATION OF NULL MODELS

In each chapter, I describe in detail the null model procedures that were used to test the predictions of competition or coevolution hypotheses on community parameters of ensembles and functional groups. Here follows a brief overview of the general null modelling procedures.

Community parameters of ensembles and functional groups (i.e. species composition, phenotypic and trophic niches) were quantified by different indices and compared with patterns expected in isolation of the biotic filter under investigation, i.e. patterns expected by chance (Fig. 3.2 and Table 3.2). Expected patterns were produced by randomization of collected (actual) data matrices or random sampling from known regional source pool matrices (Fig. 3.2). To generate a statistical p-value, observed patterns were compared to the distribution of many expected patterns (Manly 1991, Fig. 3.2). I used the deviation of the observed patterns from the expected patterns produced by the null model to evaluate predictions from the relevant hypothesis (Table 3.2).

Table 3.2 The community parameters of ensembles and functional groups investigated in the thesis, and the indices and simulations used to test the predictions from hypotheses of two biotic filters, competition and coevolution (See Fig. 3.2).

Biotic filter	Observed parameter	Chap.	Index (a)	Simulation (b)	Prediction (c)
Coevolution & Competition	Phenotypic niche	5	Minimum segment-length ratio	Random sampling	Obs>Exp / Obs<Exp
			Variance of segment-length ratios		Obs<Exp
Competition	Trophic niche	6	Pianka	Randomization	Obs<Exp
			Variance of Pianka		Obs<Exp
			Electivity		Obs<Exp
			Variance of electivity		Obs<Exp
Competition	Species composition	7	C-score	Randomization	Obs>Exp
			No. combination		Obs>Exp
			V-ratio		Obs<Exp

I did not construct null models to test the predictions of the allotonic frequency hypothesis (Chapter 2). Instead, I used multivariate techniques (described in Chapter 6) to investigate which phenotypic trait (size, wing morphology, or echolocation) was the better predictor of diet. This, combined with the null model analyses of Chapter 5, allowed me to evaluate the relative influence of coevolution on the phenotypic and trophic niche structures of ensembles.

Chapter 4

LOCAL AND REGIONAL SPECIES RICHNESS OF INSECTIVOROUS BATS IN SOUTHERN AFRICA

INTRODUCTION

> "The beginning of wisdom is to call things by the right names"
>
> *Chinese Proverb*

I surveyed the species richness of insectivorous bat ensembles and regional source pools using active and passive sampling methods. To compare species richness of ensembles and regional pools, sampling effort was standardized with rarefaction. In addition, accuracy of species inventories was assessed using species richness estimators.

There can be little progress in understanding the workings of an animal ensemble until basic aspects have been quantified such as the number of species, the abundance of each, and their identities and characteristics (Gaston & Blackburn 2000, Lawton 2000). Species richness, or the number of species (McIntosh 1967), is the simplest index to describe local ensembles and regional source pools (Peet 1975, Magurran 1988), and forms the basis of various models of community structure (McArthur & Wilson 1967, Connell 1975, Stevens 1989). More importantly, comparative and null model analyses used to investigate community structure (e.g. Chapters 5, 6, and 7) are more robust when based on relatively accurate estimates of species richness at a local scale (Gotelli & Graves 1996, Patterson, Willig & Stevens 2004). However, estimating species richness at a local and regional scale is difficult (May 1988, Colwell & Coddington 1994).

Accurate estimates of species richness may be particularly difficult when sampling elusive species such as insectivorous bats (Patterson, Willig & Stevens 2004). Nocturnal habits, flight, and the use of echolocation render bats difficult to detect and capture. During one night bats may cover large distances, crossing different vegetation and landscape types that are barriers to other mammals (Fleming 1988, de Jong 1994, Kalko *et al.* 1999, Jacobs, Schoeman & Barclay 2005). Furthermore, coexisting insectivorous bats feed at different times of the night (McDonald, Rautenbach & Nell 1990), for different periods (Fenton *et al.* 1998a), and in different habitats (Aldridge & Rautenbach 1987). Moreover, differences in the flying and echolocation abilities among bat species make some less susceptible to certain trapping techniques. For example, high-flying molossids are difficult to catch using mist nets set from the ground, and high duty-cycle echolocating bats such as rhinolophids, are more often captured using harp traps than mist nets (Rautenbach, Fenton & Whiting 1996). In such cases, passive monitoring of echolocation calls can be helpful in assessing distribution range and habitat use of bats seldom captured in mist nets or harp traps (Ochoa, O'Farrel & Miller 2000, Biscardi *et al.* 2004).

Accurate estimates of species richness at a local scale are highly dependent on the number of individuals counted and the amount of area sampled (Williams 1964). The area sampled may represent different sampling units such as oceanic islands, quadrats, or insectivorous bat ensembles. Even within a well-defined area, however, the number of species detected depends primarily on thoroughness of sampling. For example, the number of botanical collecting trips to the Galapagos Islands was a better predictor of the number of plant species than area, elevation, or isolation (Connor & Simberloff 1978). Thus, unless multiple ensembles are sampled equally and exhaustively, their species richness cannot be statistically compared (Colwell & Winkler 1984, Gotelli & Graves 1996).

Rarefaction can be used to standardize comparisons of species richness between ensembles (Soberon & Llorente 1993, Colwell & Coddington 1994, Gotelli & Graves 1996, Gotelli & Colwell 2001, Gotelli 2004). Rarefaction asks: for a collection of N individuals of S species, what is the expected number of species in a small sub-sample of n individuals? (Gotelli & Graves 1996). If the rarefaction algorithm is repeated many times, a rarefaction curve can be plotted with the number of individuals on the x-axis, and number of species on the y-axis. Rarefaction curves for different ensembles can then be used to compare their species richness based on an identical number of individuals sampled.

Species richness estimators can be used to assess the accuracy of the estimated species richness surveyed in ensembles. In contrast to rarefaction, species richness estimators extrapolate the number of species expected if enough individuals were sampled (Gotelli & Colwell 2001, Gotelli 2004). Extrapolation of species richness is achieved by fitting asymptotic and non-asymptotic functions to species rarefaction curves, fitting parametric distribution models of relative abundance, and non-parametric methods based on the distribution of individuals among species or of species among samples (Colwell & Coddington 1994, Colwell, Xuan Mao & Chang 2004). However, accurate fits of parametric models require counts of individuals on a logarithmic scale of accuracy and thus seldom practical (Colwell & Coddington 1994). Colwell & Coddington (1994) compared non-parametric methods to the asymptotic function most commonly used, the Michael Mentis function, using a large plant species data set. They found that the best predictor of total species richness was the Chao 2 (Chao 1989) non-parametric estimator. The Jackknife 2 (Burnham & Overton 1978) estimator provided the second least bias estimates of species richness for small samples.

In this chapter, active and passive surveying methods are used to estimate species richness of insectivorous bat ensembles and regional source pools. Sample-based rarefaction is used to standardize comparisons of species richness between ensembles and regional species pools. To extrapolate the expected species richness for ensembles and regional pools, the non-parametric Chao 2 and Jackknife 2 estimators, and the Michael Mentis asymptotic function are used. Finally, results from the analyses are discussed in light of published records.

METHODS

SAMPLING METHODS

Capture methods

I used different methods to catch the bat species of ensembles and 16 additional sites described in Chapter 3. I captured bats with harp traps and mist nets placed at the entrances of potential day and night roosts, including mines, caves, and suspected roost entrances in buildings. I used hand nets if bats hanging from the roof of a roost were accessible. I also set three to six mist nets at a time, which ranged in length from 9 m to 12 m, a half hour before dusk across and along potential flyways, forest edges, and riverbeds. Nets were monitored up to at least 24h00 each night. In addition, at each trapping location, I opened nets and monitored them for at least one full night (from dusk to dawn) to ensure that I was catching species that might be foraging after 24h00. Nets were checked regularly, every five to ten minutes during the first two hours, and at least every hour during the rest of the night to ensure that the bats were not injured while caught in the nets. I distinguished juvenile bats from adults by the presence of cartilaginous epiphyseal plates in their finger bones (Anthony 1988). Bats were identified in the field using taxonomic keys (Skinner & Smithers 1990, Taylor 2000). Species identification was subsequently confirmed by genetic analyses from wing tissue taken from most captured bats (Chapter 5).

Passive echolocation monitoring

I periodically monitored the echolocation calls of foraging bats in habitats of the fynbos, forest, and Nama-Karoo ensembles where species richness was low and netting was ineffective (Rautenbach, Fenton & Whiting 1996, Bernard & Fenton 2002). Coexisting bats can be distinguished from each other based on features of their echolocation signals (Fenton & Bell 1981, O'Farrel & Miller 1997, 1999, Russo & Jones 2002, Miller-Butterworth *et al.* 2005). Signal features such as lowest frequency (Fenton & Bell 1981) and peak frequency (Kalko 1995) are useful to identify coexisting vespertilionids and emballonurids. Statistical analyses such as discriminant function analysis (Obrist 1995, Barclay 1999, Jones, Vaughan & Parsons 2000, Parsons & Jones 2000) and artificial neural networks (Parsons & Jones 2000) can be used to quantify and objectify identification of bats based on signal features. However, the reliability of such statistical methods are strongly influenced by the variability of echolocation signals and sample size (Biscardi *et al.* 2004). Thus, I did not passively monitor echolocation calls in the savanna biome because bat species richness was much higher here than in other biomes (Rautenbach, Fenton & Whiting 1996, this study), and many echolocation parameters of coexisting bats showed marked overlap (Taylor 1999, 2000, Chapter 5).

I used three different passive monitoring systems. The first was an Anabat II bat detector with Anabat Zero Crossing Analysis Interface Module and Anabat 6 software installed on a Dell laptop computer. The resultant wave files were analysed using Analyze software (version 2.3, 1999, Computer software, IBM). The second was a Pettersson D980 bat detector (Pettersson Electronik AB, Uppsala, Sweden) connected to a Compaq Presario 1400 personal computer using a DAQ 6062E sound card (National Instruments, Austin, Texas) via an anti-aliasing filter (F2000, Pettersson Electronik AB, Uppsala, Sweden). The third was an Avisoft UltraSoundGate 416 fitted with two UltraSoundGate CM16 microphones (Avisoft Bioacoustics, Berlin, Germany) and Avisoft-RECORDER software (Avisoft Bioacoustics, Berlin, Germany) installed on a Compaq Presario 1400 personal computer. The resultant wave files obtained from the latter two monitoring systems were analysed using BatSound Pro software (version 3.20; Pettersson Elektronik AB, Uppsala, Sweden). I sampled at 500 000 Hz (16 bits, mono), with a threshold of 16.

Sampling effort

Different units have been used to quantify sampling effort. These include, (i) number of nights sampled (Fleming, Hooper & Wilson 1972, Moreno & Halffter 2000), (ii) number of hours sampled / number of nets used (Fenton *et al.* 1992), (iii) length of nets used / hour sampled (Clarke & Downie 2001), (iv) and number of bats captured (Brosset *et al.* 1996, Rautenbach, Fenton & Whiting 1996). However, I used active and passive methods to sample bats (see above), hence standardizing the sampling effort by number of nets, number of hours, or a combination of the two was not possible. For example, nets placed near roosts capture a larger number of bats in a shorter period thereby significantly increasing capture rates with lower effort compared with nets placed away from roosts (Bernard & Fenton 2002). In addition, in all the ensembles, I increased sampling effort towards capturing rare species. Thus, I used the number of trapping nights at a site as a measure of the sampling effort, which resulted in an adequate fit to the sample-based rarefaction curves (see below). I regarded the sample effort of a 24-hour period as 1 “trapping night”.

STATISTICAL ANALYSES

Sample-based rarefaction curves

Individual-based and sample-based rarefaction make different assumptions about the patchiness of data (Gotelli and Colwell 2001, Colwell, Xuan Mao & Chang 2004). Individual-based rarefaction explicitly accounts for the relative abundance of species and assumes all individuals of a species occur randomly and independently among samples of the data set (Colwell, Xuan Mao & Chang 2004). However, aggregated spatial and temporal distribution of individuals is quite common (Colwell, Xuan Mao & Chang 2004). Conversely, sample-based rarefaction curves implicitly reflect empirical levels of individual aggregation within species by considering only the presence or absence of a species in a sample (Colwell, Xuan Mao & Chang 2004). When tested, sample-based-rarefaction proved effective to standardize a collection of published plant and animal data sets (Colwell & Coddington 1994, Gotelli & Colwell 2001, Ugland, Gray & Ellingsen 2003).

Using EstimateS (version 7.7, Colwell 2004) software, I plotted the expected number of species per unit of trapping night for each ensemble based on sample-based rarefaction (Gotelli & Colwell 2001, Colwell, Xuan Mao & Chang 2004). Using the census data, a matrix was generated for each ensemble and regional pool. Each column of the matrix represented a trapping night and each row a species. If a species was present in an ensemble or regional pool, the corresponding cell was assigned a score of 1. Species not sampled during a trapping night were assigned a score of 0. If S_j was the number of species found in exactly *j* samples of the data set totaling H samples, then the expected species richness (S_{obs}) was:

$$S_{obs} = \sum_{j=1}^{H} S_j$$

For sample-based rarefaction, *i(h)* is an unbiased estimator of the species richness expected in *h* samples pooled, where

$$h = 1, 2, \ldots\ldots .H$$

This estimator was based on the S_j, appropriately weighted by the combinatorial coefficients (Colwell, Xuan Mao & Chang 2004):

$$\tau(h) = \sum_{j=1}^{H} (1 - \alpha_{jh})S_j$$

$$= S_{obs} - \sum_{j=1}^{H} \alpha_{jh} S_j \qquad h = 1, 2, \ldots\ldots .H$$

Where the combinatorial coefficients were defined by:

$$\alpha_{jh} = \begin{cases} \dfrac{(H - h)!(H - j)!}{(H - h - j)!H!} & \text{for } (j + h \leq H) \\ 0 & \text{for } (j + h > H) \end{cases}$$

Because the coefficient alpha in the sample-based estimator is 0 for h = H, estimated richness for the full data set was (Colwell 2004):

$$\tau(h) - S_{obs}$$

Species richness estimators

Using EstimateS software (version 7.7, Colwell 2004), I calculated the Chao 2 and Jackknife 2 non-parametric estimators, and the Michael Mentis (MMMeans) asymptotic estimator to estimate the species richness of each ensemble and regional species pool. First, the sample order was randomized 1000 times to eliminate the influence of the order in which nights were added to the total (Colwell 2004).

The Chao 2 (Chao 1989) non-parametric estimator was calculated as:

$$S_{Chao2} = S_{obs} + \frac{Q_1^2}{2(Q_2 + 1)} - \frac{Q_1 Q_2}{m(Q_2 - 1)^2}$$

The Jackknife 2 (Burnham & Overton 1978) estimator was calculated as:

$$S_{jack2} = S_{obs} + \left[\frac{Q_1 (2m - 3)}{m} - \frac{Q_2 (2m - 3)^2}{m\,(m-1)} \right],$$

Where S_{tot} was the estimate of the total number of species, S_{obs} was the observed number of species, Q_j was the number of species that occurred in *j* samples (Q_1 was the frequency of unique species, Q_2 was the frequency of duplicate species), and m was the total number of samples.

The Michael Menton richness estimator was computed based on the sample-based rarefaction curve (MMMeans, Colwell 2004). The Michael Menton estimator can also be calculated using the MMRuns method where estimates are computed for each pooling level, and for each randomization run, and then averaged over the total number of randomization runs. However, the MMMeans method is less erratic than the MMRuns method (Colwell & Coddington 1994)

The species richness estimators provided me with three different estimates of the expected species richness of ensembles and regional pools, to assess the accuracy of their observed species inventories.

RESULTS

LOCAL AND REGIONAL SPECIES RICHNESS IN SOUTHERN AFRICA

Total bat captures

In total, 1186 insectivorous bats representing 45 species, 22 genera and 7 families were captured over 181 trapping nights (Table 4.1). The three most captured species, representing 36.7 % of all captures, were the vespertilionid, *Neoromicia capensis*, the miniopterid, *Miniopterus natalensis* (formerly *Miniopterus schreibersii* – Appleton *et al.* 2004; Miller-Butterworth *et al.* 2005), and the molossid, *Tadarida aegyptiaca*. These three and *Rhinolophus clivosus* were the only bat species recorded in each of the seven local ensembles. The 12 most frequently captured species accounted for 68.6 % of captures, while 23 other species had fewer than 10 captures each and accounted for 5.8 % of total captures (Table 4.1). The most speciose family was Vespertilionidae (20 species), followed by Rhinolophidae (10 species), Molossidae (6 species), Nycteridae and Hipposideridae (3 species each), Miniopteridae (2 species), and Emballonuridae (1 species). Except for *Mops niveiventer* (Family Molossidae), bats captured at the Zambian sites (Table 3.1) exhibit distribution ranges that extend south into South Africa (Skinner & Smithers 1990, Taylor 2000). *Scotophilus sp. nov.* is a cryptic *Scotophilus species* (Jacobs *et al.* 2006).

CFK regional and local species richness

The CFK regional species pool inventory totaled 13 insectivorous bat species representing 11 genera and five families captured over 97 trapping nights. Five CFK species, *Neoromicia capensis*, *Miniopterus natalensis*, *Tadarida aegyptiaca*, *Rhinolophus clivosus*, and *R. capensis* were present at every CFK ensemble, while a sixth, *Myotis tricolor*, was captured in every fynbos ensemble. Four species were found only at Algeria. These included the endemic *Cistugo leseueri*, *Laephotus wintoni*, *Eptesicus hottentotus*, and one molossid, *Sauromys petrophilus*. One species, *Pipistrellus hesperidus*, was restricted to the Knysna forests. I did not capture *R. capensis* at Algeria, but I recorded echolocation calls of foraging individuals at the site during November 2004.

Table 4.1 Number of individual insectivorous bats representing 45 species, captured at the Algeria, Die Hel, De Hoop, Goodhouse, Koegelbeen, and Sudwala ensembles, and 16 additional local sites (location codes from Table 3.1) in southern Africa between 2001 and 2004 (see text for details on capture methods).

Species	Code	Algeria	Die Hel	De Hoop	Knysna	Ghouse	Kheen	Sudwala	Rest of southern African locations
Chaerephon pumilus	CP							5	17 (Sm) (Sp) (Sp) (Sz3)
Cistugo lesueuri #	CL	5							
Cistugo seabrai #	CS					2			
Cloeotis percivali	CPV							16	
Eptesicus hottentotus	EH	18				2			
Glauconycteris variegatus #	CV								1 (Sk)
*Hipposideros caffer **	HC					7		5	12 (Sm) (Sp)
H. commersoni #	HCO								2 (Sz1)
Laephotus wintoni #	LW	5							
Mimetillus moloneyi #	MM								1 (Sz3)
Miniopterus fraterculus	MF				16				
*M. natalensis **	MS	3	30	32	11	6	5	25	14 (Sz1) (Sz4) (Sl)
*Mops condylurus **	MC								50 (Sk) (Sl) (Sm2)
Mops niveiventer	MN								14 (Sz3)
Myotis bocagei #	MB								25 (Sk) (Sl) (Sz3)
*Myotis tricolor **	MT	1	8	34				18	
Myotis welwitschii #	MW								1 (Sk)
Neoromicia africanus	NA							11	9 (Sp) 2 (Ss) (Sl) (Sm2)
*Neoromicia capensis **	NC	22	2	57	42	4		2	14 (Gf) (Sz1) (Sz2) (Sz) (Sz4)
Nycteris hispida #	NH								2 (Sm1)
Nycteris macrotis #	NM								5 (Sz3)
*Nycteris thebaica **	NT	9		10		4		1	5 (Sp) (Sz1) (Sz3)
Nycticeius schlieffeni #	NS								2 (Sk)
Otomops martiensseni #	OM								2 (Sd)
Pipistrellus hesperidus	PK				14				11 (Sk) (Sl)
Pipistrellus rusticus	PR								22 (Sk) (Sz1) (Sz2) (Sz3) (Sz4)
Pipistrellus zuluensis #	PZ							1	2 (Sk) (Sz2)
Rhinolophus blasii #	RB							2	
*Rhinolophus capensis **	RC		6	41	12				
*Rhinolophus clivosus **	RCL	6	3	13	7	2	5	20	4 (Gk)
Rhinolophus darlingi	RD					2	1	11	3 (Sm)
Rhinolophus denti	RDT						14		
Rhinolophus fumigatus #	RF								3 (Sp) (Sz4)
Rhinolophus hildebrandti	RH							15	4 (Sp) (Sz1)
Rhinolophus landeri #	RL								2 (Sp)
*Rhinolophus simulator **	RS							53	3 (Sz1)
Rhinolophus swinnyi	RSW								24 (Gk) (Tp)
*Sauromys petrophilus **	SP	73							
Scotoecus albigula #	SA								2 (Sz3)
Scotoecus albofuscus #	SAL								2 (Sl) (Sz1)
Scotophilus viridis #	SV								4 (Sm2)
*Scotophilus dinganii **	SD							2	48 (Ss) (Sd) (Sl) (Sz2) (Sz1) (Sz3) (Sm2)
Scotophilus sp. nov.	SD2								14 (Sz1) (Sz3) (Sl),
*Tadarida aegyptiaca **	TA	124	2	11	6	2		1	18 (Fa) (Sz2)
Taphozous mauritianus #	TM							1	5 (Sz2)

* shows 11 most captured species, and # shows < 10 individuals captured

Savanna regional and local species richness

The savanna regional species pool inventory totaled 33 insectivorous bat species representing 18 genera and seven families captured over 56 trapping nights. Eighteen species, representing 12 genera and seven families were caught in the Sudwala ensemble. Rare bat species caught in the savanna biome included *Rhinolophus swinnyi*, *Myotis welwitschii*, *Scotoecus albofuscus*, *Mimetillus moloneyi*, and *Glauconycteris variegatus*.

Nama-Karoo regional and local species richness

Eleven species representing nine genera and six families were captured in the Nama-Karoo biome over 11 trapping nights. Nine species representing eight genera and six families were captured at Goodhouse. The passive echolocation monitoring also revealed the presence of *Sauromys petrophilus*, a species previously recorded in the area (Skinner & Smithers 1990). Hence, the inventory for the Goodhouse ensemble totalled 10. Three of the species in the Goodhouse inventory, *M. natalensis*, *R. clivosus*, and *R. darlingi* also roosted in the cave at Koegelbeen. The fourth species in the cave, *R. denti*, was not captured at Goodhouse.

SAMPLE-BASED RAREFACTION AND SPECIES RICHNESS ESTIMATORS

Ensembles

Sample-based rarefaction curves of the CFK and savanna ensembles show that at a local scale, the savanna ensemble, Sudwala, exhibited the highest species richness (Fig. 4.1). Among CFK ensembles, the Algeria ensemble was relatively species rich, while species richness of the remaining three ensembles was markedly similar (Fig. 4.1). The sample based rarefaction curves of the Nama-Karoo ensembles are not shown because of the low number of trapping nights at each site. Species richness estimators indicated that inventories of the ensembles were between 86 and 100 % complete (Table 4.2).

Regional species pools

Sample-based rarefaction clearly showed that species richness of the savanna regional pool was significantly higher than the CFK regional pool (Fig. 4.2). Species richness estimators indicated that the inventory of the CFK regional pool was 100 % complete (Table 4.2). However, the inventory of the savanna regional pool was only between 69 and 85 % complete (Table 4.2).

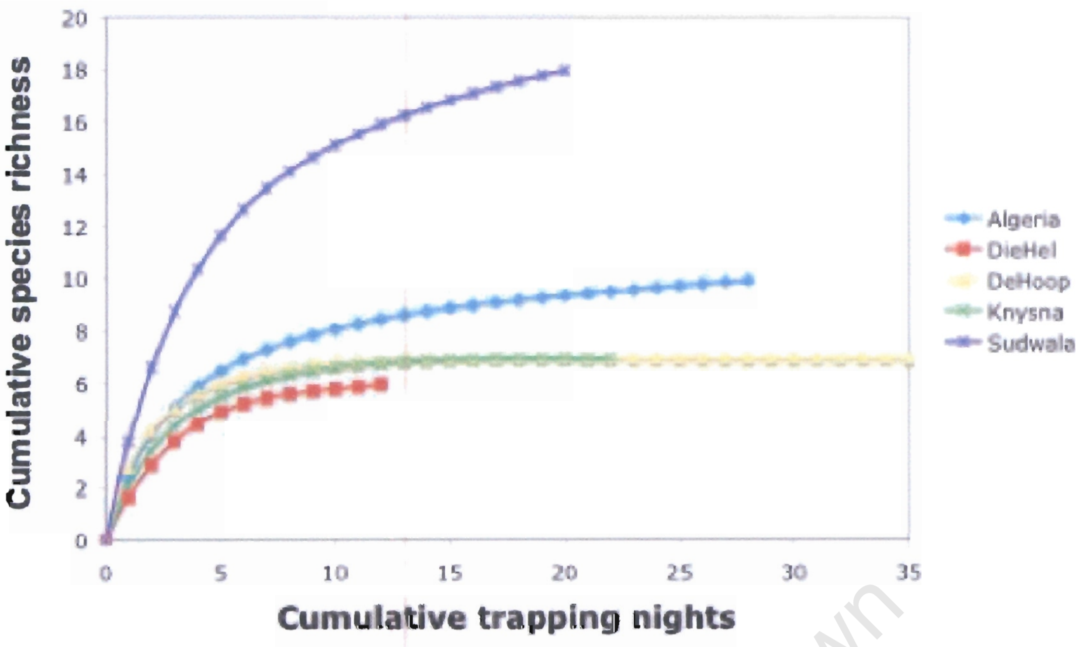

Fig.4.1 Sample-based rarefaction curves depicting mean species richness of insectivorous bat species inventories obtained from the randomized orders of trapping nights in the fynbos ensembles, Algeria (SD = 1.29), Die Hel (SD = 0.68), De Hoop (SD = 0), forest ensemble, Knysna (SD = 0), and savanna ensemble, Sudwala (SD = 1.77). Greatest species richness was in the savanna ensemble. Amongst fynbos and forest ensembles, Algeria exhibited the greatest species richness.

Table 4.2 Observed number (italics) and expected number of bat species - based on Chao 2 (Chao 1989), Jackknife 2 (JK2, Burnham & Overton 1978), and Michael Mentis Means (MMM, Colwell, Xuan Mao & Chang 2004) species-richness estimators - of ensembles (Algeria, Die Hel, De Hoop, Knysna, Goodhouse, Koegelbeen, and Sudwala) and regional pools (Cape Floristic Kingdom and savanna biome). Numbers in parentheses show the % completeness of species inventories, calculated as the number of species observed divided by the expected number.

	Algeria		Die Hel		De Hoop		Knysna		CFK		GHouse		Kbeen		Sudwala		Savanna	
Estimator	*10 spp*		*6 spp*		*7 spp*		*7 spp*		*13 spp*		*10 spp*		*4 spp*		*18 spp*		*33 spp*	
Chao2	10.4	(96)	6.5	(92)	7	(100)	7	(100)	13	(100)	10.2	(98)	4	(100)	18.4	(98)	46	(72)
JK2	10.5	(95)	6.9	(87)	7	(100)	7	(100)	13	(100)	10.7	(94)	4	(100)	18.7	(96)	47.6	(69)
MMM	11	(91)	8	(75)	7	(100)	8	(88)	13	(100)	14.7	(68)	4.2	(95)	21.1	(86)	39	(85)

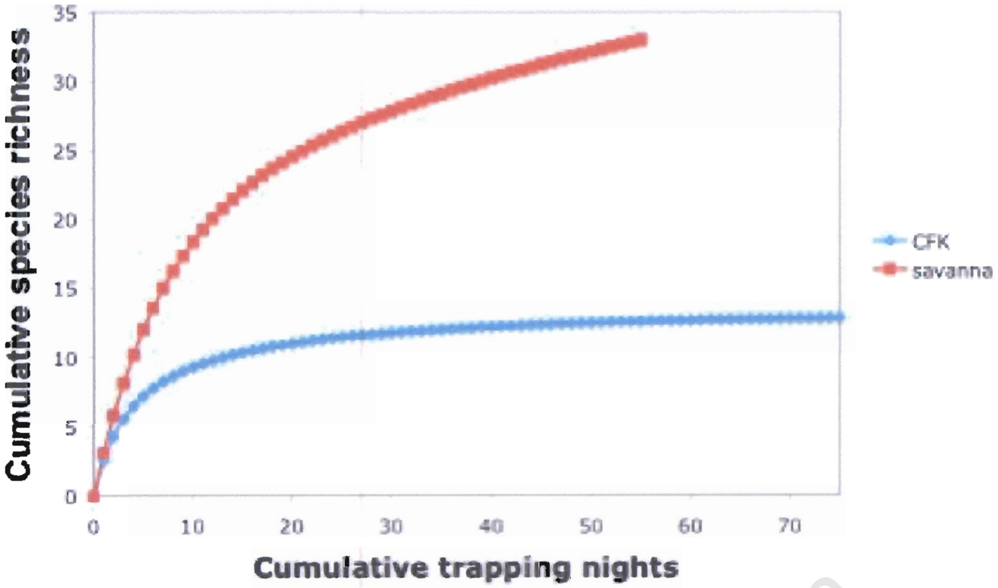

Fig. 4.2 Sample-based rarefaction curves depicting mean species richness of insectivorous bat species inventories obtained from randomized orders of trapping nights in the Cape Floristic Kingdom (SD = 0) and savanna biome (SD = 3.1). Species richness was significantly higher in the savanna biome.

DISCUSSION

SPECIES MISSING FROM REGIONAL SOUTHERN AFRICAN INVENTORIES

Based on total captures, southern Africa has at least 45 species of bats from 22 genera and seven families. Highest local and regional species richness was in the savanna biome (18 and 33 species respectively). By comparison, the Red Data Book of the Mammals of South Africa (Friedmann & Daly 2004) lists 47 insectivorous bat species of the region. Except for *Chaerephon ansorgei* and *Mops midas*, species listed but not captured in this study are known from less than eight records (*Kerivoula argentata, K. lanosa, Laephotus botswanae, L. namibensis*, *Neoromicia rendalli*, and *Nycteris woodi*). Most of these bat species are associated with the sub-tropical savannas of southern Africa. Two additional vespertilionid species were captured very recently, *Scotoecus hirundo* at Zinave National Park in Mozambique (Taylor 2000, W. Cotterill pers. comm.), and *Scotophilus nigrita* near the border of South Africa and Mozambique (D.S. Jacobs pers. comm.). Based on species richness indicators, it is estimated that the inventory of the savanna regional pool was between 69 and 89 % complete. Thus, more surveys of the savanna biome are necessary, particularly in Botswana and Mozambique, to establish population numbers and distribution ranges of recently discovered species, and assess the presence of other insectivorous bat species not known from the region (D.S. Jacobs & W. Cotterill pers. comm.).

SPECIES RICHNESS OF ENSEMBLES

Based on species richness estimators, the species inventories of ensembles are at least 90% accurate. Inventories of the CFK, Nama-Karoo, and savanna biomes also corresponded well with known distribution ranges of insectivorous bats in South Africa (Friedmann & Daly 2004). Nonetheless, I made amendments to the inventories of two ensembles used in subsequent analyses (Chapters 5, 6 and 7).

Previous surveys indicate that the inventories of two CFK ensembles may not be complete. At Die Hel, Prof. D.S. Jacobs captured one male *Miniopterus fraterculus* in 1998 (Miller-Butterworth, Jacobs & Harley 2003). Species abundance was estimated to be low (D.S. Jacobs per. comm.). Because my sampling effort was low at Die Hel (12 trapping nights, compared to > 20 trapping nights at other CFK ensembles), I included *M. fraterculus* in Die Hel's inventory for subsequent analyses. At Knysna Forest, Herselman & Norton (1985) captured one *Kerivoula lanosa* male in 1979. This bat is special for using abandoned hanging nests of birds, such as weavers, as day roosts (Roberts 1951). Using mist nets and passive monitoring systems, I intensively surveyed the bat fauna of the Knysna forest at many different locations and habitats, including the exact place where the last *K. lanosa* was captured in 1979 (Herselman & Norton 1985, pers. comm. J.C. Herselman). In addition, I examined more than 250 abandoned weaver nests. Nothing indicated the presence of *K. lanosa*. Recent attempts to verify the presence of *K. lanosa* at one of the two eastern Cape locations (Pirie Forest) where the bat was recorded also proved unsuccessful (pers. comm. D. S. Jacobs). Thus, I did not include *K. lanosa* in Knysna's inventory for subsequent analyses.

Four species were captured in the Koegelbeen ensemble, including the rare rhinolophid, *Rhinolophus denti*. Preliminary genetic analyses confirmed that *R. denti* is phylogenetically distinct from *R. swinnyi* (Stoffberg, Jacobs & Matthee unpublished data), a previous disputed fact (Hayman & Hill 1971, Rautenbach 1986, Gelderblom, Bronner & Lombard 1995). Distribution records suggest that three widespread species, *Tadarida aegyptiaca*, *Neoromicia capensis*, and *Nycteris thebaica* (Skinner & Smithers 1990, Taylor 2000, Friedman & Daly 2004) should occur in the Koegelbeen ensemble. Since these bats were recorded at most of the other ensembles, including Goodhouse, and sample effort at Koegelbeen was particularly low, they were included in Koegelbeen's inventory to total seven bats in subsequent analyses.

SPECIES RECORDED ACROSS SOUTHERN AFRICA

Three species, the vespertilionid, *Neoromicia capensis*, the miniopterid, *Miniopterus natalensis* (formerly *Miniopterus schreibersii* – Appleton *et al.* 2004; Miller-Butterworth *et al.* 2005), and the molossid, *Tadarida aegyptiaca*, comprised 36.7 % of all individual bat captures. These three and *Rhinolophus clivosus* were the only species that were recorded in every ensemble. These patterns are consistent with those found in bat surveys of the Neotropics (e.g. Moreno & Halffter 2000, Bernard & Fenton 2002), and savanna biome of southern Africa. For example, 26 insectivorous bat species were captured using mist nets and harp traps at a variety of sites near Pafuri in the north of the Kruger National Park (Aldridge & Rautenbach 1987). However, 43 % of total captures comprised only four species, *Hipposideros caffer, Neoromicia capensis, Nycticeius schlieffeni*, and *Scotophilus dinganii*. Similarly, from a total of 568 individuals representing 25 species netted in a longitudinal survey of bats in the Kruger National Park, 83 % of captures involved individuals of seven species, *Mops condylurus, Nycticeius schlieffeni, Scotophilus dinganii, S. borbonicus, Pipistrellus nanus*, and *Neoromicia capensis* (Rautenbach, Fenton & Whiting 1996). During a study on the effects of elephant disturbance in Miombo woodland in northern Zimbabwe, four insectivorous vespertilionids, *Neoromicia capensis, Scotophilus viridis, Scotophilus* 'other', and *Nycticeius schlieffeni*, represented 85 % of total captures (Fenton *et al.* 1999). The phenomenon of a few bat species present in local ensembles across the regional landscape is therefore not unusual.

WHY IS BAT RICHNESS LOW IN THE CAPE FLORISTIC KINGDOM?

In contrast to low numbers of birds and mammals (Bigalke 1979), the flora of the CFK is characterized by an unusually high number and density of plant species exceeding that of most, if not all, equivalent-sized regions of the world (Bond & Goldblatt 1984, Cowling & Holmes 1992). Environmental factors that promoted speciation in CFK plants such as soil diversity, dissected landscape, moisture gradients, and the transient, fire created niches (Bond & Goldblatt 1984, Cowling & Holmes 1992), did not promote similar speciation in the herbivorous insects of the region (Gilliomee 2003). Indeed, adverse factors associated with the flora such as the sclerophyllous leaves that contain high levels of toxic compounds, the low litter production of the leaves, and shrubby architecture, make the CFK plants a poor source of food and/or niches to occupy for herbivorous insects (Gilliomee 2003). The result is low insect numbers, low insect biomass, and probably also low insect diversity (Gilliomee 2003). Consequently, low availability of insects may negatively impact species richness of insectivorous bats in the CFK region, and/or increase competition among sympatric bats for limiting prey resources.

Chapter 5

PHENOTYPIC NICHE PATTERNS SUPPORT COMPETITION AND COEVOLUTION HYPOTHESES

INTRODUCTION

It can be assumed that the evolution of an organism's phenotype by natural selection resulted in much of the variation amongst species and is largely adaptive with respect to ecological function. Body size, wing morphology, and echolocation are dimensions of the phenotypic niche that can give valuable insight into the biotic processes that have shaped insectivorous bats and their community structure. I used null models to investigate the influence of the two biotic filters, competition and coevolution, on phenotypic patterns of insectivorous bat species of seven insectivorous bat ensembles and their functional groups. This was done as follows. I removed the influence of body mass from the wing morphology and echolocation parameters taken from species comprising these ensembles, and generated multivariate plots of the wing morphology and echolocation such that distances between any two species on these plots were representative of the wing and echolocation differences between them. Prior to generating these plots, I set up predictions in terms of the phenotypic distances between species, and how these distances should differ from distances chosen at random, if competition or coevolution structured the ensembles.

PREDICTIONS FROM COMPETITION AND PREY-PREDATOR INTERACTIONS

If competition influenced the phenotypic niche structure of ensembles, two predictions can be made (Lack 1947). First, phenotypic distances between species of ensembles should be greater than distances chosen at random from a particular distribution of distances. Second, phenotypic distances between species should be less variable - i.e. species should be more evenly spaced - than the variance of distances expected by chance (Case & Sidell 1983). On the other hand, if coevolution between consumers and their food sources influenced niche structure, then the phenotypic distances between coexisting species should be smaller, i.e. species should be more similar, than differences between species expected by chance (Bowers & Brown 1985, Willig & Moulton 1989).

Demonstrating unusual patterns of phenotypic differences and variances requires an appropriate context in which to assess the probability of chance producing similar patterns (Gotelli & Graves 1996, Stevens & Willig 1999, Patterson, Willig & Stevens 2004). The chance patterns expected in the absence of competition and/or coevolution can be simulated by random sampling from known or imagined source pools using null models. Deviations of the observed pattern from the expected pattern may elucidate the ecological/evolutionary processes responsible for the observed phenotypic pattern. However, choice of the known or imaginary source pool from which chance patterns are simulated has proven controversial (Gotelli & Graves 1996).

Construction of realistic regional source pools is difficult, requiring a great deal of historic and phylogenetic information (Gotelli & Graves 1996, Stevens & Willig 1999, Gotelli & Entsminger 2004). Such information is necessary because, for example, particular historic events may have selected for a strong phylogenetic signal in a taxon to create a particular pattern of morphology within a clade. A random assembly of species from this clade will likely recapitulate that pattern (Stevens & Willig 1999), obfuscating the patterns caused by the processes of interest. Ideally, regional source pools should consist of species that have a reasonable chance of reaching a local ensemble (Gotelli & Graves 1996). For example, a forest specialist from the mainland is unlikely to colonize a relatively barren island off the coast. One way to solve problems of phylogeny, dispersal ability, and habitat, is to randomly sample expected patterns from multiple biologically and geographically realistic regional source pools (Harvey & Pagel 1991, Brown 1995, Gotelli & Graves 1996).

CONTROL FOR BODY SIZE AND PHYLOGENY

Body size has the most profound impact on how animals function (Peters 1983, Calder 1984, West *et al.* 1997, Reich 2001, Lovegrove & Haines 2004). Body size is a comprehensive phenotypic trait that incorporates elements of evolution at levels of morphology, physiology, behaviour, and ecology (Barclay & Harder 2004. Simmons & Conway 2004, Speakman & Thomas 2004, Swartz, Freeman & Stockwell 2004, Willig, Patterson & Stevens 2004). Thus, if biotic filters structure ensembles, theoretically body size should be influenced (Brown & Nicoletto 1991, Brown, Marquet & Taper 1993, Brown 1995, Gotelli & Graves 1996, Gaston & Blackburn 2000). However, body size is not the only important phenotypic trait that defines the ecological niche position of a bat species within an ensemble. Wing morphology and echolocation parameters are also good predictors of diet and habitat use of sympatric bats (Aldridge & Rautenbach 1987, Norberg & Rayner 1987, Bogdanowicz, Fenton &Daleszczyk 1999, Schnitzler & Kalko 1999, 2001, Jacobs 2000, Schoeman & Jacobs 2003).

Body size has a significant allometric relationship with many ecomorphological traits (West *et al.* 1997, Swartz, Freeman & Stockwell 2004), including flight and echolocation parameters of bats (Norberg & Rayner 1987, Barclay & Brigham 1991, Jones 1994, 1996, Norberg 1998). As size increases, volume changes more rapidly than surface area, dictating many patterns of body structure such as wingspan and wing area (Speakman & Thomas 2004). Similarly, peak echolocation call frequency and body size are negatively correlated (Jones 1994, 2996, Jones & Rydell 2004). Hence, comparative analyses of phenotypic traits need to account specifically for the effect of body size (Swartz, Freeman & Stockwell 2004). The allometric relationship between body size and wing or echolocation parameters of interest can serve as a criterion on which to remove the effects of size from the phenotypic parameters (Harvey & Pagel 1991).

Apart from its influence on species patterns, phylogeny can also affect the treatment of species as independent data points (Felsenstein 1985). In some analyses, it may be necessary to take into account the phylogenetic relationships between species to examine whether the evolution of two characters is correlated, using, for example, Felsenstein's (1985) method of independent contrasts (Harvey & Pagel 1991, Blomstein, Garland & Ives 2003). Felsenstein's method is based statistically on a Brownian motion model. The model assumes that successive genetic changes of a parameter of a species is independent of changes in another species, and that the expected total change summed over many independent changes will be zero (Harvey & Pagel 1991). If so, pair-wise comparisons between species or higher nodes of a phylogenetic tree that share a common ancestor is independent of each other because the difference of a morphological character reflect only the evolutionary changes in that character that have taken place since they split from their common ancestor (Harvey & Pagel 1991). Felsenstein's method of independent contrasts is particularly efficient when the phylogenetic relationships amongst the species are well resolved (Harvey & Pagel 1991).

In this chapter, I test the contrasting predictions of competition and coevolution hypotheses on observed patterns of phenotypic differences (body size, wing morphology, and echolocation) between species of ensembles and functional groups. Phenotypic differences between species are quantified with two indices, minimum segment length ratio and variance of segment length ratios, and compared with corresponding patterns expected by chance that are derived by random sampling from three known regional source pools. Before null modelling phenotypic niche patterns, the influence of body size is removed from wing and echolocation parameters, taking the phylogenetic relationships among bat species into account.

METHODS

Phenotypic data of coexisting insectivorous bats of southern African ensembles were collected between 2001 and 2004 (Chapter 4). The study ensembles are described in more detail in Chapter 3. To compile accurate species inventories, ensembles were surveyed during wet and dry seasons, and the estimated species richness of ensembles was verified statistically using rarefaction and species richness estimators (Chapter 4).

BODY SIZE, WING, AND ECHOLOCATION PARAMETERS

Body size

I measured body mass (to nearest 0.5 g) of each captured bat with a Pasola scale. Forearm length is a good measure of body size, and frequently used to compare interspecific differences of body size between bats (e.g. Aldridge & Rautenbach 1987, Jones 1994, Bogdanowicz, Fenton &Daleszczyk 1999, Jacobs 2000). However, mass is an effective measure of body size, irrespective of the shape or taxonomic affiliation of the species (Brown 1995), and therefore well suited to compare body size of different taxa (e.g. Gaston & Blackburn 2000, Barclay & Harder 2004, Speakman & Thomas 2004). I excluded measurements from juveniles and gravid females to avoid biasing means of species.

Wing morphology

I used wing area and wingspan as measures of absolute wing size (Norberg & Rayner 1987). I photographed the extended right wing of each captured bat (after Saunders & Barclay 1992) with an Olympus C730 digital camera (Olympus America Inc., New York, USA) ensuring that the camera was positioned at a 90° angle above the flattened wing. Each wing was extended at a similar angle flat on graph paper until the wing membrane was stretched tight, and the right hind limb and tail membrane could be opened and secured in position to the graph paper with masking tape. I calibrated these wing images with the graph paper to measure wingspan (WSP, to nearest 0.1 mm) and wing area (WA, including body area without the head, and the area of the uropatagium (after Norberg & Rayner 1987) to nearest 0.1 mm^2), using SigmaScan Pro 5 software (version 5.0.0, SPSS Inc., Aspire Software International, Leesburg, USA). Measurements were doubled to get WA and WSP for the whole bat.

Echolocation

I recorded echolocation signals of low duty-cycle echolocation bats from hand-released bats. Bats were followed for as long as possible after release to ensure that search phase calls were recorded (O'Farrell *et al.* 1999). I released the bats just before dusk the day after they were captured. This ensured that there was sufficient light for me to follow them. Bats were released in open spaces, at least 15 m from the nearest obstacles to minimize variability in signal parameters due to proximity to obstacles (Kalko & Schnitzler 1993, Kalko 1995, Obrist 1995). I recorded echolocation signals of high duty-cycle echolocation bats held in the hand, eliminating any possible Doppler shift or compensation for it by the bat when in flight (Heller & v. Helversen 1989). I released each bat in the habitat in which I caught it.

I used duration (DUR), bandwidth (BW), and peak echolocation frequency (PF) as indicators of sensory ability in low duty-cycle echolocating bats (Chapter 1). I only used duration and peak echolocation frequency as indicators of sensory ability in high duty-cycle echolocating bats (Chapter 1).

I digitally recorded the echolocation calls of bats in real time on a Compaq Presario 1400 personal computer using a DAQ 6062E high speed sound card (National Instruments, Austin, Texas) connected to the high frequency output of a Pettersson D980 bat detector (Pettersson Electronik AB, Uppsala, Sweden) via an anti-aliasing filter (F2000, Pettersson Electronik AB, Uppsala, Sweden).

The resultant wave file was analysed using BatSound Pro software (version 3.20; Pettersson Elektronik AB, Uppsala, Sweden). I set the sampling frequency at 500 000 Hz (16 bits, mono), with a threshold of 16. I randomly selected one signal pulse for each bat to avoid pseudo-replication. Choice of signal pulse was subject to the following three criteria. First, signals with a high signal-to-noise ratio, i.e. signal from the bat was at least three times stronger than the background noise as displayed on the time-amplitude window. Second, only signals that were not saturated were analyzed (Fenton *et al.* 2001). Finally, for low duty-cycle echolocating bats, only search phase signals that were recorded at least three seconds after releasing the bat, were considered. The dominant harmonic from each call was taken from the Fast Fourier Transform (FFT) power spectrum (Obrist 1995, Parsons & Jones 2000, Russo & Jones 2002; size 512). A Hanning window was used to eliminate effects of background noise. I measured PF from the peak of the power spectrum (Obrist 1995, Parsons & Jones 2000). I measured BW in signals of low duty-cycle echolocating bats at ±18 dB from the PF on the FFT power spectrum (Fullard, Dawson & Jacobs 2003). I measured DUR from the time-amplitude display (Biscardi *et al.* 2004).

Species means

Where possible, I randomly selected 10 individuals (five male and five female) to represent a species' mean. If fewer than five individuals of either sex were caught, or fewer than 10 individuals in total, I selected all the individuals available. Averaging parameters for males and females (Schoener 1984) may represent a phenotype that does not occur in nature (Gotelli & Graves 1996). On the other hand, if each sex is treated as two morphospecies when using null models (Dayan *et al.* 1989, 1990), the results will be difficult to interpret since overlap within a species may not be statistically or biologically equivalent to overlap between species (Gotelli & Graves 1996). Furthermore, small sample sizes for some species precluded me from treating each sex separately. However, preliminary ANOVA analyses detected only limited sexual dimorphism in some species. Small sample sizes also precluded me from taking geographic variation of parameters into account. Using source pool averages for geographically highly variable species may reduce the size of the source pool if the average parameter in the source pool characterizes only a small fraction of all the populations representing the pool (Gotelli & Graves 1996). However, preliminary ANOVA analyses detected limited geographic variation in widespread species such as *Neoromicia capensis* and *Nycteris thebaica*. Thus, I used the average mass, WSP, WA, PF, BW (for low duty-cycle echolocating bats), and DUR for each species. Means were Log10 transformed to enhance normality of the data (Kolmogorov one sample test, all $p > 0.02$, except DUR, $d = 0.18$, $p < 0.02$).

STATISTICAL ANALYSES

Control for size and phylogeny

To remove the influence of body size and phylogeny on wing or echolocation parameters, the allometric relationship between mass on the one hand, and WSP, WA, PF, BW, and DUR, were calculated with the method of independent contrasts (Felsenstein 1985), using the PDAP package (Midford, Garland & Maddison 2004) of Mesquite phylogenetic software (v1.05, Maddison & Maddison 2004).

The phylogeny for the bats was derived from genetic analyses conducted by Dr. Geeta Eick and Samantha Stoffberg on DNA material taken from captured bats. Paired wing tissue samples were taken from captured bats with a 3 mm biopsy punch and stored in 0.2 ml epindorf vials filled with 70 % ethanol (Miller-Butterworth, Jacobs & Harley 2003). The punctures clearly marked the bats and ensured that recaptures were not included in subsequent analyses.

Dr. Geeta Eick and Samantha Stoffberg generated partial sequences from two mitochondria genes and one nuclear gene for 42 southern African bat taxa. A 527 bp fragment of the cytochrome b gene, a 505 bp fragment of the 16S ribosomal gene and a 466 bp fragment of the STAT5A gene were combined to form a supermatrix data set for phylogenetic analysis comprising 545 parsimony informative characters out of a total of 1498 alignment positions. The combined data set was analysed using parsimony (MP) in PAUP v4.0b10 (Swofford 2002). For topology searches, trees were generated using equal weighting and the heuristic search option with tree-bisection-reconnection branch-swapping and stepwise addition of taxa using 1000 random sequence addition replicates, with one tree retained per stepwise addition replicate.

If the lengths of the branches of the tree in units of expected variance in evolutionary change are known, Felsenstein's independent contrast method assumes a gradualist model of evolution (Harvey & Pagel 1991). In some cases a diversity of different branch length definitions will yield essentially the same results (Garland, Harvey & Ives 1992). I lacked branch-length information on actual times of divergence for standardizing contrasts, and therefore, following Grafen (1989), I set all branch lengths equal, thereby defining a branch length as the number of steps along higher branches as indicated by the cladistic analysis (Garland et al. 1992). This assumes a punctuational mode of evolution (Grafen 1989). Previous work has indicated that the use of branch lengths so defined is preferable to obtaining correlations with no correction for phylogeny (Martin & Garland 1991).

I used a least-squares regression to compare the allometric relationship between independent contrasts of mass, and wing and echolocation parameters (Zar 1999). If the least-squares regression through the origin was significant, I noted the slope, *b* (allometric exponent), and calculated new (size corrected) values for the original wing and echolocation parameters as:

Size corrected parameter = old parameter/mass^b (Blomberg, Garland & Ives 2003)

Principal component analyses

To remove any correlation between size corrected values of wing morphology (WSP and WA) and echolocation (PF, BW, and DUR), I created unique parameters using principal component analysis (PCA, Statistica version 7, Statsoft). PCA eliminates redundancy of highly correlated characters yet maintains morphological distances among species by constructing linear models from original variables. By extraction from a covariance matrix, new variables (principal components) are produced that retain the original relationships among species in wing and echolocation space (Stevens 1986).

Bandwidth was not measured from high duty-cycle echolocation bats, hence not included in the PCA of all captured species. Separate PCAs for each of the three functional foraging groups were conducted using PF, BW, DUR, WA, and WSP parameters for the open and clutter-edge species (low-duty cycle echolocation bats), and PF, DUR, WA, and WSP for the clutter species (mainly high duty-cycle echolocation bats).

Testing the predictions of competition and coevolution

Segment-length ratio indices

Segment-length ratio indices are more appropriate than indices of absolute distance when testing predictions of competition or coevolution hypotheses on size or morphology patterns (Gotelli & Entsminger 2004). Parameters were Log10 transformed, thus:

$$\text{Log}\,(A/B) = \text{Log}\,(A) - \text{Log}\,(B)$$

where, A and B were trait values for adjacent species (Gotelli & Entsminger 2004). Data were sorted from largest to smallest, and a n - 1 set of segment-length ratios calculated for n species of an ensemble or functional group.

The first index, minimum segment-length ratio, was the segment-length ratio between the two species nearest in morphospace, i.e. the lowest segment-length ratio among the set of segment-length ratios. This index allowed me to test Hutchinson's (1957) prediction that there should be a minimum spacing between species if competition structured the phenotypic niche of ensembles or functional groups. It also allowed me to test the contrasting prediction of the coevolution hypothesis that the two species should be closer in morphospace than otherwise expected (Gotelli & Entsminger 2004). If the minimum segment-length ratio between species was significantly larger than 95% of simulated minimum segment-length ratios, I concluded that competition influenced the phenotypic structure of an ensemble or functional group. Conversely, if the minimum segment-length ratio between species was significantly smaller than 95% of random values, I concluded that coevolution structured the phenotypic niche.

The second index, the variance of segment-length ratios among adjacent species in ensembles or functional groups, tested the prediction that species should be regularly spaced if competition influenced the phenotypic niche (Poole & Rathcke 1979, Gotelli & Entsminger 2004). Thus, if the observed variance was significantly smaller than 95% of simulated values, I concluded that competition structured the phenotypic niche of ensembles or functional groups.

Regional source pools

I compared values of segment-length indices calculated for observed ensembles with values calculated for simulated ensembles that were assembled at random from regional source pools (Gotelli & Graves 1996, Stevens & Willig 1999, Gotelli & Entsminger 2004). Because no *a priori* regional pool size is preferred (Gotelli and Graves 1996, Stevens and Willig 1999), I used two different regional source pools for each ensemble. The first regional source pool included bat species whose distribution overlapped in the biome in which the ensemble occurs - based on distribution records from Skinner & Smithers (1990) and Friedmann & Daly (2004), and personal capture records (Chapter 4). Hence, the CFK ensembles were compared with simulated ensembles drawn from the CFK regional pool (13 species, Chapter 4), the Nama Karoo ensembles with simulated ensembles drawn from the Nama-Karoo regional pool (17 species), and the savanna ensemble with simulated ensembles drawn from the savanna regional pool (38 species). The second regional pool included all the species caught in southern Africa (Chapter 4).

Simulations and statistics

Using the Size Ratio module of Ecosim null model software (version 7.7, Gotelli & Entsminger 2004), I statistically compared segment-length indices of observed ensembles and functional groups with those of simulated ensembles and functional groups assembled at random from the regional source pools. For each phenotypic parameter and ensemble, I created a matrix of all the species that were sampled at the site, and three separate matrices of species classified to functional groups (Chapter 3, Table 5.1). Each row represented the mean parameter value of a species.

Simulated ensembles or functional groups were constructed by drawing the same number of species present in the observed ensemble or functional group, at random from the regional source pool. Species in regional source pools were drawn with equal probability. Once drawn, species could not be drawn again for that particular simulated ensemble or functional group. Minimum segment length ratios and variances were calculated for every simulated ensemble or functional group.

For each ensemble and regional species pool, I calculated the number of simulation ensembles or functional groups that could be assembled from the algorithm:

$$C = S! / \{N!(S - N)!\}$$

where, C was the number of ensembles or groups, N was the number of species in the ensemble or functional group, and S was the number of species in the regional source pool (Moulton & Pimm 1987, Willig & Moulton 1989). C was often very large so when $C > 1000$, I selected a random 1000 simulated ensembles or functional groups to calculate probability statistics. When $C < 1000$, I calculated statistics based on the actual number of simulations possible.

Log-Uniform Null Models

To test if results from the above null models were peculiar to the regional source pools that were used, I compared the segment-length values of ensembles and regional source pools with those sampled randomly from a log-uniform null distribution, i.e. where there were approximately equal numbers of species in each of the segment-length ratio classes (Gotelli & Entsminger 2004). The endpoints of the log-uniform null distribution were fixed by the largest (*Hipposideros commersoni*, 68.7 g) and the smallest (*Cistugo seabrai*, 3.8 g) bat species caught during the study. Ecosim generated a set of default values: the default minimum was 10% less than the observed minimum, and the default maximum was 10% more than the observed maximum (Gotelli & Entsminger 2004). For 1000 simulations, Ecosim randomly and uniformly selected a point greater than or equal to the smallest boundary and less than or equal to the largest boundary, for *n* species in an ensemble or regional source pool.

If more than 95% of the minimum segment-length or variance in segment-lengths of the simulated ensembles were larger or smaller than the observed ensemble, I concluded that patterns of the observed ensemble were non-random (Manly 1991). In addition, experiment-wise error of the significance tests (i.e. *p* values) was held constant at five percent for ensembles separately from functional groups at each site by application of Bonferroni sequential adjustments (Rice 1989).

RESULTS

RELATIONSHIP BETWEEN MASS, AND WING MORPHOLOGY AND ECHOLOCATION

Rarefaction and species richness estimators indicated that species inventories of the fynbos, forest, and savanna ensembles were complete (Chapter 4). Size, wing, and echolocation parameters of 42 insectivorous bat species were measured (Table 5.1). Although three other species, *Mimetillus moloneyi, Nycteris hispida* and *Scotoecus albigula*, were captured (Chapter 4), it was not possible to record their echolocation calls and were therefore not included in analyses. In any case, these species were very rare. Fig. 5.1 shows the phylogenetic relationship between the species recovered from parsimony analysis by Dr.. Geeta Eick and Samantha Stoffberg of the combined 16S, cytochrome b & STAT5A data sets, derived by DNA analyses of skin material obtained from captured bats (Length = 2214, Consistency Index (CI) = 0.4503, and Retention index (RI) = 0.604). The topology of Fig. 5.1 is largely consistent with existing family-level molecular phylogenies of bats (Teeling *et al* 2002, Hutcheon & Kirch 2004, Eick, Jacobs & Matthee 2005). In addition, phylogenetic relationships among certain species have been confirmed by more detailed genetic analyses (Stadelmann et al. 2003, Eick, Jacobs and Matthee 2005, Miller-Butterworth et al. 2006, Jacobs et al. 2006, Stoffberg, Jacobs and Matthee unpubl. data).

Significant allometric relationships were found between mass, and four of the wing and echolocation parameters. Only BW of the echolocation signal was not significantly correlated with mass (Product-Moment Correlation Coefficient; $r = 0.15$, d.f. = 29, $p = 0.26$). The other two echolocation parameters, PF ($y = -0.3x$; $r = 0.93$, d.f. = 41, $p < 0.001$) and DUR ($y = 0.55x$; $r = 0.91$, d.f. = 41, $p < 0.001$), and both wing parameters, WSP ($y = 0.51x$; $r = 0.73$, d.f. = 42, $p < 0.001$) and WA ($y = 0.39x$; $r = 0.41$, d.f. = 41, $p < 0.001$), were significantly correlated with mass.

PRINCIPAL COMPONENT ANALYSES

The first two unrotated principal components (PCs) accounted for 96.9% of the total variance of the echolocation and wing morphology among the 42 species, and grouped species along family and functional group divisions (Fig. 5.2A). The only exceptions were the high duty-cycle echolocation bats *Hipposideros commersoni*, that grouped with the molossids and the emballonurid, *Taphozous mauritianus*, and not near the conspecific, *H. caffer*, and *Rhinolophus hildebrandti* that grouped on its own. In addition, *Chaerephon pumilus* and *Sauromys petrophilus* grouped with the clutter-edge bats and not with the open-air bat species. Plotting the factor loadings resulted in the clear separation of PF and DUR on opposite sides from the two wing parameters (Fig. 5.2B). Varimax rotation did not alter or clarify these patterns appreciably.

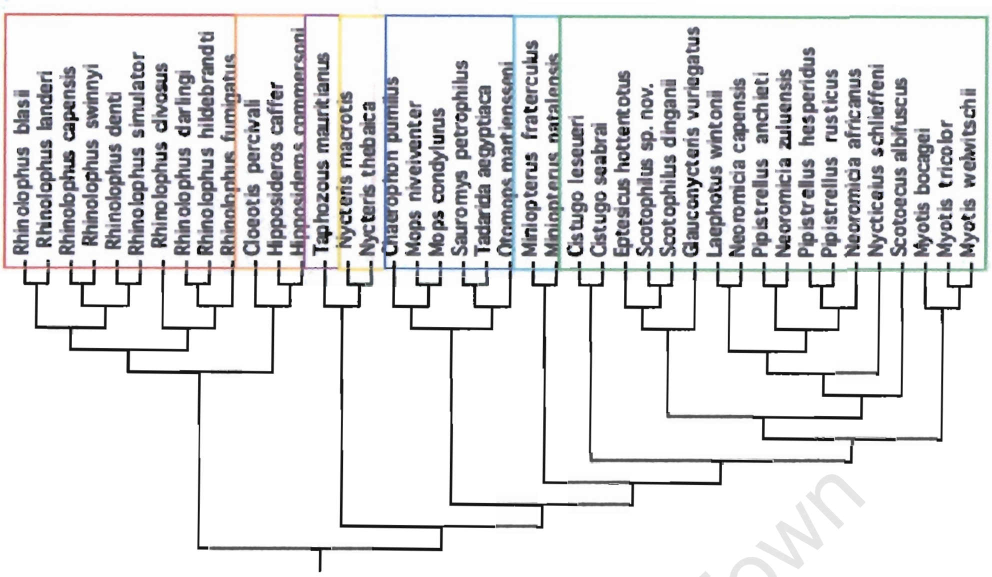

Fig. 5.1 The phylogeny of 42 southern African insectivorous bat species recovered from parsimony analysis by Dr. Geeta Eick and Samantha Stoffberg (see text for details). Coloured squares denote different bat families: Emballonuridae = purple; Hipposideridae = orange; Miniopteridae = cyan; Molossidae = blue; Nycteridae = yellow; Rhinolophidae = red; Vespertilionidae = green.

These patterns were interpreted as follows. Firstly, PC1 was a measure of differences in DUR and bats that loaded high on PC1 had echolocation calls of much longer DUR than bats that loaded low on PC1 (Table 5.1). For example, *Rhinolophus* species use high duty-cycle echolocation that avoid masking effects of clutter by compensating for the Doppler shifts in frequency caused by movement of flight and prey (Schnitzler 1987). Echolocation signals typically consist of constant peak frequencies of long duration (CF). These bats loaded high on PC1. On the other hand, *Nycteris* species that forage in similar clutter conditions compensate for masking effects with low intensity echolocation signals, comprising two or three steeply frequency modulated (FM) harmonics, of very short duration (Fenton & Thomas 1981). These bats loaded low on PC1. Secondly, PC2 was a measure of differences in PF, and bats that loaded high on PC2 had echolocation calls of much higher PF than bats that loaded low on PC2 (Table 5.1). For example, the bat with the lowest peak echolocation frequency, *Otomops martiensseni* (14 kHz) loaded highest on PC2, and the bat with the highest peak echolocation frequency, *Cloeotis percivali* (240 kHz) loaded lowest on PC2. Thus, the first two principal components grouped the bat species based on their echolocation characteristics

Table 5.1 Mean ±SD mass, wing (WSP = wingspan, and WA = wing area), and echolocation (PF = peak echolocation frequency, BW = bandwidth for low-duty-cycle-echolocation bats, and DUR = duration) parameters of 42 insectivorous bat species caught in southern Africa between 2001 and 2004. FG = functional feeding group (O = open-air, CE = clutter-edge, and C = clutter).

					Wing parameters				Echolocation parameters					
			Mass (g)		WSP (cm)		WA (cm^2)		PF (kHz)		BW (kHz)		DUR (ms)	
Species	n	FG	Mean	±SD	Mean	±SD	Mean	±SD	Mean	±SD	Mean	±SD	Mean	±SD
Chaerephon pumilus	10	O	11.2	1.3	26.6	1.2	96.2	9.3	29.9	1.5	15.7	2.3	4.1	0.1
Glauconycteris variegatus	1	CE	13		30.4		148.4		41.1		21.1		2.3	
Cistugo lesueuri	5	CE	6.7	1.2	24	0.9	93.2	1.1	46.5	1.8	45.8	22.7	2.9	0.2
Cistugo seabrai	2	CE	3.8	0.4	21.2	1.1	65.2	7.3	45.8	0.7	24.4	10.8	3.1	0.7
Cloeotis percivali	6	C	5.3	0.6	20.9	1.3	83.7	5.2	207.8	3			4.6	1.2
Eptesicus hottentotus	10	CE	18.1	1.5	33.1	0.6	180.8	13.3	30.6	1.7	16.8	5.5	5.5	2.1
Hipposideros caffer	10	C	8.5	1.1	27.7	1.4	139.6	10.6	142.3	0.6			8.4	0.7
H. commersoni	2	C	68.7	9.4	52.4	1.2	438.2	44.9	65	0.2			13.1	0.1
Laephotus wintoni	5	CE	10.3	1.6	27.4	1	134.4	14.6	22.4	0	16.3	0.7	2.1	0
Miniopterus fraterculus	10	CE	8.9	0.5	29.4	1.2	136.5	8.9	62.1	1.5	17.2	6.3	3.7	0.7
Miniopterus natalensis	10	CE	11.6	0.8	30.6	1.3	146	7.8	51.4	1.1	13.1	3.4	3.4	0.3
Mops condylurus	10	O	28.3	5.6	33.6	1.1	149.7	5.8	26.7	0.9	9.2	1.9	10	1.6
Mops niveiventer	6	O	28.7	2	31.7	1.3	129.7	10.9	20.3	0.2	10.6	0.8	8.1	0.6
Myotis bocagei	5	CE	9.1	0.8	25.8	0.9	120.7	9.9	44.6	2.4	23.6	2.9	2.5	0.5
Myotis tricolor	10	CE	13.1	2.2	31.8	1.6	175.7	18.9	47.8	3.1	46	23.9	3.3	0.6
Myotis welwitschii	1	CE	18		36.6		234.9		34		16.4		2.4	
Neoromicia africanus	10	CE	4.2	0.3	21.4	0.9	83.5	5.8	69.4	1.5	11.8	5.7	4.6	0.9
Neoromicia capensis	10	CE	7.3	0.9	22.6	1	93	6.6	39.4	1.6	14.4	3	5.1	1.3

Table 5.1 Continued

Neoromicia zuluensis	2	CE	5.8	0.4	21.4	1.2	81.4	1.9	48.4	1.1	19.9	17.7	2.7	0.4
Nycteris macrotis	2	C	17.8	0.4	35.1	1	237.3	9.5	76.7	13.2	20.3	0.4	1.2	0.5
Nycteris thebaica	10	C	12.6	1.5	29.3	1.6	167.3	9.8	77.5	10.3	30.2	11.9	1.7	0.2
Nycticeius schlieffeni	2	CE	6.3	0.4	21.4	0.1	78.2	1.8	42.5	0.3	16.1	1.3	3.5	0.2
Otomops martiensseni	2	O	32	2.8	40.4	0.1	209.2	12.6	11.8	0.3	7.8	0.3	27	1.4
Pipistrellus anchietai	1	CE	6		21.7		86.9		55.9		25.2		2.1	
Pipistrellus hesperidus	10	CE	7.3	0.6	21.4	0.8	84.4	4.6	59.1	1.5	30.1	6.8	2.5	0.2
Pipistrellus rusticus	10	CE	6.3	1.5	20.1	0.8	74.2	5.8	55.7	2.9	15.9	7.6	4.5	2.2
Rhinolophus blasii	2	C	10	1.4	27	1	130.3	8.4	86.5	0.6			27.7	12.6
Rhinolophus capensis	10	C	10.8	0.6	29.7	1.6	147.3	12.9	83.8	0.8			41.2	3.2
Rhinolophus clivosus	10	C	19	2.5	33.6	1.2	204.3	14.7	91.7	1			37.4	6.2
Rhinolophus darlingi	10	C	8.8	1.6	28.5	1.3	146.1	11.8	87.1	2.1			39.5	10.6
Rhinolophus denti	10	C	5.9	0.2	27.1	0.8	123	7	111.2	1.8			23.4	4
Rhinolophus fumigatus	2	C	12.3	0.4	30.8	2.1	169.6	37.5	53.7	0.2			40.3	0.9
R. hildebrandti	10	C	28.9	1.4	40.1	1.5	287.8	20.4	33.2	0.8			44.8	5.7
Rhinolophus landeri	2	C	7.5	0.7	27	0.1	140.1	0.1	107.3	2			40	14.5
Rhinolophus simulator	10	C	8.2	1.4	26.9	1.1	132.1	8.4	80.1	1.2			31.3	7.5
Rhinolophus swinnyi	10	C	7.7	0.5	27.9	0.6	135.3	5.2	106.6	0.4			22.3	3.3
Sauromys petrophilus	10	O	9.8	0.8	26	1.1	88.9	11.3	29.3	0.6	13.9	4.1	4.7	2.5
Scotoecus albofuscus	1	CE	10.5		21.1		84		39.3		24		3.3	
Scotophilus dinganii	10	CE	28.7	5.9	34.3	1.1	200.4	20.8	33.6	1.3	16.8	4.9	4.9	0.6
Scotophilus sp. nov.	10	CE	27.8	5.7	30.8	1.4	172.1	12.5	45.3	1.2	19.6	5.3	3.9	0.9
Tadarida aegyptiaca	10	O	16	1.4	30.7	1.2	116	10.7	22.7	2.2	11.7	6.1	9.6	3.4
Taphozous mauritianus	6	O	34	5	39.5	1.3	216.2	15.7	25.9	0.9	2.8	0.9	7.4	4.6

rather than wing morphology characteristics

First and second principal components of the PCAs for the three functional groups accounted for 64.8 to 67.3% and 19.6 to 33.8%, respectively, of the total variance of the echolocation and wing morphology among species (Table 5.2). However, separation of bat species was not particularly clear, and different parameters contributed to the first and second principal components. Nevertheless, only echolocation parameters contributed to the first two principal components in all functional groups (Table 5.3).

SEGMENT-LENGTH RATIO NULL MODELS

Non-random patterns predicted by competition

Mass

Except at Goodhouse, the variance of mass segment-length ratios between species was significantly small, irrespective of regional source pool used (Table 5.4). These non-random patterns indicate that mass was more evenly spaced among the species of ensembles than otherwise expected by chance. I also compared the mass segment-length ratios of the CFK and Nama-Karoo regional source pools to those assembled at random from the largest southern African regional source pool. Variance of segment-length ratios was significantly small in both biome regional pools (observed = 0.0006 and 0.002 versus expected = 0.009 and 0.006, respectively, $p < 0.001$). Conversely, non-random patterns of mass was less ubiquitous among species of the clutter-edge and clutter functional groups (Tables 5.5 and 5.6, respectively). Similarly, the variance of segment-length ratios among the four common species caught at every ensemble (Chapter 4), *Miniopterus natalensis* (Miniopteridae),

Table 5.2 Eigenvalues and percent variation of the first two principal components (PCs) derived from principal component analyses of Log10 wing and echolocation parameters of bat species classified to three functional groups.

		PC1		PC2	
Foraging guild	Spp richness	Eigenvalue	% Variation	Eigenvalue	% Variation
Clutter-edge	20	0.1	67.3	0.03	19.6
Clutter	15	0.3	64.8	0.2	33.8
Open-air	7	0.1	65.1	0.05	25.7

Table 5.3 Contribution of the first two principal components (PCs) derived from principal component analyses of Log10-transformed wing and echolocation parameters of bat species classified to functional groups (boldface print indicates parameters contributing most to the covariances of bat species).

	Functional groups					
	Clutter-edge		Clutter		Open-air	
Parameter	PC1	PC2	PC1	PC2	PC1	PC2
WSP	0.149	0.011	0.081	-0.153	-0.126	0.029
WA	0.077	0.007	0.04	-0.079	-0.05	0.005
PF	**0.246**	0.025	0.092	**-0.342**	**-0.261**	-0.047
BW	0.003	**0.146**			-0.174	**0.17**
DUR	0.105	-0.083	**0.528**	0.089	0.141	0.148

Neoromicia capensis (Vespertilionidae), *Tadarida aegyptiaca* (Molossidae), and *Rhinolophus clivosus* (Rhinolophidae), was also not significantly small (observed = 0.004 versus expected = 0.007, 0.02, and 0.04 based on random sampling from the CFK, Nama-Karoo and southern African regional source pool, respectively, all $p > 0.05$).

Distribution of masses of the bat species, revealed different patterns at a local and regional scales. Fig. 5.4 shows the distribution of masses of bat species classified to the regional source pools. At the scale of the largest regional source pool (all species caught in southern Africa), the distribution of masses on a logarithmic scale was unimodal and right-skewed (g_l = 0.64), but did not depart significantly from a log-normal distribution (Kolmogorov-Smirnov one sample test; d = 0.09, p = n.s., Fig. 5.3). However, the distribution of masses appear scale dependant, becoming progressively more even, and less right-skewed, at savanna, Nama-Karoo, and CFK regional scales (g_l = 0.65, - 0.1 and 0.15, respectively, Fig. 5.3), to the local scale (Fig. 5.4). The distribution of masses at Goodhouse was clearly more random than at other ensembles (Fig. 5.4), and therefore consistent with null model results. Random mass patterns of the Goodhouse ensemble was linked to the presence of the small and very rare vespertilionid, *Cistugo seabrai* (Stadelmann et al. 2004). When I excluded *C. seabrai* from the Goodhouse matrix, and reanalysed the mass data, variance of segment-length ratios between species was significantly small (observed = 0.0009 versus expected = 0.013, $p < 0.001$, based on random sampling from the SA regional source pool).

Principal components

Only certain ensembles and functional groups displayed non-random principal component patterns predicted by competition hypotheses. Minimum PC1 segment-length ratios of the Algeria ensemble and Sudwala clutter-edge functional group were significantly larger than expected by chance. Variance of PC2 segment-length ratios between bats of the Sudwala

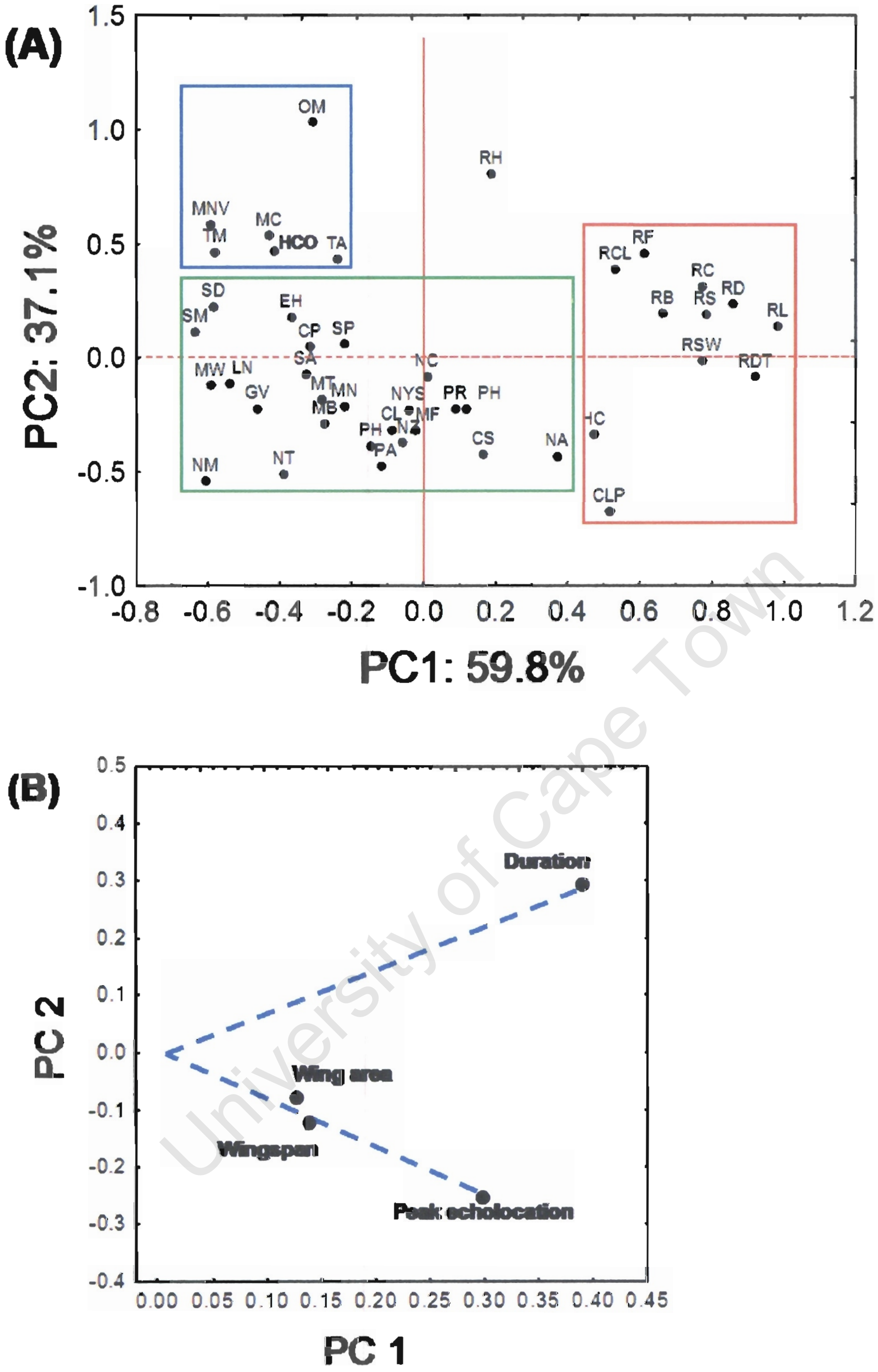

Fig. 5.2 Principal component analysis of size corrected, Log10 wing (WA and WSP) and echolocation (PF and DUR) parameters of 42 insectivorous bat species. (A) Plot of component scores of species on the first two principal components (PC1 and PC2) Coloured squares denote functional groups: clutter (red), open-air (blue), and clutter-edge (green) feeders. (B) Plot of component weights for echolocation and wing parameters on the first two principal components. Dotted line shows distance to midpoint (0, 0) of graph.

Table 5.4 Observed and expected segment-length ratio indices - minimum segment-length (MSL) and variance of segment length ratios - of body size (mass) and principal component (PC1 and PC2) parameters of bats of fynbos (Algeria, Die Hel, De Hoop), forest, (Knysna), Nama-Karoo (Goodhouse and Koegelbeen), and savanna (Sudwala) ensembles. Observed minimum segment-length ratios greater than, and observed variances smaller than, 95% of the expected values, suggest that competition influenced the phenotypic structure (red boldface print). Observed minimum segment lengths smaller than 95% of the expected values, suggest that coevolution influenced the phenotypic niche structure (blue boldface print).Experiment-wide error was held at five percent by Bonferroni sequential adjustment. C is the number of unique simulation ensembles that could be randomly assembled from the source pool (see text for details).

			Algeria		Die Hel		De Hoop		Knysna		Good House		Koegelbeen		Sudwala	
Parameter	Source Pool	Index	Obs	Exp	Obs	Exp	Obs	Exp	Obs	Exp	Obs	Exp	Obs	Exp	Obs	Exp
Mass	Biome	MSL	0.02	0.02	0.03	0.02	0.02	0.03	0.03	0.03	0.02	0.02	0.04	0.03	**0.009**	0.003
	Biome	Variance	0.001	0.001	**0.0005**	0.003	0.003	0.003	0.001	0.004	0.007	0.005	**0.0008**	0.008	**0.002**	0.006
PC1	Biome	MSL	**0.01**	0.007	0.01	0.01	0.006	0.01	0.03	0.02	0.006	0.01	**0.006**	0.03	0.006	0.005
	Biome	Variance	0.002	0.004	0.03	0.007	0.03	0.008	0.03	0.009	0.01	0.01	0.03	0.02	0.005	0.007
PC2	Biome	MSL	0.008	0.007	0.006	0.01	0.02	0.02	0.006	0.02	0.008	0.006	0.02	0.01	**0.0002**	0.003
	Biome	Variance	0.02	0.02	0.04	0.04	0.03	0.04	0.04	0.05	0.02	0.01	0.01	0.03	0.005	0.006
C				*78*		*1716*		*1716*		*1716*		*1.6E+7*		*1.6E+7*		*3E+7*
Mass	SA	MSL	**0.02**	0.007	0.03	0.02	0.02	0.02	0.03	0.02	0.02	0.008	0.04	0.02	**0.009**	0.003
	SA	Variance	**0.001**	0.01	**0.0005**	0.02	0.003	0.02	**0.001**	0.02	0.007	0.01	**0.0008**	0.02	**0.002**	0.006
PC1	SA	MSL	0.01	0.01	0.01	0.03	**0.006**	0.03	0.03	0.04	0.006	0.02	**0.006**	0.03	0.006	0.005
	SA	Variance	**0.002**	0.01	0.03	0.02	0.03	0.02	0.03	0.02	0.01	0.01	0.03	0.02	0.005	0.007
PC2	SA	MSL	0.008	0.007	0.006	0.02	0.02	0.02	0.006	0.02	0.008	0.008	0.02	0.02	**0.0002**	0.003
	SA	Variance	0.02	0.02	0.04	0.04	0.03	0.04	0.04	0.04	0.02	0.02	0.01	0.04	0.005	0.006
C				*3.9E+8*		*3.2E+7*		*3.2E+7*		*3.7E+7*		*1.9E+9*		*1.2E+5*		*4E+14*
Mass	LUM	MSL	0.02	0.01	0.03	0.03	0.02	0.03	0.03	0.03	0.02	0.02	0.04	0.02	**0.009**	0.003
	LUM	Variance	**0.001**	0.01	**0.0005**	0.02	**0.003**	0.02	**0.001**	0.02	0.007	0.01	**0.0008**	0.02	**0.002**	0.004
PC1	LUM	MSL	0.01	0.01	0.01	0.03	**0.006**	0.03	0.03	0.04	0.006	0.02	**0.006**	0.03	0.006	0.01
	LUM	Variance	**0.002**	0.01	0.03	0.02	0.03	0.02	0.03	0.02	0.01	0.01	0.03	0.02	0.005	0.02
PC2	LUM	MSL	0.008	0.03	0.006	0.02	0.02	0.02	0.006	0.02	0.008	0.01	0.02	0.02	**0.0002**	0.01
	LUM	Variance	0.02	0.02	0.04	0.04	0.03	0.04	0.04	0.03	0.02	0.02	0.01	0.04	0.005	0.04

Table 5.5 Observed and expected segment-length ratio indices - minimum segment-length (MSL) and variance of segment length ratios - of body size (mass) and principal component (PC1 and PC2) parameters of clutter (CLUT), and open-air (OPEN) bats caught in the fynbos (Algeria, Die Hel, De Hoop), forest, (Knysna), Nama-Karoo (Goodhouse and Koegelbeen), and savanna (Sudwala) ensembles. Observed minimum segment-lengths greater than, and observed variances smaller than, 95% of the expected values, suggest that competition influenced the phenotypic structure (red boldface print). Observed minimum segment lengths smaller than 95% of the expected values, suggest that coevolution influenced the phenotypic niche structure (blue boldface print). Experiment-wide error was held at five percent by Bonferroni sequential adjustment. C is the number of unique simulation ensembles that could be randomly assembled from the source pool (see text for details).

			Algeria		De Hoop		Goodhouse		Koegelbeen		Sudwala			
			CLUT		CLUT		CLUT		CLUT		CLUT		OPEN	
Parameters	Source Pool	Index	Obs	Exp	Obs	Exp	Obs	Exp	Obs	Exp	Obs	Exp	Obs	Exp
Mass	Biome	MSL					0.02	0.05	0.2	0.09	0.02	0.02	**0.08**	0.02
	Biome	Variance					0.008	0.06	**0.0001**	0.06	**0.007**	0.02	0.007	0.03
PC1	Biome	MSL					0.009	0.07	0.04	0.07	**0.009**	0.02	**0.22**	0.1
	Biome	Variance					0.05	0.03	0.04	0.03	0.01	0.02	0.04	0.07
PC2	Biome	MSL					0.02	0.04	0.02	0.04	**0.02**	0.007	0.2	0.1
	Biome	Variance					0.1	0.04	0.3	0.04	0.04	0.03	0.0007	0.01
C								*35*		*35*		3003		*56*
Mass	SA	MSL	0.02	0.1	0.07	0.2	0.02	0.1	0.2	0.1	0.02	0.02	**0.08**	0.02
	SA	Variance	0.007	0.06	0.006	0.08	0.008	0.05	**0.0001**	0.05	**0.007**	0.02	0.007	0.03
PC1	SA	MSL	0.04	0.07	0.04	0.1	0.009	0.07	0.04	0.07	**0.009**	0.02	**0.22**	0.1
	SA	Variance	0.01	0.03	0.03	0.04	0.05	0.03	0.04	0.03	0.01	0.02	0.04	0.07
PC2	SA	MSL	0.02	0.04	0.02	0.07	0.02	0.04	0.02	0.04	**0.02**	0.007	0.2	0.1
	SA	Variance	0.4	0.05	0.8	0.05	0.1	0.05	0.3	0.04	0.04	0.03	0.0007	0.01
C				*330*		*330*		*1820*		*1820*				*56*
Mass	LUM	MSL	0.02	0.08	0.07	0.2	0.02	0.1	0.2	0.1	0.02	0.02	**0.08**	0.08
	LUM	Variance	0.007	0.05	0.006	0.05	0.008	0.05	**0.0001**	0.05	**0.007**	0.02	0.007	0.05
PC1	LUM	MSL	0.04	0.1	0.04	0.1	0.009	0.09	0.04	0.09	**0.009**	0.02	**0.22**	0.1
	LUM	Variance	0.01	0.03	0.03	0.04	0.05	0.03	0.04	0.03	0.01	0.02	0.04	0.04
PC2	LUM	MSL	0.02	0.04	0.02	0.05	0.02	0.04	0.02	0.04	**0.02**	0.04	0.2	0.1
	LUM	Variance	0.4	0.05	0.8	0.05	0.1	0.04	0.3	0.04	0.04	0.03	0.0007	0.01
C				*330*		*330*		*330*		*330*		*165*		*56*

Table 5.6 Observed and expected segment-length ratio indices - minimum segment-length (MSL) and variance of segment length ratios - of body size (mass) and principal component (PC1 and PC2) parameters of clutter-edge (EDGE) bats caught in of the fynbos (Algeria, Die Hel, De Hoop), forest, (Knysna), Nama-Karoo (Goodhouse and Koegelbeen), and savanna (Sudwala) ensembles. Observed minimum segment-lengths greater than, and observed variances smaller than, 95% of the expected values, suggest that competition influenced the phenotypic structure (red boldface print). Observed minimum segment lengths smaller than 95% of the expected values, suggest that coevolution influenced the phenotypic niche structure (blue boldface print). Experiment-wide error was held at five percent separately by Bonferroni sequential adjustment. C is the number of unique simulation ensembles that could be randomly assembled from the source pool (see text for details).

			Algeria		Die Hel		De Hoop		Knysna		Goodhouse		Sudwala	
			EDGE		EDGE		EDGE		EDGE		EDGE		EDGE	
Parameters	Source Pool	Index	Obs	Exp	Obs	Exp	Obs	Exp	Obs	Exp	Obs	Exp	Obs	Exp
Mass	Biome	MSL	0.04	0.05	0.06	0.07	0.05	0.1	0.09	0.07	**0.2**	0.1	0.01	0.01
	Biome	Variance	0.006	0.004	0.001	0.006	0.01	0.01	**0.0002**	0.006	0.003	0.02	0.01	0.01
PC1	Biome	MSL	0.04	0.03	0.01	0.06	0.04	0.3	0.03	0.07	0.04	0.2	**0.04**	0.004
	Biome	Variance	0.04	0.05	0.04	0.06	0.06	0.07	0.03	0.06	0.2	0.06	0.1	0.04
PC2	Biome	MSL	0.1	0.1	0.2	0.1	**0.5**	0.2	**0.06**	0.1	**0.006**	0.08	0.05	0.03
	Biome	Variance	0.03	0.02	0.02	0.02	**0.0004**	0.03	0.01	0.02	0.06	0.05	0.03	0.02
C				*21*		*56*		*35*		*78*		*126*		*792*
Mass	SA	MSL	0.04	0.04	0.06	0.06	0.05	0.1	0.09	0.06	**0.2**	0.07	0.01	0.01
	SA	Variance	0.006	0.02	0.001	0.02	0.02	0.04	**0.0002**	0.02	0.003	0.03	0.01	0.01
PC1	SA	MSL	0.04	0.03	0.01	0.07	0.04	0.2	0.03	0.07	0.04	0.07	**0.04**	0.004
	SA	Variance	0.04	0.08	0.04	0.1	0.06	0.2	0.03	0.1	0.2	0.1	0.1	0.04
PC2	SA	MSL	0.1	0.06	0.2	0.1	**0.5**	0.2	0.06	0.09	**0.006**	0.1	0.05	0.03
	SA	Variance	0.03	0.04	0.02	0.04	0.0004	0.06	0.01	0.04	0.06	0.04	0.03	0.02
C				*792*		*494*		*220*		*792*		*792*		*792*
Mass	LUM	MSL	0.04	0.04	0.06	0.06	0.05	0.1	0.09	0.06	**0.2**	0.07	0.01	0.01
	LUM	Variance	0.006	0.02	0.001	0.02	0.02	0.04	**0.0002**	0.02	0.003	0.03	0.01	0.01
PC1	LUM	MSL	0.04	0.03	0.01	0.07	0.04	0.2	0.03	0.07	0.04	0.07	**0.04**	0.004
	LUM	Variance	0.04	0.08	0.04	0.1	0.06	0.2	0.03	0.1	0.2	0.1	0.1	0.04
PC2	LUM	MSL	0.1	0.06	0.2	0.1	**0.5**	0.2	0.06	0.09	**0.006**	0.1	0.05	0.03
	LUM	Variance	0.03	0.04	0.02	0.04	0.0004	0.06	0.01	0.04	0.06	0.04	0.03	0.02

clutter functional group and the De Hoop clutter-edge functional group was significantly small, based on biogeographic and log-uniform regional pools (Tables 5.4, 5.5, and 5.6). However, values of segment-length ratio indices of the 350km and 750km regional pools were not significantly different from those expected by chance (all $p > 0.05$).

Non-random patterns predicted by coevolution

Minimum segment length ratios of mass never exhibited non-random patterns predicted by the coevolution hypothesis. Conversely, the minimum segment-length ratios of PC1 and PC2 were significantly small at De Hoop, Koegelbeen, Goodhouse and Sudwala, based on biogeographic and log-uniform regional pools (Tables 5.4, 5.5, and 5.6). However, minimum segment-length ratios of the 350km and 750km regional source pools were not significantly small (all $p > 0.05$).

DISCUSSION

My null model analyses of body size and principal component (i.e. echolocation) parameters found non-random patterns consistent with competition and coevolution hypotheses in the phenotypic structures of ensembles and functional groups. However, the ensembles, functional groups in ensembles, and functional groups in general, differed in the manner and degree to which they were structured, and non-random patterns were ubiquitous only for body size.

NON-RANDOM PATTERNS OF BODY SIZE

Body size (mass) was evenly spaced (i.e. exhibited a significantly small variance of segment-length ratios between species) at a local scale (i.e. every ensemble except Goodhouse), and at an intermediate regional scale (i.e. the Cape Floristic Kingdom and Nama-Karoo biome regional source pools). My findings are consistent with evidence from detailed studies of coexisting vertebrate species that show similar non-random patterns of body size (Gotelli & Ellison 2002). These include North American desert rodents (Bowers & Brown 1982, Brown & Nicoletto 1991), Middle Eastern mammalian carnivores (Dayan *et al.* 1989, 1990), Caribbean *Anoles* lizards (Haefner 1988, Losos 1990), Galapagos finches (Schluter, Price & Grant 1985), and North American stickleback fishes (Schluter & McPhail 1992).

However, body size distribution of bats was scale-dependant, becoming progressively more right-skewed and less evenly spaced from local to regional level. The right-skewed body size distribution at the greatest regional scale is consistent with body size distributions of non-volant and volant New World mammals at regional and continental scales (Brown & Nicoletto 1991, Arita & Figueroa 1999, Willig, Patterson & Stevens 2004). My results are

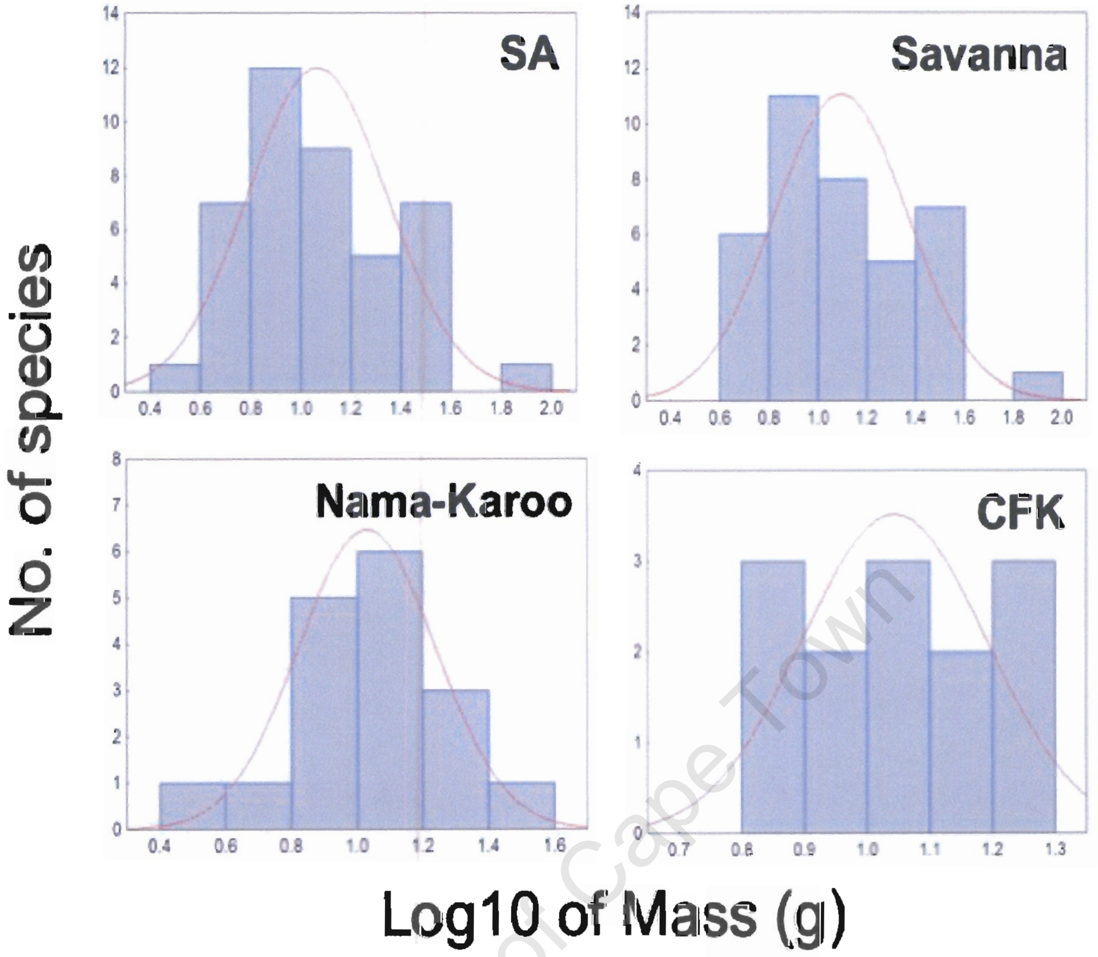

Fig. 5.3 Hierarchical evaluation of the Log10 distribution of body size at the scale of the whole southern African source pool, the savanna source pool, the Nama-Karoo source pool and the CFK source pool. The expected normal distribution curve is in red.

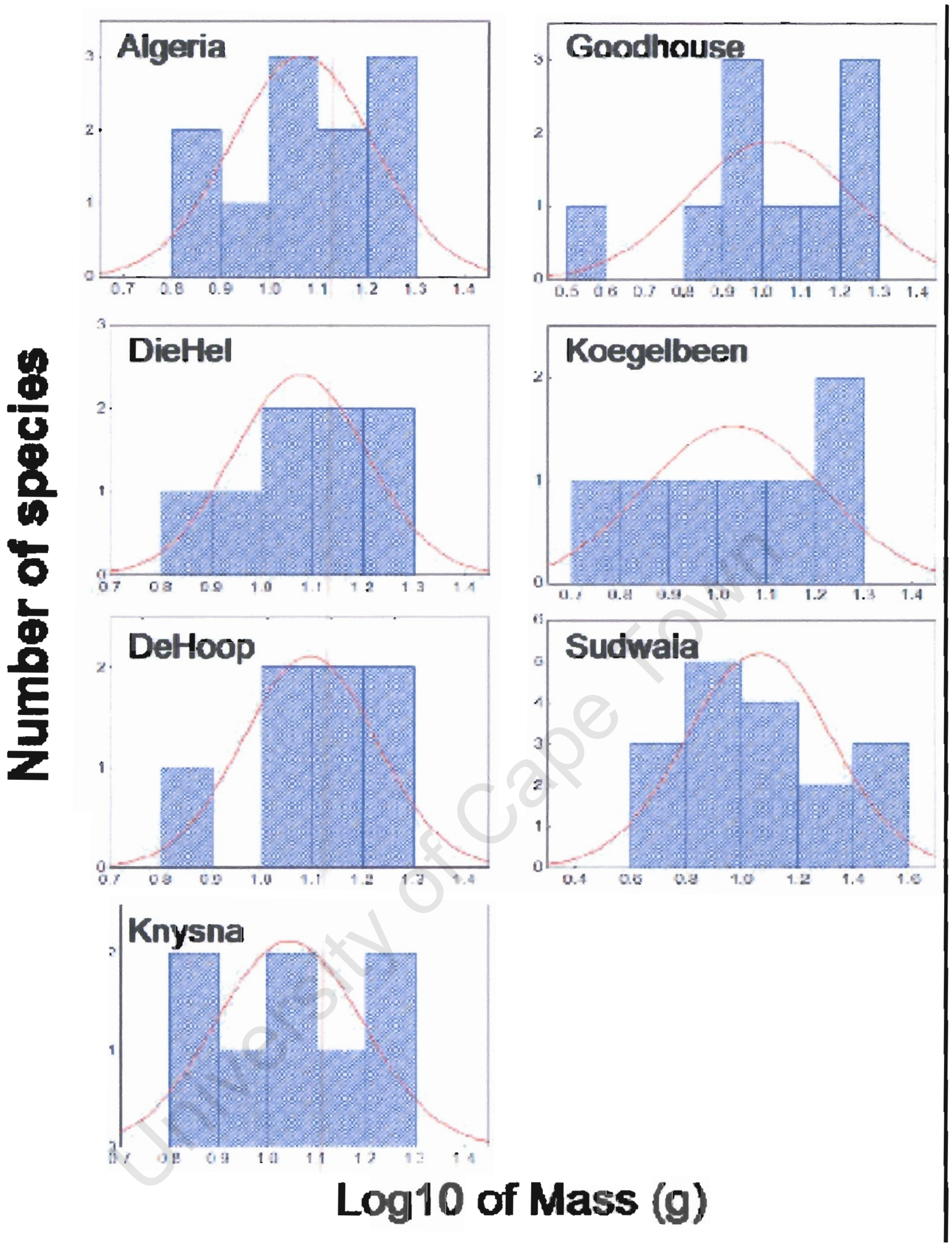

Fig. 5.4 Distributions of insectivorous bat body size (mass) at the ensemble scale. The expected normal distribution curve is in red.

also consistent with the observation that body sizes of non-volant mammals tend to be evenly distributed at a local scale (Brown & Nicolleto 1991, Arita & Figueroa 1999). They differ, however, with body size patterns of Mexican bat assemblages where the frequency distribution of body sizes was right-skewed at local, intermediate and regional scale (Arita & Figueroa 1999). The inclusion of fruit-eating bats in the data matrix of the latter study may explain the right-skewed size distribution at local scale. Average body size of fruit-eating bats is significantly larger than average body size of insectivorous bats (Jones 1996, Jones & McLarnon 2000). In contrast to New World volant and non-volant mammals (Brown & Nicoletto 1991, Arita & Figueroa 1999, Willig, Patterson & Stevens 2004), however, the range of southern African insectivorous bat body sizes was narrower at a local scale than at a regional scale. Small and large-bodied bat species caught in the sub-tropical savannas were absent from the temperate fynbos and forest ensembles.

Brown & Nicoletto (1991) explained the differences of body size distribution between local and regional scales as an effect of local competitive exclusion, higher extinction for large species with small range sizes, and higher specialization of modal species. They propose that competitive exclusion is the most likely biotic process to explain why faunas at local scale harbour few modal-sized species and display an even distribution of body masses. If so, competitive interactions should be limited to those species utilizing similar food resources (Brown & Nicoletto 1991, Brown 1995). Thus, there should be evidence for interspecific competition at a local scale among bat species with similar diets (Chapter 6). However, I found no support for the prediction that non-random patterns should be more apparent within functional groups (Diamond & Gilpin 1982). Indeed, the limited range of body sizes at a local scale suggest that filters other than competitive interactions may prevent small and large-bodied species from establishing themselves in ensembles.

The fact that large- and small-bodied bat species were poorly represented in the regional source pools of intermediate size suggests that there may be a low replacement rate of these species between the local and regional scale (Brown & Nicoletto 1991). Consequently, certain large-scale abiotic processes may prevent the accumulation of small-bodied and/or large-bodied bat species in regional source pools (Brown & Nicolleto 1991, Brown 1995). One hypothesized process is the selective extinction of species with large (or small) body sizes and small geographic ranges (Brown & Nicolleto 1991). Large individuals have large resource requirements, thus they require large home ranges and occur at low population densities (Brown & Maurer 1987, 1989, Speakman & Thomas 2004). Thus, large-bodied bat species with small geographic ranges and small total population sizes should have a high probability of extinction (Willig, Patterson & Stevens 2004). It is also hypothesized that small-bodied bat species should be more sensitive to density independent environmental perturbations (i.e. abiotic filters), diminishing the probability of their persistence over broad geographic areas (Gaston 1990, but see Gaston 1988). Although my data do not directly test these hypotheses, there is evidence that lends some support. For example, the extinction risk of bat species is significantly correlated with small geographic ranges (Jones, Purvis & Gittleman 2003). Furthermore, there is no significant relationship between body mass and range size (Willig, Patterson & Stevens 2004). Thus, large-bodied bat species do not necessarily have larger geographic range sizes than small-bodied bat species. For example, large-bodied African bat species such as *Nycteris grandis* (39 g) and *Hipposideros commersoni* (68 g) have smaller geographic ranges than their smaller-bodied congenerics such as *N. thebaica* (13 g) and *H. caffer* (9 g), respectively (Skinner & Smithers 1990, Taylor 2000).

The right-skewed distribution of body size among mammalian species has been modelled by Brown, Marquet & Taper (1993), who suggest that reproductive power – i.e. the rate at which energy from the environment is channelled into offspring production – is maximized at an intermediate modal size (c.a. 100 g for non-volant mammal species). Hence, modal-sized species are more frequently limited by variation in the physical environment and/ or the presence of other organisms than their larger relatives (Brown & Nicoletto 1991). Consequently, physiological constraints on food quality reinforced by life history traits may force smaller (especially modal-sized) animals to specialize on higher-quality foods and restrict their foraging to habitats where suitable foods are abundant (Brown and Nicoletto 1991). However, the particular energetic definition of this hypothesis has been criticized (Kozlowski 1996, Brown, Taper & Marquet 1996). Moreover, data on life history parameters of bats contradicted a key prediction of the hypothesis - components of reproductive power should not scale linearly with body size but change sign at some intermediate (modal) body size (Jones & Purvis 1997). Thus, filters other than local competitive exclusion, range sizes, or higher specialization of modal species may be partially or wholly responsible for the even distribution of body sizes of insectivorous bat ensembles.

The physics of flight and sound combined with the small size of volant prey severely limits the viable body size range displayed by echolocating bats (Brigham and Barclay 1991, Jones 1994, 1996,). The mechanics of prey capture in flight, coupled with the small effective range of echolocation, selects for a small body size capable of the maneuverability and agility necessary to hunt small, volant prey at short range (Norberg & Rayner 1987, Barclay & Brigham 1991, Jones 1996). Furthermore, the coupling of flight and echolocation mechanisms puts a lower limit on echolocation frequencies, and therefore an upper limit to body size, necessary to detect and catch small flying prey (Jones 1994, 1996). Thus, the smaller range of masses of insectivorous bats at a local scale, and to a lesser degree at an intermediate regional scale, may be an artefact of the constraints of flight and echolocation.

An important assumption of the competition hypothesis is that the phenotypic trait can be linked to the resource utilized (Gotelli & Graves 1996). Ultimately, body size must influence the amount and types of food that bats require to sustain cellular and metabolic processes with the necessary energy and nutrients (Speakman & Thomas 2004). However, body size is a comprehensive phenotypic character that incorporates elements of morphology, physiology, behaviour, and ecology (Barclay & Harder 2004. Simmons & Conway 2004, Speakman & Thomas 2004, Swartz, Freeman & Stockwell 2004, Willig, Patterson & Stevens 2004). Furthermore, mass is significantly correlated with wing morphology and echolocation parameters (Jones 1996, this study), and consistent with evidence that they are part of the same adaptive complex (Arita & Fenton 1997). Thus, it is difficult to link body size *per se* to the particular resource that is being partitioned.

NON-RANDOM PATTERNS OF PRINCIPAL COMPONENTS

Principal components linked to the echolocation characteristics of bat species displayed non-random patterns predicted by competition theory, but only in species-rich ensembles and functional groups. The high species richness of the Algeria and Sudwala ensembles (Chapter 4) might have led to competitive interactions between coexisting bats to partition available resources. Similarly, more than 250 000 *Miniopterus natalensis* bats roost for c.a. eight months of the year at De Hoop, consuming approximately 100 tons of insects (McDonald, Rautenbach & Nell 1990, Taylor 2000). Consequently, intraspecific variation in wingspan and echolocation flexibility enables the species to utilize open and cluttered habitats at De Hoop (Jacobs 1999). Thus, resource utilization of the other coexisting bats, especially clutter-edge species, is probably severely affected. Thus, under conditions of high species richness or abundance, competition for resources might have been intense enough to influence the echolocation structure of coexisting bats.

Principal components also displayed non-random patterns predicted by the coevolution hypothesis. Sympatric bat species of four ensembles were more similar in echolocation parameters than expected by the null model. Similarly, temperate North American hummingbirds were more similar in mass, bill length, and wing length than predicted by several null models (Brown & Bowers 1985). These morphological patterns were attributed to mutualist coevolutionary processes with flowers. Conversely, neither nectarivore nor foliage-gleaning bat ensembles from Caatinga or Cerrado in Brazil exhibited non-random patterns predicted by coevolutionary hypotheses (Willig & Moulton 1989).

In contrast to competition analyses, body size (mass) never exhibited non-random patterns predicted by coevolution hypotheses. This is probably because, if bats and their insect prey coevolved, there would have been stronger and more direct interaction, over evolutionary time, between insect hearing and bat echolocation than between insect hearing and the body size of bats. This is supported by studies that found that echolocation parameters such as peak echolocation frequency were better predictors of diet than size or wing parameters of insectivorous bats (Bogdanowicz, Fenton &Daleszczyk 1999, Jacobs 2000, Schoeman &

Jacobs 2003).

There may be forces other than coevolution, however, that promote animals to be more similar than otherwise expected by chance. If certain resource states are very abundant, for example, similar patterns of phenotype among species may be favoured because there is no competition for those resources (Gotelli & Entsminger 2004). Nevertheless, coevolution patterns were evident in ensembles of three different biomes (fynbos, Nama-Karoo, and savanna), and the ensembles differed in species composition, elevation, dominant vegetation, and rainfall (Chapters 3 and 4). Thus, non-random patterns of similarity were probably not the cause of shared abiotic conditions, or an abundance of resources, at the ensembles. Alternatively, 20 to 60 kHz is the peak frequency range used by most echolocating bats (Fenton & Fullard 1979, Fullard & Thomas 1981, Fullard 1987, Rydell, Jones & Waters 1995, Fenton *et al.* 1998b), because of the frequency dependent effects of atmospheric attenuation and target strength (Jones & Rydell 2004). Thus, in relatively species-poor bat ensembles, non-random patterns of phenotypic similarity may reflect the limited range of echolocation frequencies used by most member bat species, and not coevolutionary processes.

CONCLUSIONS

I found evidence for competition and coevolution influencing the phenotypic structure of insectivorous bat ensembles in southern Africa. There was evidence that interspecific competitive interactions influenced body size in ensembles, and to a lesser degree echolocation in ensembles with high species richness or bat abundance. Coevolution, on the other hand, influenced the structure of ensembles only through echolocation and not body size. However, abiotic filters such as geographic distribution ranges of small and large-bodied bat species, extinction risk, and the physics of flight and sound probably also interact at regional and continental scales to influence the phenotypic structure of coexisting insectivorous bats at a local scale.

Chapter 6

TROPHIC NICHE PATTERNS SUPPORT COMPETITION AND COEVOLUTION HYPOTHESES

INTRODUCTION

The diet of an organism can be regarded a consequence of the interaction between an organism's phenotype and the environmental forces and processes, e.g. competition and coevolution, that impinge upon the organism, limiting what it is able to do with its phenotype. Diet is therefore a dimension of an organism's trophic niche that can give great insight into the processes that have shaped that organism and its ensemble. I used null models to investigate the influence of competition on dietary overlap patterns exhibited by the insectivorous bat ensembles and their functional groups. I also investigated which phenotypic trait (size, wing, or echolocation parameters) was the better predictor of diet as a means of determining the influence of coevolution on the diets of bats in the seven ensembles. This was done by testing the predictions of the allotonic frequency hypothesis.

COMPETITION AND DIETARY OVERLAP

Measuring the dietary overlap between all members of an insectivorous bat ensemble is of interest, because the hypothesis of diffuse competition predicts that resource use should be affected by many competing species (MacArthur 1972, Pianka 1974, Findley and Black 1983). Mean or median overlap is a useful summary statistic, but may hide a great deal of information at the ensemble level (Pianka 1980). Mean dietary overlap of species caught in ensembles can be augmented with more sensitive measures of dietary overlap, such as overlap between species of functional groups or guilds in ensembles (Winemiller & Pianka 1990, Gotelli & Graves 1996).

Early investigations into the influence of competition on the trophic niche structure focused on describing and quantifying differences of resource use between coexisting species (Schoener 1986). Reasoning was that if the biotic processes of limiting similarity and character displacement were important, utilization differences between coexisting species should reflect resource partitioning as minimal dietary niche overlap between species. On the other hand, dietary overlap between coexisting species should not prohibit coexistence, and in fact, may be more likely on theoretical grounds, because complete non-overlap would result in available resources being under-utilized (May 1974). Instead, competition may structure the trophic niche by significantly reducing the variance of dietary overlap between coexisting species (Gotelli & Entsminger 2004). However, it became apparent that even in the absence of competition, different species utilize resources in different ways (Connell 1980). In response, some researchers have shifted their attention to simulate dietary overlap patterns that are expected in the absence of competition, and then compare these (chance) patterns with the observed overlap patterns (Lawlor 1980, Case 1983, Winemiller &Pianka 1990, Gotelli & Graves 1996, Gotelli & Entsminger 2004). However, because of the assumptions of dietary overlap measurements, it may still be difficult to infer that competition was responsible for non-random overlap patterns (Gotelli & Graves 1996).

Underlying most dietary overlap indices is the important assumption that all resources are equally available to coexisting species (Lawlor 1980). If resource categories such as different insect types are not equally available to species, however, high dietary overlap between species may not necessarily reflect shared resource use (Lawlor 1980). Alternatively, some prey types may be more accessible to certain species but not to others because of differences in their phenotype. Schoener (1974) and Lawlor (1980) suggested, therefore, that niche overlap indices should be based on electivity of resources rather than utilization of resources (Gotelli & Graves 1996). The "electivity" is the relative ability or preference of a species to catch and eat a particular insect type (Lawlor 1980). However, incorporating electivity may greatly affect measures of overlap (Pianka 1986, Pianka and Winemiller 1990). Therefore, when possible, both utilization and electivity dietary overlap indices should be calculated when null modelling dietary overlap between species (Gotelli & Entsminger 2004).

THE ALLOTONIC FREQUENCY HYPOTHESIS

The allotonic frequency hypothesis (AFH) predicts that the incidence of eared moths should be highest in the diet of coexisting bats whose peak echolocation frequencies fall outside the range at which moths hear best, i.e. 20 to 60 kHz (Fenton & Fullard 1979, Fullard 1982, 1987, Chapter 2). Thus, across bat species with calls dominated by frequencies > 20 kHz the incidence of tympanate moths in their diet should increase with increasing echolocation frequency. This seems to be the case whether the focus of the study is global, incorporating a number of families of bats (Jones 1992, Bogdanowicz, Fenton & Daleszczyk 1999), or local focusing on a single ensemble of bats (Pavey & Burwell 1998, Jacobs 2000, Schoeman & Jacobs 2003).

A corollary prediction is that peak echolocation frequency should be a better predictor of diet than size or wing parameters (Bogdanowicz, Fenton & Daleszczyk 1999, Jacobs 2000, Schoeman & Jacobs 2003). In support of this prediction, echolocation frequency was a better predictor of diet than wing parameters in two South African bat ensembles, and suggests that selection pressure exerted by moth hearing might have acted directly on echolocation frequency and secondarily on wing parameters (Jacobs 2000, Schoeman & Jacobs 2003).

However, the predictions of the AFH remain to be tested on diet, size, wing, and echolocation parameters of coexisting bats of several different ensembles across a large geographical landscape.

In this chapter, I use null models to investigate the influence of competition on the trophic niche structure of insectivorous bat ensembles. I quantify dietary overlap between bats using utilization (Pianka 1973) and electivity (Gotelli & Entsminger 2004) indices. Observed overlap values are compared with simulated overlap values expected in the absence of competition that are generated by appropriate randomization procedures of original data matrices. In addition, I elucidate relationships between peak echolocation frequency and the proportion of moths in the diets of bat species to test the predictions of the Allotonic Frequency Hypothesis.

METHODS

I sampled the diets of insectivorous bat species caught in various ensembles of southern Africa (Chapter 4). The study sites are described in more detail in Chapter 3. Ensembles were surveyed during wet and dry seasons using a combination of capture techniques (Chapters 3 and 4).

DIET

I examined faecal pellets collected from captured bats to estimate diet of species. Despite some potential sources of bias (Rabinowitz & Tuttle 1982), faecal analysis is a reliable method for examining the food habits of insectivorous bats (Kunz & Whitaker 1983, Whitaker 1988). Furthermore, stomach analysis (Whitaker 1988) requires killing the animal, and is therefore less used. Bats were kept for at least one hour in cotton bags to ensure the collection of enough faecal pellets. I released bats unharmed after clipping the fur on their backs to avoid sampling the same bat twice. A minimum of 20 pellets were analysed from each species (Whitaker *et al.* 1999). I teased apart each pellet under 70% ethanol and identified the arthropod exoskeleton fragments to order using a taxonomic text (Scholtz & Holm 1985) and a reference collection of insects trapped at each site (see below). I calculated the percent volume of each insect order in each faecal sample as described by Whitaker (1988). However, classification to ordinal levels may cause some bias in results because coexisting bats may partition insect resources below the ordinal level - i.e. at familial or genus level (e.g Barlow 1997).

INSECT AVAILABILITY

I sampled insect availability at ensembles using one or two 22W battery-operated black-light insect traps (BioQuip Products, 1320 East Franclin Avenue, El Segundo, California). When possible, I operated the traps at the same time that I captured bats. The traps were placed at 1 m and 4 m above the ground, about 100 m from the mist nets to ensure that the light-traps did not affect bat activity at the nets. I classified all insects to order. Moths were pinned and classified to morpho-species (Oliver & Beattie 1993) for later identification to family. Morpho-species have been shown to be useful as surrogates for species, particularly in estimates of invertebrate biodiversity and species turnover (Oliver & Beattie 1993, 1996).

STATISTICAL ANALYSES

Testing predictions of competition

For every ensemble, I created a dietary data matrix of species captured, and three separate matrices of the species classified to functional groups (Chapter 3, Table 5.1). Each row represented a different species, and each column represented a different prey category (insect order). Each cell represented the percentage volume of the prey in the diet of bats.

Pianka's utilization index

Many different indices have been proposed to quantify dietary overlap between individual species pairs (e.g. MacArthur & Levins 1967, Colwell & Futuyma 1971, Feinsinger *et al.* 1981). Although choice of index may be arbitrary, Pianka's (1973) index has been recommended for null models (Gotelli & Graves 1996). Pianka's index is symmetrical, i.e. the overlap of species 1 on species 2 is equivalent to the overlap of species 2 on species 1. For a pair of species, the overlap in resource use of species 1 on species 2 with resource utilization (percentage insect order) p_1 and p_2, respectively, was calculated as:

$$O_{12} = O_{21} = \frac{\sum_{i=1}^{n} p_{2i} p_{1i}}{\sqrt{\sum_{i=1}^{n} \left(p_{2i}^{2}\right)\left(p_{1i}^{2}\right)}}$$

Based on Pianka's index, dietary overlap between species ranged from 0 (no prey type in common) to 1 (complete overlap).

Electivity index

Lawlor (1980) originally suggested that electivity of species could be calculated by scaling the observed utilization values to the column totals of the matrix itself, but this approach leads to Type 1 errors (Gotelli & Entsminger 2004). Therefore, I used the electivity index provided by Ecosim null model software (version 7.7, Gotelli & Entsminger 2004):

$$e_{ij} = p_{ij} / R_j$$

where, R_j was a measure of the availability of resource state j (i.e. the proportion of insect order caught in the light traps). In other words, each utilization value was divided by the estimated resource availability. The "e" values were then substituted for the "p" values in Pianka's index.

Pianka's utilization index and the electivity index enabled me to test predictions of competition theory: there should be a significantly low dietary overlap between coexisting species (Schoener 1974), and there should be a significantly low variance of dietary overlap between coexisting species.

Simulation procedures

Using the Niche module of Ecosim software (version 7.7, Gotelli & Entsminger 2004), I statistically compared values of the dietary overlap indices between species of ensembles and functional groups with overlap values of 1000 simulated ensembles and functional groups. Simulation ensembles and functional groups were constructed by randomizing the original data matrices. Four randomization algorithms (RA1 – RA4) can be used to simulate overlap patterns expected in isolation of competitive interactions between species (Gotelli & Graves 1996). Following Winemiller & Pianka (1990) who showed that the RA3 algorithm is robust to Type 1 and Type 2 errors, I used the RA3 algorithm, i.e. utilization and electivity overlap between species were reshuffled within each row of the matrix, to simulate dietary overlap patterns expected in the absence of competition (Gotelli & Entsminger 2004).

When measuring overlap with Pianka's index, resource states were set to "equiprobable". Conversely, when I measured overlap with the electivity index, the user-defined option was chosen, and each of the percentages of prey types caught in the light traps were allotted to the cells provided.

If the dietary overlap or variance in dietary overlap between bats of the observed ensemble or functional group was smaller than 95% of the values of simulated ensembles or functional groups, I concluded that competition structured the observed trophic patterns. In addition, experiment-wise error of the significance tests (i.e. p values) was held constant at five percent for ensembles separately from functional groups at each site by application of Bonferroni sequential adjustments (Rice 1989).

Testing predictions of the allotonic frequency hypothesis

Methods used to measure size (mass), wing (wingspan and wing area), and echolocation (peak echolocation frequency and duration of call) parameters from captured bats are described in

Chapter 5.

Relationship between % moth in the diet and peak echolocation frequency

I regressed the arcsine of the mean percentage volume of moths in the bats' diet against the Log10 of their mean peak echolocation frequency (PF) to determine if there was a significant relationship between % moth and PF. To control for phylogeny, the relationship between PF and diet was analysed by the method of independent contrast (Felsenstein 1985) using the PDAP package (Midford, Garland & Maddison 2004) in Mesquite (version 1.05, Maddison & Madison 2004) software. The phylogeny for the bats was derived from analyses conducted by Dr Geeta Eick and Samantha Stoffberg on DNA material obtained from captured bats (Chapter 5).

Best predictor of diet

I did a stepwise multiple regression of polynomial terms for a suite of independent variables (Zar 1999) to determine whether size, flight or echolocation is the better predictor of diet. This regression entails a sequential process of testing goodness of fit of the response variable to linear, quadratic, cubic, etc. functions of the predictor. The procedure was terminated when the higher order regression equation provided no significant increase in fit. First, the influence (allometric relationship) of mass on wingspan (WSP), wing area (WA), PF, and duration (DUR) was removed (Chapter 5). In regressions, arcsine percentage order insect in the diet was taken as the dependent variable, and Log10 transformed size, flight and echolocation parameters as independent variables. In all regressions, I plotted the residuals against their normal scores to test the normality of the residuals. The residuals were normally distributed in all regression models.

RESULTS

TROPHIC STRUCTURE OF BATS AND INSECT AVAILABILITY

Rarefaction and species richness estimators confirmed that species inventories of the fynbos, forest, and savanna ensembles were accurate (Chapter 4). At Koegelbeen, faecal pellets were collected from only three species hence data for the ensemble was not included in the null model analyses. In addition, dietary data of two species caught at two sites were not included in analyses because I did not collect faecal pellets from these species at these sites: *Sauromys petrophilus* (Goodhouse) and *Miniopterus fraterculus* (Die Hel). Less than 20 pellets were analysed for *M. tricolor* at Algeria, *N. capensis* and *R. clivosus* at Die Hel, *Eptesicus hottentotus*, *Rhinolophus darlingi*, and *Tadarida aegyptiaca* at Goodhouse, and *Pipistrellus anchietai*, *P. zuluensis*, *Tadarida aegyptiaca*, and *Taphozous mauritianus* at Sudwala (Tables 6.1A – F). However, dietary composition of these bats corresponded well with dietary composition of the same species caught at other sites of southern Africa (Tables 6.1A – F). In many cases, I did not collect any or enough faecal pellets (i.e. > 20 pellets) from species during the winter or summer season, and therefore I was not able to compare seasonal changes in diet of bats at ensembles.

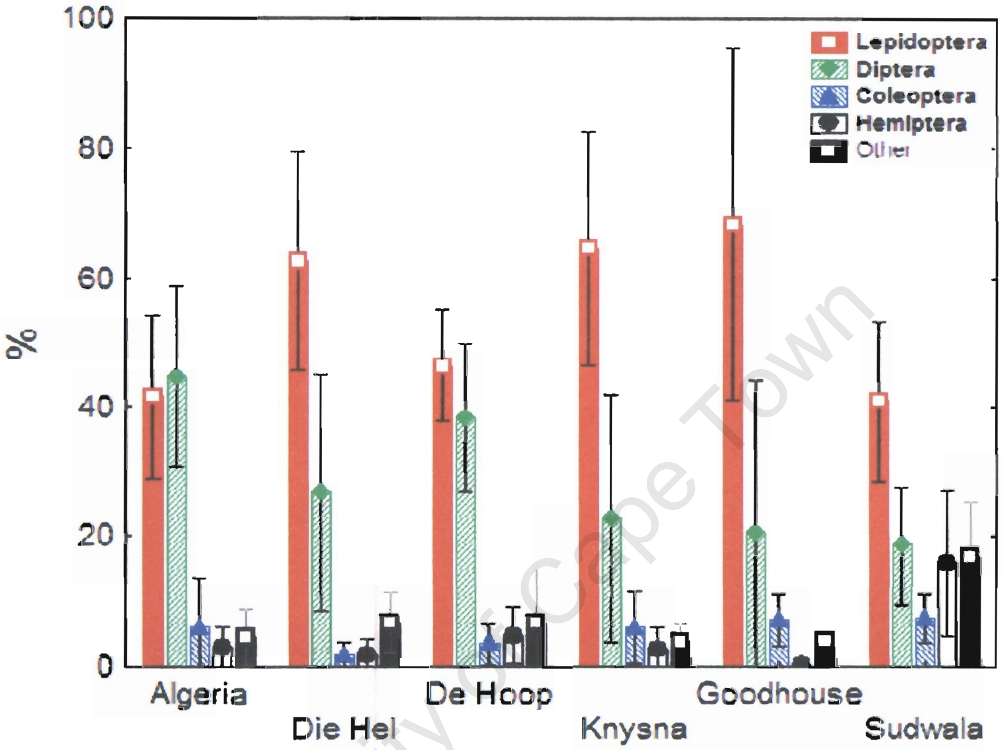

Fig. 6.1 Shows mean ± SD (bars) of percentage insect order caught in black-light traps during summer and winter months at six insectivorous bat ensembles of southern Africa. 'Other' insect order include Neuroptera, Ephemeroptera,

Diptera and Lepidoptera (moths) dominated the nocturnal insect fauna at all ensembles throughout the data collecting periods (Fig. 6.1). These two insect categories represented, respectively, 42% and 45% at Algeria (n = 8048), 27% and 63% at Die Hel (n = 722), 38% and 47% at De Hoop (n = 2472), 23% and 65% at Knysna (n = 879), 20% and 68.2% at Goodhouse (n = 495), and 19% and 41 % at Sudwala (n = 2846), of the total number of insects caught in the light traps. However, ca. 90% of the dipterans were small (< 7 mm body length). Moths were the most abundant medium and large sized insect prey found in the light traps. Insect abundance declined to low levels during the winter months at all ensembles, consistent with evidence from other studies that sampled insect availability in the fynbos (McDonald,

Table 6.1 Mean (M) ± SD volume of prey categories in the diet of bats (number of individuals in brackets) caught at six ensembles, (A) Algeria, (B) Die Hel, (C) De Hoop, (D) Knysna, (E) Goodhouse, and (F) Sudwala, of southern Africa. Species abbreviations follow Table 4.1.

(A) Algeria

Bat Species	NC (10)		EH (12)		LW (8)		CL (4)		MN (1)	MT (1)	NT (8)		RCL (10)		SP (51)		TA (43)	
No. pellets	89		118		63		39		20	11	51		72		464		387	
Prey Category	M	SD	M	SD	M	SD	M	SD	M	M	M	SD	M	SD	M	SD	M	SD
Lepidoptera	0		0		43.5	±48.1	0		6	0	34.9	±27.3	34.2	±30.4	0.3	±2.2	5.4	±13.4
Coleoptera	12.5	±21.5	92.8	±11	36	±43.2	6.3	±4.9	6	50	21.3	±17.6	51.3	±34.6	19.5	±23.1	25.5	±30.7
Hemiptera	44.6	±33.7	3.8	±9.6	3.5	±4.9	32.5	±22.8	33	25	1.5	±4.5	11.1	±26.2	32.9	±23.7	19.2	±25.6
Diptera	37.6	±28.4	1.5	±5.2	0		47.3	±37.3	49	0	3.8	±10.6	0		37.8	±31.2	34.6	±33.4
Hymenoptera	0		1.6	±4	0		6.8	±13.5	0	25	1.6	±4.6	0.8	±2.3	7.9	±16.2	8.4	±22.2
Trichoptera	0		0		0		2.5	±5.0	6	0	0		0		0.4	±2.9	0	
Orthoptera	0		0		0		0		0	0	23.5	±19.6	0		0		0.6	±3.4
Neuroptera	0		0		13	±29.1	0		0	0	0		1.1	±3.3	0.6	±3.0	1.5	±6.5
Ephemeroptera	2.3	±5.5	0		4	±5.5	1.5	±3.0	0	0	0		0		0		2.7	±7.7
Arachnida	0		0		0		0		0	0	13.5	±27.4	0		0		0	
Other	1	±3.2	0.3	±1.2	0		3.3	±6.5	0	0	0		1.4	±4.3	1	±3.3	1.4	±7.1

Table 6.1 Continued

(B) Die Hel

Bat Species	NC (2)		MN (30)		MT (10)		RC (6)		RCL (3)	
No. pellets	16		197		21		47		17	
Prey Category	M	SD	M	SD	M	SD	M	SD	M	SD
Lepidoptera	0		7.7	±16.2	0	0	74.7	±27.4	18.3	±7.6
Coleoptera	0		4.5	±10	33	±15.7	15	±25.1	55	±48.2
Hemiptera	14.2	±1.2	50.1	±28.2	42	±23.9	0		26.7	±46.2
Diptera	74.2	±1.2	26.3	±20.9	10	±14.1	0		0	
Trichoptera	0		1.6	±6.2	0		5.3	±6.7	0	
Neuroptera	0		0.52	±2.1	6	±13.4	0		0	
Ephemeroptera	9.2	±5.9	3.4	±10.9	0		0		0	
Other	2.5	±3.5	5.82	±9.0	4	±8.9	5	±12.3	0	

Table 6.1 Continued

(C) De Hoop

Bat Species	NC (12)		MN (25)		MT (13)		NT (5)		RC (22)		RCL (9)		TA (10)	
No. pellets	87		138		78		30		119		93		88	
Prey Category	M	SD	M	SD	M	SD	M	SD	M	SD	M	SD	M	SD
Lepidoptera	0.6	±2.1	8.7	±19.9	0		50	±21.6	49.3	±38.3	18.9	±36.2	5	±15.8
Coleoptera	40	±40	2.3	±3.9	43.6	±34.6	18.8	±17.5	39.6	±36.1	81.1	±36.2	19.5	±26.5
Hemiptera	30.4	±24.7	51.5	±29.8	31.1	±35.9	2.5	±5	5.9	±9.1	0		15.3	±20.1
Diptera	17.5	±24.9	25	±20.6	12.9	±28.9	0		1.4	±6.4	0		54	±30.5
Trichoptera	0		4	±9.7	0		0		0		0		0	
Orthoptera	0		0		0		11	±13	0.9	±4.3	0		0	
Isoptera	10	±20	0		0		0		0		0		0	
Neuroptera	0		1.3	±3.2	7	±15.4	0		0		0		0	
Ephemeroptera	0		6.2	±15.6	0		0		0		0		5.2	±11
Arachnida	0		0		0		5	±10	0		0		0	
Other	1.1	±2.9	1	±2.3	5.4	±11.3	7.5	±11.9	3.2	±4.2	0		0	

Table 6.1 Continued

(D) Knysna

Bat Species	NC (24)		PH (8)		MN (11)		MF (12)		RC (9)		RCL (6)		TA (6)	
No. pellets	209		79		71		72		70		35		51	
Prey Category	M	SD	M	SD	M	SD	M	SD	M	SD	M	SD	M	SD
Lepidoptera	3.7	±12.4	30.4	±25.3	19	±17.4	33.8	±23.9	80	±28.3	18.3	±16.2	49.3	±42.8
Coleoptera	15.1	±20.6	6.6	±9.5	23.2	±29.1	2.7	±7.8	18.9	±27.9	78.3	±18.3	21.2	±19.2
Hemiptera	22	±24.3	33.8	±15.1	23.9	±30	29.5	±24.4	0		0		11.7	±17.1
Diptera	57.1	±32.5	28	±13.5	27.6	±29.8	27.8	±23.8	1.1	±2.3	0		16.2	±18
Trichoptera	0		0		0		0		0		0		0	
Hymenoptera	0		0		2.7	±9.1	0		0		0		0	
Neuroptera	0		0		0		0		0		0		0	
Ephemeroptera	1.3	±6.1	0		0		0		0		0		0	
Other	0.4	±2	1.2	±4.1	3.6	±9.2	6.3	±10.3	0		3.3	±8.2	0	

Table 6.1 Continued

(E) Goodhouse

Bat Species	NC (2)		EH (1)	CS (2)		MN (2)		NT (3)		RD (2)		RCL (2)		HC (6)		TA (2)	
No. pellets	23		14	20		21		30		17		21		41		16	
Prey Category	M	SD	M	M	SD	M	SD	M	SD	M	SD	M	SD	M	SD	M	SD
Lepidoptera	0		0	0		0		66.7	±15.3	82.5	±3.5	15	±7.1	93.3	±15.2	8.5	±2.2
Coleoptera	15	±21.2	100	10	±14.1	3.4	±4.8	3.3	±5.8	15	±7.1	55	±7.1	5.3	±6.7	0	
Hemiptera	30	±14	0	12.5	±3.5	65	±7.1	0		0		0		0		60	±4.2
Diptera	55	±7.1	0	49.2	±22.2	24.2	±12.9	0		0		0		0		26.5	±13.4
Trichoptera	0		0	23.3	±33	0		0		0		0		0		0	
Orthoptera	0		0	0		0		23.3	±25.2	0		25	±7.1	0		0	
Neuroptera	0		0	0		5	±7.1	0		0		5	±7.1	0		0	
Ephemeroptera	0		0	0		2.5	±3.5	0		0		0		0		0	
Arachnida	0		0	0		0		6.7	±12	0		0		0		0	
Other	0		0	5	±7.1	0		0		2.5	±3.5	0		1.3	±4.3	0	

Table 6.1 Continued

(F) Sudwala

Bat Species	NC (2)		NA (11)		PA (1)	PZ (1)	SD (2)	MN (8)		MT (4)	NT (2)		RB (2)	
No. Pellets	20		66		5	8	15	52		38	22		20	
Prey Category	M	SD	M	SD	M	M	M	M	SD	M	M	SD	M	SD
Lepidoptera	0		44.2	±23.2	0	10	0	12.5	±6.7		45	±7.1	82.1	±7.7
Coleoptera	15	±21.2	2.8	±4.4	15	10	100	0		100	0		6.7	±9.4
Hemiptera	30	±14.1	15	±18.4	65	0	0	37.5	±27.7	0	0		5	±7.1
Diptera	55	±7.1	31.7	±15	20	70	0	24.2	±23.7	0	0		0	
Trichoptera	0		2.7	±3.9	0	0	0	0		0	0		0	
Isoptera	0		0		0	0	0	25	±39.3	0	0		0	
Orthoptera	0		0		0	0	0	0		0	17.5	±10.6	0	
Neuroptera	0		3.5	±4.5	0	10	0	0		0	0		2.5	±3.5
Ephemeroptera	0		0		0	0	0	0		0	0		0	
Plecoptera	0		0		0	0	0	0		0	0		0	
Mantodea	0		0		0	0	0	0		0	25	±34.4	0	
Arachnida	0		0		0	0	0	0		0	12.5	±17.7	0	
Other	0		0		0	0	0	0.8	±1.2	0	0		3.8	±5.3

Table 6.1 Continued

(F) Sudwala

Bat Species	RCL (19)		RD (10)		RH (13)		RS (11)		HC (5)		CLP (5)		CP (2)		TA (1)	TM (1)
No. Pellets	90		57		69		99		49		37		20		10	6
Prey Category	M	SD	M	SD	M	SD	M	SD	M	SD	M	SD	M	SD	M	M
Lepidoptera	18.2	±33.8	41.8	±25.5	42.3	±25.6	70	±29.4	97	±4.5	98	±4.5	4.5	±1.2	3.3	30
Coleoptera	46.2	±40.8	38.7	±30.5	50	±22.8	4.2	±4.7	0		0		15	±7.1	0	60
Hemiptera	1.8	±7.3	16.5	±21.4	0		6.2	±11.5	0		0		72	±3.4	3.3	0
Diptera	0		0		0		3.2	±7.2	2	±4.5	0		8.5	±12	93.3	0
Trichoptera	0		0		0		3.3	±6.8	0		0		0		0	0
Isoptera	0.0		0				0		0		0		0		0	0
Orthoptera	4.1	±11.8	0		3.1	±8.5	0		0		0		0		0	10
Neuroptera	0		0		0		0.9	±3	0		0		0		0	0
Ephemeroptera	0		0		0		7.9	±12.3	0		0		0		0	0
Plecoptera	23.2	±43.7	0		0		0		0		0		0		0	0
Mantodea	0		0		0		0		0		0		0		0	0
Arachnida	0		0		0		0		0		0		0		0	0
Other	6.5	±11.7	2.8	±0.5	4.2	±11.4	3.8	±6.4	1	±2.2	2	±4.5	0		0	0

Table 6.2 Observed and expected mean dietary niche overlap and variance of dietary overlap based on Pianka's utilization and electivity indices (see text for details) of bat species caught in ensembles, and classified to three functional groups (clutter-edge, clutter, and open-air foragers). Significantly low dietary overlap and variance of overlap relative to the null model (expected values) indicated that interspecific competition structured the trophic niche (bold print).

Site	Niche Overlap Index	All species				Clutter-edge				Clutter				Open-air			
		Mean		Variance		Mean		Variance		Mean		Variance		Mean		Variance	
		Obs	Exp	Obs	Exp	Obs	Exp	Obs	Exp	Obs	Exp	Obs	Exp	Obs	Exp	Obs	Exp
Algeria	Pianka	0.53	0.26*	0.09	0.06*	0.45	0.24*	0.1	0.06	0.82	0.28*	0.009	0.05	0.96	0.34*		
	Selectivity	0.24	0.21	0.07	0.07	0.11	0.14	0.07	0.08	0.1	0.22	0.03	0.06	0.01	0.16		
Die Hel	Pianka	0.39	0.3	0.09	0.07	0.58	0.32	0.05	0.06	0.45	0.29						
	Selectivity	0.52	0.27	0.1	0.08	0.8	0.38*	0.014	0.05	0.4	0.3						
De Hoop	Pianka	0.52	0.24*	0.06	0.06	0.75	0.29*	0.04	0.05	0.75	0.21*	0.04	0.07				
	Selectivity	0.36	0.19*	0.11	0.07	0.77	0.26*	0.003	0.05	0.36	0.12	0.27	0.08				
Knysna	Pianka	0.62	0.3*	0.07	0.06	0.85	0.38*	**0.01**	**0.05***	0.45	0.17						
	Selectivity	0.62	0.21*	0.12	0.08	0.93	0.22*	**0.002**	**0.07***	0.93	0.17*						
Ghouse	Pianka	0.31	0.2	0.12	0.09	0.43	0.2*	0.11	0.07	0.68	0.18*	0.09	0.07				
	Selectivity	0.23	0.13*	0.14	0.08*	0.3	0.12	0.14	0.08	0.34	0.14	0.26	0.08*				
Sudwala	Pianka	0.4	0.15*	0.11	0.06*	0.4	0.16*	0.09	0.06	0.72	0.16*	0.05	0.06	0.12	0.13	0.01	0.06
	Selectivity	0.22	0.15*	0.08	0.06	0.32	0.13*	0.13	0.06	0.22	0.17	0.07	0.06	0.06	0.1	0.004	0.06

*, Observed score is significantly different from the expected score (P < 0.05) after Bonferroni sequential adjustments applied separately for each ensemble (Rice 1989)

Rautenbach & Nell 1990, Schoeman & Jacobs 2003), and savanna (Rautenbach, Kemp & Scholtz 1988) biomes.

DIETARY OVERLAP

Ensembles

My null model analyses found no evidence that interspecific competition limited dietary overlap between coexisting bats of ensembles. Contrary to predictions, average dietary overlap between species was significantly high (Table 6.2). In addition, variance of dietary overlap between bats of the Algeria, Goodhouse, and Sudwala ensembles was significantly high (Table 6.2). This indicated an internal guild structure among bat species of these ensembles, where some species were very similar in resource use and others very dissimilar (Winemiller & Pianka 1990).

I used multidimensional scaling (MDS, Primer version 5.2.2, PRIMER-E Ltd, 2001) to identify the structure and species members of the dietary guilds. MDS is a powerful tool to ordinate ecological data such as dietary data (that do not follow standard statistical distributions) by similarity indices or other measures of distance (Legendre and Legendre 1998). Species of each ensemble were ordinated by Euclidian distance measures of their diets, as a measure of interspecific distance (Ricklefs and Travis 1980). Small stress values of the MDS-plots indicated that the goodness-of-fit of the reproduced distance matrices to the observed distance matrices were satisfactory (Figs. 6.2A – C).

Three dietary guilds were identified. The first guild (Guild 1) included bats with a high incidence of small, soft-bodied insects such as flies, lacewings, and bugs in their diet. Diet of bats of the second dietary guild (Guild 2), comprised a high proportion of hard-bodied beetles, and those of the third guild (Guild 3) consisted mainly of moth. Allocation of species to dietary guilds was relatively easy for the Algeria and Goodhouse ensembles (Figs. 6.2A and B), but more difficult for the Sudwala ensemble (Fig. 6.2C). Species richness of Guild 1 was different at every ensemble: five bats at Algeria (*Cistugo lesueuri*, *Miniopterus natalensis*, *Neoromicia capensis*, *Sauromys petrophilus*, and *Tadarida aegyptiaca*), four bats at Goodhouse (*Cistugo seabrai*, *M. natalensis*, *N. capensis*, and *T. aegyptiaca*), and six bats at Sudwala (*Pipistrellus anchietai*, *P. zuluensis*, *M. natalensis*, *N. capensis*, *Chaerephon pumilus*, and *T. aegyptiaca*). Species richness of Guild 2 included two bats at Algeria (*Eptesicus hottentotus* and *Myotis tricolor*) and Goodhouse (*E. hottentotus* and *Rhinolophus clivosus*), and five bats at Sudwala (*Taphozous mauritianus*, *M. tricolor*, *Scotophilus dinganii*, *R. clivosus*, and *R. hildebrandti*). Species richness of Guild 3 totalled three at Algeria (*Rhinolophus clivosus*, *Nycteris thebaica*, and *Laephotus wintoni*) and Goodhouse (*R. darlingi*, *Hipposideros caffer*, and *Nycteris thebaica*), and seven at Sudwala (*R. blasii*, *R. darlingi*, *R. simulator*, *H. caffer*,

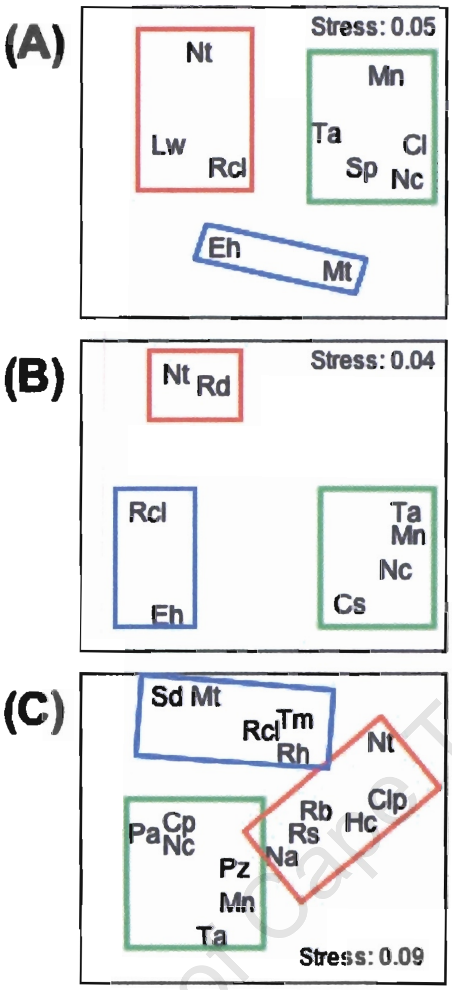

Fig. 6.2 Shows MDS-plots of dietary overlap between bat species of the Algeria (A), Goodhouse (B), and Sudwala (C) ensembles. Abbreviations are from Table 5.1. Stress values indicated satisfactory goodness of fit of the reproduced distance matrix to the observed distance matrix of species in ensembles. Dietary guilds are demarcated with coloured squares as follows: Guild1 = soft-bodied insect eaters (Green), Guild 2 = beetle eaters (Blue), and Guild 3 = moth eaters (Red).

Cloeotis percivali and *Neoromicia africanus*). Thus, with the exception of *Rhinolophus clivosus*, species were classified to the same guild irrespective of ensemble. In contrast, *Rhinolophus clivosus* was classified to Guilds 2 or 3, depending on ensemble. In addition, species from different functional groups were classified in the same guild e.g. *Tadarida aegyptiaca* (open-air) and *Miniopterus natalensis* (clutter-edge) were classified to Guild 1.

Mean dietary overlap between species of dietary guilds at Algeria, Goodhouse, and Sudwala was significantly high (Table 6.3). However, variance in overlap between species of Guild 1 at Algeria, and of Guild 2 and Guild 3 at Sudwala was significantly small (Table 6.3). This suggests that diffuse competition may have influenced the trophic niche structure (Gotelli & Entsminger 2004). However, variance of dietary overlap between species was not significantly small when measured by the electivity index (Table 6.3).

Functional groups

Null model analyses of dietary overlap between bats of functional groups found no evidence that interspecific competition influenced the trophic structure. Contrary to predictions, there was frequently a significantly high dietary overlap between bats (Table 6.2). However, variance of dietary overlap between the clutter-edge bats of the Knysna ensemble (*Neoromicia capensis, Pipistrellus hesperidus, Miniopterus natalensis,* and *M. fraterculus*) was significantly small, regardless of overlap index used (Table 6.2). Thus, the trophic niche structure may be mediated by diffuse competition and a limit to similarity. The significantly high variance of dietary overlap between clutter-edge bats at Algeria and Sudwala, and clutter bats at Goodhouse (Table 6.2), supported the earlier finding of an internal dietary guild structure in these ensembles.

ALLOTONIC FREQUENCY HYPOTHESIS

Relationship between % moth and peak echolocation frequency

I found strong support for the predictions of the allotonic frequency hypothesis. There was a significant relationship between PF and the proportion of moths in diet of bats at Algeria, De Hoop, Goodhouse, and Sudwala. The relationship was parabolic at Algeria ($\%\text{moth} = 73.7 - 2.9 * \text{PF} + 0.03 * \text{PF}^2$, $r = 0.64$, $p < 0.05$, Fig. 6.3A), but linear at De Hoop, Goodhouse, and Sudwala ($\%\text{moth} = -21.3 + 0.66 * \text{PF}$, $r = 0.82$, $p < 0.05$; $\%\text{moth} = -20.5 + 0.8 * \text{PF}$, $r = 0.81$, $p < 0.01$; $\%\text{moth} = -6.7 + 0.59 * \text{PF}$, $r = 0.8$, $p < 0.01$; respectively, Figs. 6.3B, E, and F). When I controlled for phylogeny using independent contrasts, the relationship between PF and moth in diet remained significant at Algeria, De Hoop and Sudwala ($r = 0.74$, $n = 9$, $p < 0.05$; $r = 0.78$, $n = 6$, $p < 0.05$; and $r = 0.76$, $n = 17$, $p < 0.05$, respectively). However, there was no significant relationship between PF and the proportion of moths in diet of bats at Die Hel and Knysna ($p > 0.05$, Figs. 6.3C and D).

Best predictor of diet

Stepwise multiple polynomial regression of Lepidoptera, Coleoptera, Hemiptera, Diptera, Hymenoptera, Trichoptera, and Other (rest of prey types) incidence in diets of bats (dependent variables) against size (mass), wing (WS and WA), and echolocation (PF and DUR) parameters (predictor variables) yielded significant models for, in order of importance, Lepidoptera ($r = 0.76$, $F_{(10, 322)} = 43.4$, $P < 0.001$, Fig. 6.4A), Coleoptera ($r = 0.59$, $F_{(10, 322)} = 17.7$, $p < 0.001$, Fig. 6.4B), Diptera ($r = 0.39$, $F_{(10, 322)} = 5.8$, $p < 0.001$, Fig. 6.4C), Hemiptera ($r = 0.36$, $F_{(10, 322)} = 4.6$, $p < 0.001$, Fig. 4D), Trichoptera ($r = 0.33$, $F_{(10, 322)} = 3.8$, $p < 0.001$, Figure 6.4E), and

Table 6.3 Observed and expected mean dietary overlap and variance of overlap, based on Pianka's and electivity indices, between bat species of dietary guilds at ensembles (see text for details). Significantly low dietary overlap and variance of overlap relative to the null model (expected values) indicated that interspecific competition influenced the trophic structure (bold print).

Site	Niche Overlap Index	Guild1				Guild2				Guild3			
		Mean		Variance		Mean		Variance		Mean		Variance	
		Obs	Exp	Obs	Exp	Obs	Exp	Obs	Exp	Obs	Exp	Obs	Exp
Algeria	Pianka	0.93	0.28*	**0.002**	**0.05***	0.84	0.15*			0.82	0.28*	0.009	0.05
	Selectivity	0.34	0.15	0.22	0.07	0.39	0.15			0.1	0.22	0.03	0.06
Ghouse	Pianka	0.74	0.24*	0.03	0.07	0.88	0.16*			0.95	0.16*	0.002	0.08
	Selectivity	0.68	0.13*	0.12	0.08	0.03	0.11			0.33	0.17	0.33	0.08
Sudwala	Pianka	0.61	0.16*	0.08	0.06	0.88	0.14*	**0.006**	**0.06***	0.81	0.15*	**0.017**	**0.06***
	Selectivity	0.47	0.13*	0.14	0.08	0.51	0.13*	0.09	0.08	0.28	0.16	0.11	0.06

*, Observed score is significantly different from the expected score ($P < 0.05$) after Bonferroni sequential adjustments applied separately for each ensemble (Rice 1989)

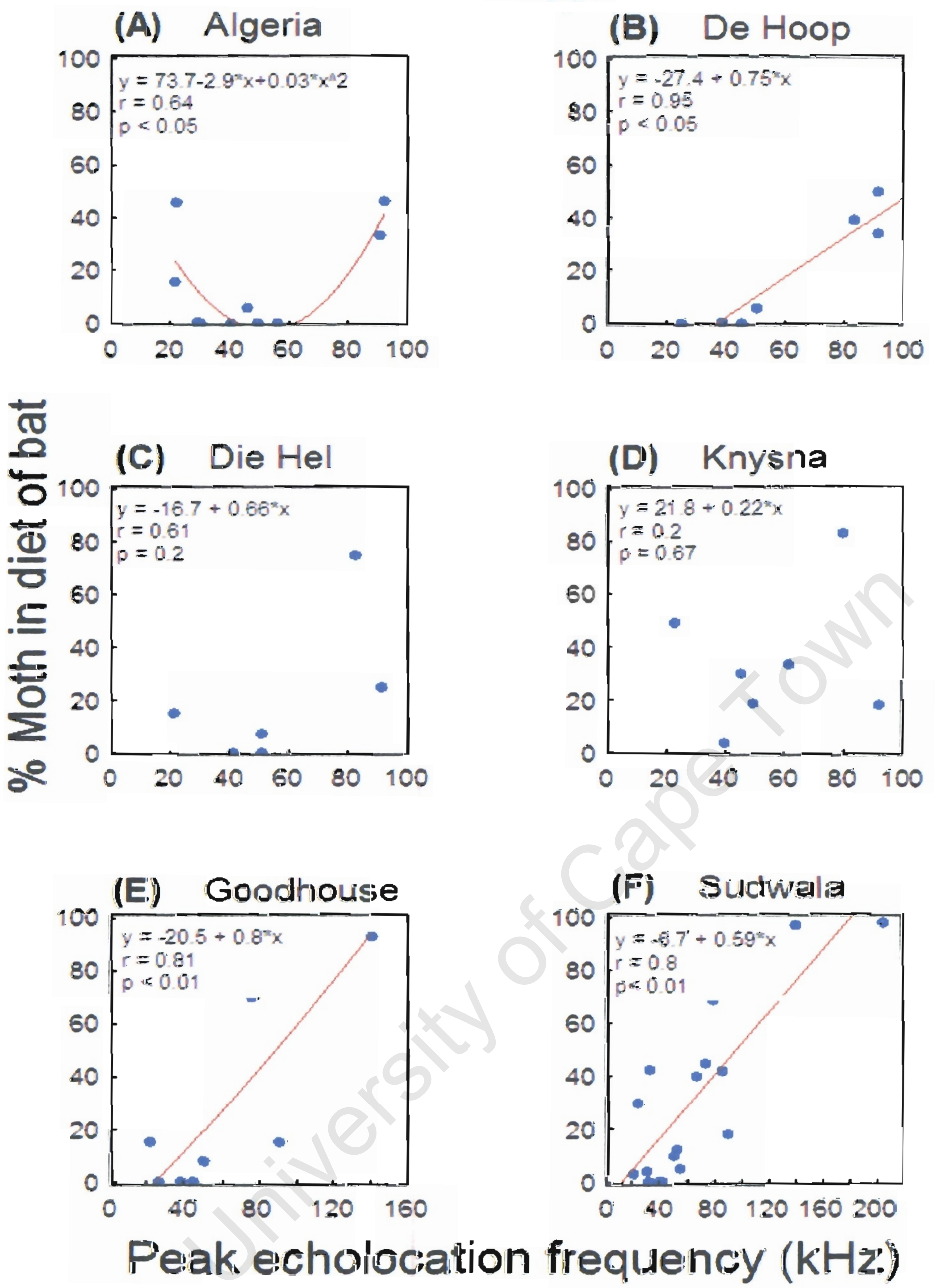

Fig. 6.3 Relationship between peak echolocation frequency and the mean percentage moth in the diet of coexisting bats captured at the (A) Algeria, (B) Die Hoop, (C) Die Hel, (D) Knysna, (E) Goodhouse, and (F) Sudwala ensembles. The solid red line shows the curve of best fit if significant, where y = arcsine (% prey item) and x = Log10 (peak echolocation frequency in kHz).

Hymenoptera ($r = 0.33$, $F_{(10, 322)} = 2.5$, $p < 0.01$, Fig. 6.4F). Because on average 91% of volume prey in diet of bats consisted of Lepidoptera, Coleoptera, Diptera, and Hemiptera, only the models for these four prey types are further discussed.

The Lepidoptera model eliminated all parameters except PF, mass, and WA (Fig. 6.4A). Peak frequency was the best predictor of moth incidence by virtue of its higher t-value (Fig. 6.4A). There was a significant parabolic relationship between incidence of moth in the diet of bats and peak echolocation frequency (Fig. 6.5A). In contrast, the significant relationships between incidence of moth, and wing area and mass, were negatively parabolic and linear, respectively (Figs. 6.5B and C). The Coleoptera model eliminated DUR (Fig. 6.4B). WA was the best predictor of beetle incidence by virtue of its t-value (Fig. 6.4B). There were significant positive linear relationships between incidence of beetles in diets of bats, and wing area, wingspan, and mass (Figs. 6.6A, B, and C). In contrast, there was a significant negative linear relationship between incidence of beetle in diet and peak echolocation frequency (Fig. 6.6D). The Diptera model eliminated all parameters except WA (Fig. 6.4C). There was a significant hyperbolic relationship between incidence of dipterans in diet of bats and wing area (Fig. 6.7A). The Hemiptera model eliminated DUR and mass (Fig. 6.4D). Peak frequency of call was the best predictor of hemipteran incidence in diet by virtue of its higher t-value (Fig. 6.4D). Relationships between incidence of hemipterans in diet of bats, and peak frequency and wing area, were hyperbolic (Figs. 6.7B and C). In addition, there was a negative linear relationship between incidence of hemipterans in diet and wingspan (Fig. 6.7D).

In summary, predictive relationships between diet of bats and their size, flight, and echolocation parameters were most significant for the moth component of bat diets (F-value = 43.4 versus 17.7 for the next most important component). The high t-value of the strong parabolic relationship between the percentage moth in the diets of bats and the peak echolocation frequency (t-value = 14), was not matched by t-values of other dietary components and parameters (2nd highest t-value = 6.1 for beetle and wing area relationship, Figs 6.4A and B). The overall parabolic relationship between PF and the incidence of moth in the diet of bats suggests that bats with dominant echolocation frequencies within the hearing range of moths (20 - 60 kHz) incorporated few or no moths into their diets. Conversely, bats that echolocate lower (< 20 kHz) or higher (> 60 kHz) than this range, incorporated more moths in their diets, and this increased as echolocation frequencies diverged further from this range.

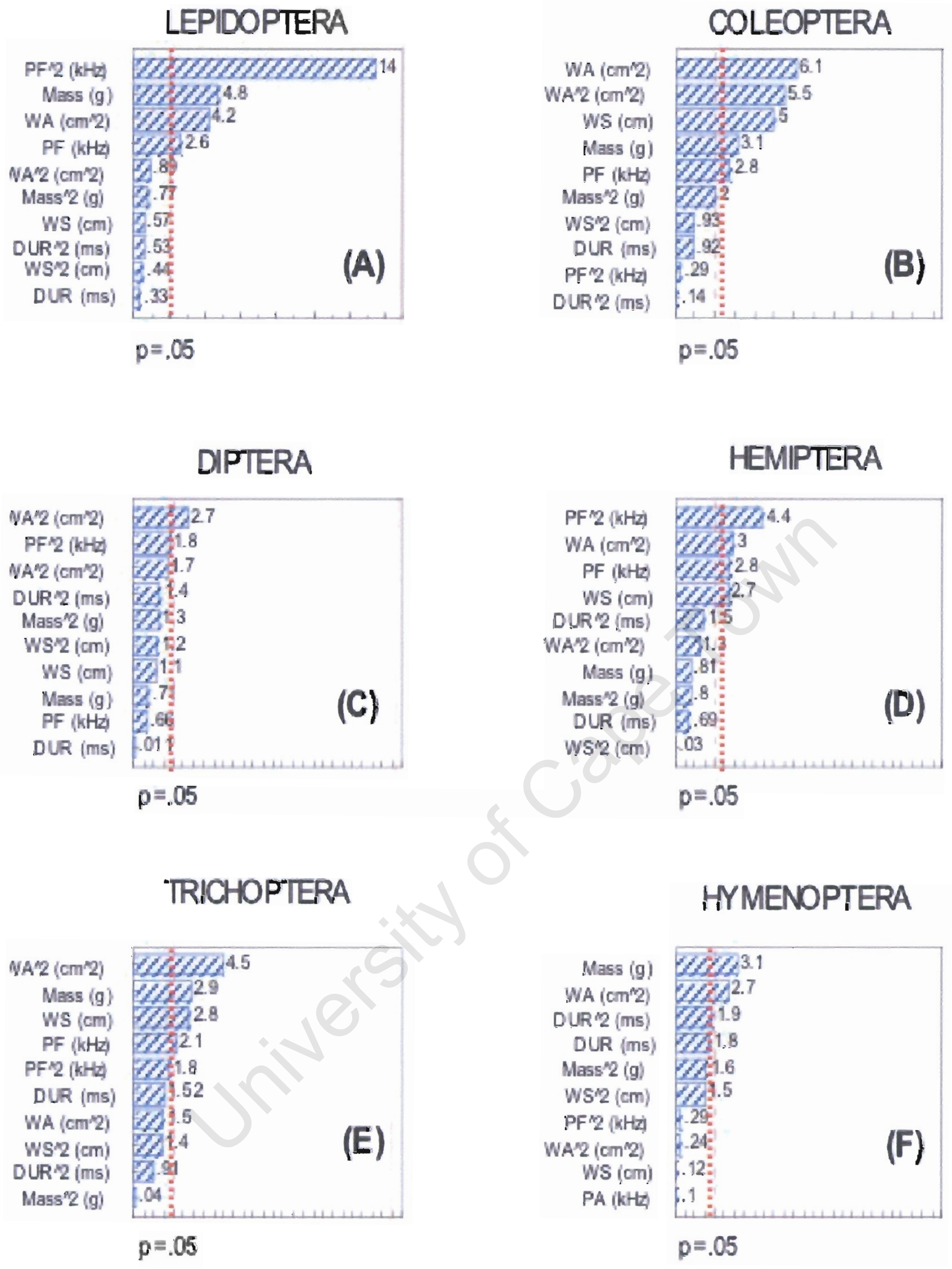

Fig. 6.4 Pareto-t graphs showing absolute t-values for the coefficients of size (mass), wing (WA = wing area and WS = wingspan), and echolocation (PF = peak echolocation frequency and DUR = duration of call) parameters, obtained from multivariate polynomial regressions of percentage (A) Lepidoptera, (B) Coleoptera, (C) Diptera, (D) Hemiptera, (E) Trichoptera, and (F) Hymenoptera in diet (dependent variables) and size, wing, and echolocation parameters (predictor variables) to estimate best predictor(s) of diet. Significant parameters ($p < 0.05$) extend beyond the red dotted line.

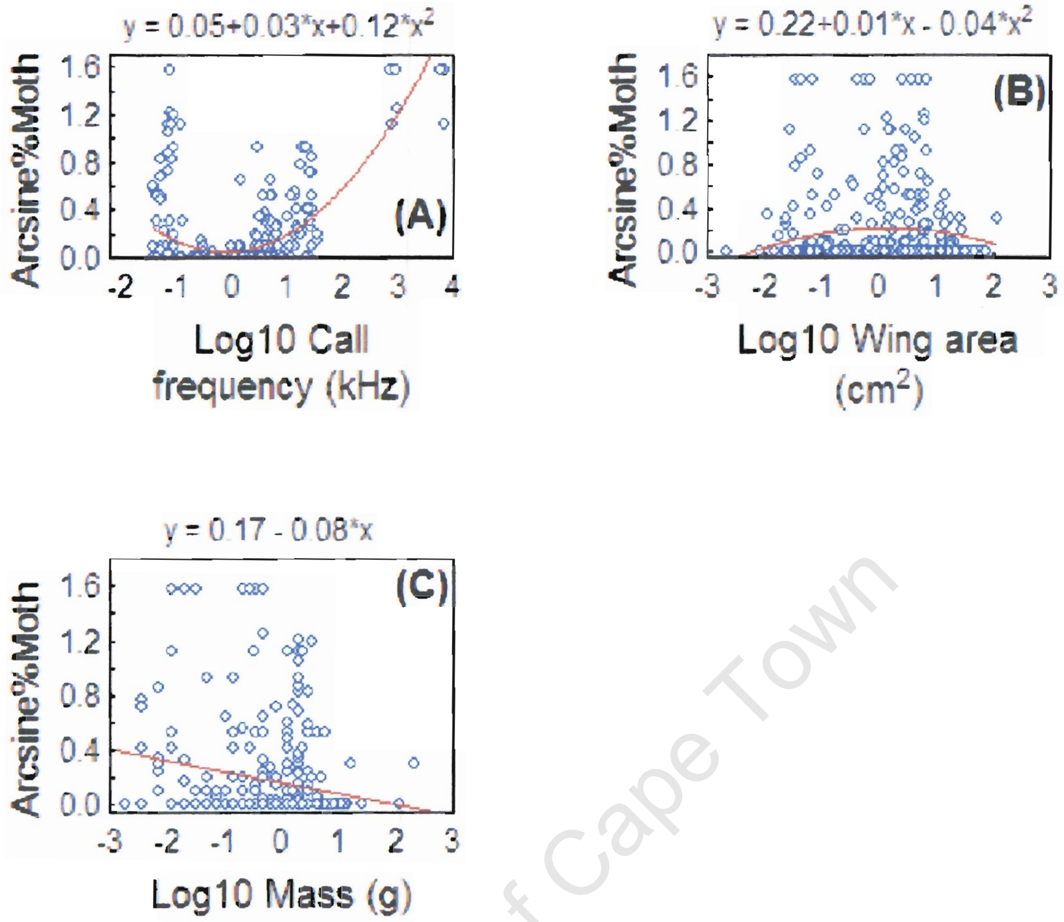

Fig.6.5 Relationship between mean percentage moth in the diet (dependent variable), and significant predictor parameters (all $p < 0.01$), in order of importance, peak call frequency (A), wing area (B), and mass (C), that were retained from multivariate polynomial regressions involving diet (as dependent variables) and size, wing, and echolocation parameters (as independent variables). Line of best fit is shown where y = arcsine (%moth in diet) and x = Log10 (peak call frequency, wing area, and mass parameters in kHz, cm^2, and g, respectively).

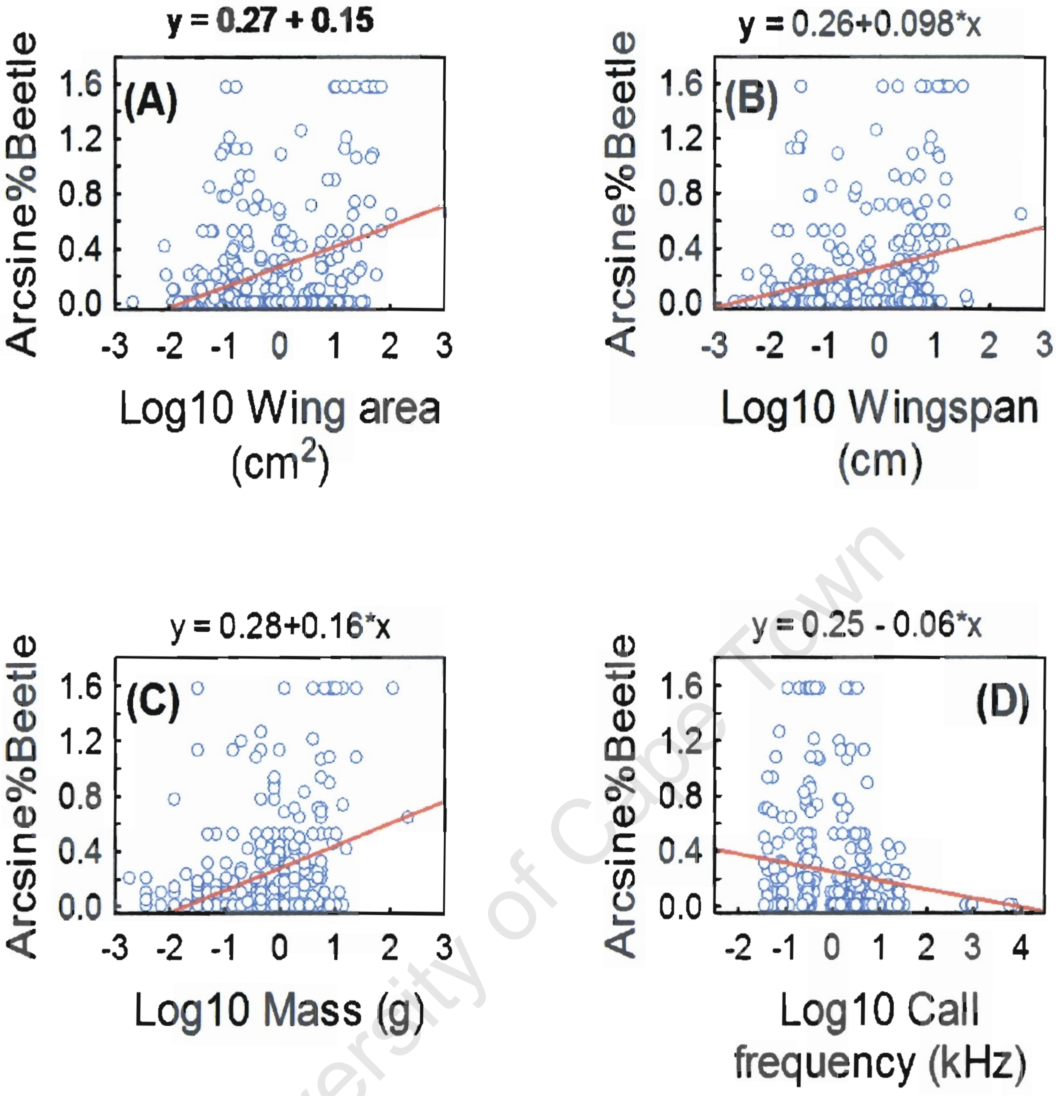

Fig.6.6 Relationship between mean percentage beetle in the diet (dependent variable), and significant predictor parameters (all $p < 0.01$), in order of importance, wing area (A), wingspan (B), mass (C), and peak echolocation frequency (D) that were retained from multivariate polynomial regressions involving diet (as dependent variables) and size, wing, and echolocation parameters (as independent variables). Line of best fit is shown where y = arcsine (%moth in diet) and x = Log10 (wing area, wingspan, mass, and peak echolocation frequency parameters in cm^2, cm, gram, and kHz, respectively).

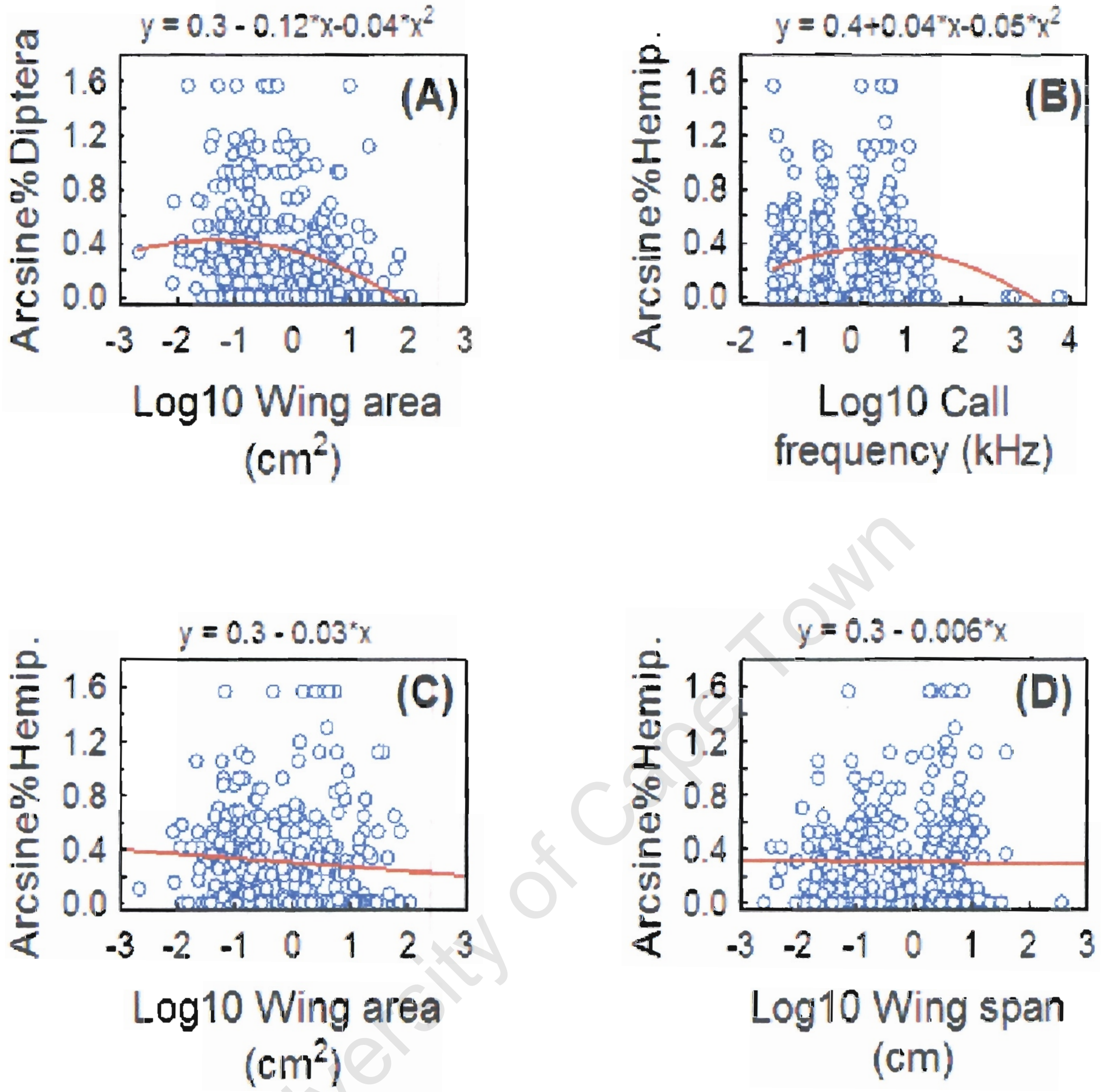

Fig. 6.7 Relationship between mean percentage Diptera (A) and Hemiptera (B – D) in the diet (dependent variables), and the significant predictor parameters (all $p < 0.01$), in order of importance for the Hemiptera model, wing area (A), peak frequency (B), wing area (C), and wingspan (D) that were retained from multivariate polynomial regressions involving diet (as dependent variables) and size, wing, and echolocation parameters (as independent variables). Line of best fit is shown as a red line where y = arcsine (%moth in diet) and **x** = Log10 (wing area, peak echolocation frequency and wingspan parameters in cm^2, kHz, and cm, respectively).

DISCUSSION

COMPETITION: DIETARY OVERLAP

I found little evidence that competition influenced the dietary structure of bats. In competitively structured ensembles, dietary overlap between sympatric species should be significantly low (Schoener 1974). Contrary to predictions, there was often a significantly high dietary overlap between sympatric bats.

In general, the average dietary overlap between coexisting insectivorous bats of functional groups and guilds was higher than the average overlap between all the species of the ensemble. In other words, insectivorous bats adapted to forage in similar habitats preyed on similar prey types. This phenomenon is well-documented (e.g. Fenton 1982, Aldridge & Rautenbach 1987). However, there was a significantly small variance of dietary overlap between the bat species of the clutter-edge functional group at Knysna, and of three dietary guilds that were identified by null models and MDS plots, Guild 1 at Algeria and Guilds 2 and 3 at Sudwala. High species richness of ensembles and dietary guilds at Algeria and Sudwala (Chapter 4, this study) might thus be mediated by diffuse competition and a limit to dietary similarity (Gotelli & Entsminger 2004). This is supported by patterns found at Knysna, where the number of species in the clutter-edge group was relatively high.

Clutter-edge bats at Knysna included four species from two families, *Neoromicia capensis, Pipistrellus hesperidus* (Vespertilionidae), *Miniopterus natalensis,* and *M. fraterculus* (Miniopteridae). The high number of species with similar morphology and ecological requirements (the first two were originally classified in the same genus) should theoretically increase the likelihood of competitive interactions between them to partition available resources (Findley & Black 1983, Saunders & Barclay 1992, Findley 1993 Arlettaz *et al.* 1997, Arlettaz 1999). Species richness of the clutter-edge functional groups at Die Hel and Algeria were similar, but included bats such as *Myotis tricolor* and *Eptesicus hottentotus* (absent from Knysna) that mainly eat beetles and that are morphologically less similar. Dietary records from additional sites where *Miniopterus natalensis* and *M. fraterculus* coexist (e.g. Die Hel) may reveal if competitive interactions between clutter-edge bats are more likely if there is more than one miniopterid present.

At Algeria, five of the ten resident bat species were classified to dietary Guild 1 because of the high incidence of small, soft-bodied insects such as flies and bugs in their diet. However, the insect fauna of Algeria is dominated by hearing moths (Schoeman & Jacobs 2003). Bats of Guild 1 seldom catch hearing moths because they echolocate within the hearing range of the moths, enabling the moths to take evasive action (see below). Consequently, availability of flies and bugs at Algeria might be limiting to the high number of bats feeding on them, hence the non-random trophic niche structure of the guild at Algeria.

Conversely, insect abundance is probably higher in the subtropical savanna than in the temperate fynbos and forest ensembles (Gilliomee 2004). Thus insect availability may not be limiting to bats of savanna ensembles, but my data do not test this hypothesis. Nevertheless, the high species richness of the dietary guilds at Sudwala may explain why their trophic niche patterns appear structured by diffuse competition. Furthermore, the large number of bat species allotted to Guild 3 - i.e. there was a high incidence of moth in their diet - might explain the high incidence of beetle in the diet of *Rhinolophus clivosus*, despite the species echolocating outside the hearing range of moths.

The results for the dietary guilds should be viewed with some caution, however. Means and variance of resource overlap could reflect the availability of different resources rather than competitive effects (Bradley and Bradley 1985). When the electivity index (Gotelli & Entsminger 2004) was used instead of Pianka's (1973) utilization index, variance of dietary overlap between the bats of the dietary guilds at Algeria or Sudwala was not significantly small. However, reliable estimates of prey availability to bats are difficult to obtain for different reasons (Whitaker 1994, Jones & Rydell 2004). For example, light traps are effective for sampling the diversity of moths and nocturnal flies, but less so for sampling nocturnal beetle diversity (Jones & Rydell 2004). Thus, electivity analyses based on estimates of prey availability using alternative capturing techniques, such as suction or sticky insect traps, may yield very different results.

The internal dietary guild structure identified at the Algeria, Goodhouse, and Sudwala ensembles was similar to the internal dietary structure exhibited by eight sympatric insectivorous bat species in Europe (Eichstadt 1997 as cited in Patterson, Willig & Stevens 2004). However, *Rhinolophus clivosus* belonged to different dietary guilds depending on the ensemble. In addition, bats such as *Neoromicia capensis* and *Tadarida aegyptiaca* that were classified to different functional groups (clutter-edge and open-air, respectively), were allotted to the same dietary guilds in ensembles. Thus, future investigations of the influence of competition on coexisting bats might be more productive by focusing on dietary sub-guilds, particular to an ensemble, rather than general functional feeding groups or taxonomy.

In addition to dietary overlap, selection of prey size classes by coexisting bats is also an important dimension along which partitioning of food resources may take place (Schoener 1974). However, I was not able to measure size of prey, because of the fine mastication of their food by some species, in the diet of all the bat species comprising ensembles and functional groups. Thus, it was not possible to investigate if prey size differences in diet of bats were significantly different from those expected by chance. Competition may have influenced the phenotypic structure of ensembles (Chapter 5), which, in turn, may be dependent on the biomass and sizes of insects available. Thus, if the size of a bat largely determines the size class of insects on which the bat can prey (Black 1974), it can be predicted that the patterns of prey size classes in the diets of bats should follow the non-random patterns of body size exhibited by the bats.

COEVOLUTION: THE ALLOTONIC FREQUENCY HYPOTHESIS

The significant relationship between peak echolocation frequency (PF) and the incidence of moths in the diet of bats in all of the ensembles, except at Die Hel and Knysna, supports the predictions of the allotonic frequency hypothesis (AFH). In addition, PF was the best predictor of dietary composition. The relationship between the proportion of moths in the diet and peak echolocation frequency of bats was a parabolic one, as predicted by the allotonic frequency hypothesis (Bogdanowicz, Fenton & Daleszczyk 1999). Jacobs (2000) and Schoeman & Jacobs (2003) found similar significant relationships between PF and the percentage moths in the diets of bats in two ensembles of southern Africa.

Different reasons may account for the lack of support for the AFH at Die Hel and Knysna. Low species richness is probably the main reason for the lack of support found at De Hel (n = 6). The positions of the six species on the regression curve (Fig. 6.3C) are markedly similar to the positions of species in the other fynbos ensembles, Algeria and De Hoop, where the relationships between PF and diet were significant (Figs. 6.3A and 3B). Furthermore, I did not collect dietary data for *Miniopterus fraterculus*, a member of the Die Hel ensemble (Chapter 4). When dietary data of *M. fraterculus* collected at Knysna was included in the Die Hel regression, the relationship between moth in the diet and peak echolocation frequency was significant ($r = 0.78$, $p < 0.05$). On the other hand, lack of support for the AFH at Knysna can be attributed to the high incidence of moths in the diet of *Tadarida aegyptiaca* (50%), despite the fact that the species used a PF (22 kHz, Chapter 5) that is within the hearing range of moths. At the other ensembles, the diet of *T. aegyptiaca* comprised mainly non-hearing, soft-bodied insects such as flies and bugs, hence ordination of dietary overlap grouped the species with bats from the clutter-edge functional group at the Algeria, Goodhouse, and Sudwala ensembles. However, the dietary data for *T. aegyptiaca* at Knysna was collected on two consecutive nights only (data not shown) and thus might not be a true reflection of the trophic niche of the species. Alternatively, the diets of clutter-edge bats (that echolocate within the hearing range of moths) at Knysna might be mediated by competition (see above), and may have increased selective pressure on *T. aegyptiaca* to feed on prey relatively unavailable to clutter-edge bats, i.e. hearing moths. In addition, moths may be particularly vulnerable to predation by bats such as *T. aegyptiaca* that echolocate at frequencies near the bottom range of their sensitivity range, c.a. 20 kHz (see below).

However, frequency might not be the only factor in the echolocation calls of bats that influence whether or not they prey on moths (Fullard & Thomas 1981). For example, although the peak frequency used by *Nycteris thebaica* is high, the calls of this species are also of low intensity and very short (Fenton, Gaudet & Leonard 1983). Both the latter characteristics are likely to make its calls less detectable by moths (Jones & Waters 2000). Nevertheless, low intensity calls may not be an adaptation *per se* to avoid detection by moths, but simply a feature of the gleaning habit (Waters 2003). This is likely the case with short duration calls, necessary to avoid pulse-echo overlap in cluttered habitats (Schnitzler & Kalko 2001). Furthermore, in this study duration of call was a poor predictor of the incidence of moths in the diets of coexisting bats.

Similarly, the high proportion of moths in the diet of the *Cloeotis*, *Rhinolophus* and *Hipposideros* species might be due to their use of high duty-cycle CF calls highly adapted for detection and classification of prey in clutter rather than their high peak echolocation frequencies (Schnitzler & Kalko 2001). Rhinolophoid bats may more easily detect large-winged insects such as moths because they are likely to produce greater amplitude modulations (glints) than smaller-winged insects (Schnitzler & Kalko 2001). Under laboratory conditions, *Rhinolophus* bats were able to distinguish between size and identity of prey species (Schnitzler 1987, von der Emde & Menne 1989, von der Emde & Schnitzler 1990), by listening to the unique acoustic glints imprinted by the fluttering wings of different insects onto the echoes of their CF calls (Neuweiler 1990, Schnitzler & Kalko 2001). Thus, the differences between the proportions of moths in the diets of high duty-cycle echolocation bats compared to low duty-cycle echolocation might simply be because the latter group of bats have greater difficulty detecting and classifying moths (Schoeman & Jacobs 2003).

Differential exploitation of moths within the genus *Rhinolophus* largely supported the AFH. However, certain species were notable exceptions to the predictions of the AFH. For example, the proportion of moth in the diet of *Rhinolophus hildebrandti* at Sudwala was notably high (42%), despite echolocating well within the hearing range of moths (44 kHz). However, there was an even higher proportion of beetles in its diet (50%), and thus its diet was more similar to the diets of bats of the beetle guild (such as *Myotis tricolor* and *Scotophilus dinganii*) than those of other high duty-cycle echolocating bats that were classified to the moth guild. Conversely, the peak frequency of the high duty-cycle echolocating bat, *R. clivosus,* is outside the hearing range of moths (92 kHz), but its diet consisted predominantly of beetle, except at Algeria. The exceptionally wide distribution range of *R. clivosus* is rivalled only by its sister species *R. ferrumequinum* (Csorba, Uyhelyi & Thomas 2004). Beetle–eating by *R. clivosus* might be a relatively new development in this species facilitating its dispersal into areas occupied by phylogenetically older resident rhinolophids hunting predominantly moths. Where many of the latter species are absent and bat abundance is low (e.g. Algeria), competition for moths may be low, allowing it to take moths in high proportions.

If most of the moths eaten by the respective species of bats were in fact non-tympanate, then the degree of difference in the percentage moths in the diets of these bats could not be used to test the allotonic frequency hypothesis (Schoeman & Jacobs 2003). Although the faecal analysis does not allow the identification of moths eaten down to species level, 90% of the moth morpho-species (n = 2956 moths, 278 morpho-species) that were caught in light traps at Algeria were tympanate (Schoeman & Jacobs 2003). Preliminary investigation indicates similar proportions of tympanate moths caught in the light traps at the other ensembles (data not shown). Based on the families of moths known to be present in southern Africa, Fenton & Fullard (1979) estimated that 85% of moths in southern Africa are tympanate. This apparent predominance of tympanate moths is not unique to southern Africa. Pavey & Burwell (1998) sampled a number of tropical and subtropical sites in Australia and found that at least 80% of moths at these sites were tympanate while Fullard (1990) reported the prevalence of tympanate moths at temperate and tropical localities to be as high as 95%.

Body size rather than call frequency may be responsible for the differences in the diet of coexisting bats. There is a strong relationship between call frequency and body size of insectivorous bats (Jones 1994, 1996, Bogdanowicz, Fenton & Daleszczyk 1999). The strong relationship between PF and diet might thus be an artefact of the relationship between PF and mass. However, after removing the influence of mass from the echolocation and wing parameters, the significant parabolic relationship between incidence of moth in diet of bats and peak echolocation frequency was notably stronger than other significant relationships between diet on the one hand, and size, wing area, wingspan or duration of echolocation call. More importantly, the relationship between moth and peak frequency was not the inverse of the positively linear relationship between moth and mass. Indeed, the significant parabolic relationship between moth in diet and PF corrected for the influence of size, is consistent with evidence that there is no relationship between mass, and moths or beetle incidence in the diet of bats that echolocate < 100 kHz if the influence of peak frequency is removed from mass (Bogdanowicz, Fenton & Daleszczyk 1999).

The increase of moth incidence in the diet of bats using echolocation frequencies > 60 kHz was gradual, but the increase of moth in diets of bats that echolocate < 20 kHz was more immediate (Fig. 6.5A). Similarly, audiograms of moths show that their hearing sensitivity decreases gradually with increasing frequency, whereas their hearing sensitivity is cut-off more abruptly at low frequencies (Fenton & Fullard 1979, Fulllard 1988, Rydell, Jones & Waters 1995). Moths cannot distinguish accurately between different frequencies of sound (Waters 2003). Consequently, hearing sensitivity of moths at low frequencies is constrained to limit the number of 'false positives' that would be triggered by the abundant sources of low frequency sound in the environment, such as cricket and frog calls (Waters 1995). Alternatively, low frequency hearing sensitivity may be constrained by the small body size of moths, given the large volume already occupied by the auditory apparatus and the limit this place on the size of the tympana (Waters 2003). Thus, selection favouring increased moth hearing sensitivity at low frequencies is probably weak. Consequently, moths may be particularly vulnerable to predation from bats echolocating at low frequencies such as *T. aegyptiaca*.

At the same time, the auditory selective pressure from bat predation may have favoured increased moth hearing sensitivity at high rather than low frequencies. In Africa, insectivorous bat ensembles are more diverse in terms of echolocation frequencies than ensembles of temperate North America (Fullard 1990). Specifically, high duty-cycle echolocating bats that emit high frequency calls such as rhinolophids and hipposiderids are relatively common in ensembles (Fullard 1982, 1987, Findley & Black 1983, Aldridge& Rautenbach 1987, Jacobs 2000, Chapter 4). In contrast, with increasing latitude bats that emit low echolocation frequencies become relatively less common (Fullard 1982, 1987, Findley & Black 1983, Aldridge & Rautenbach 1987, McDonald, Rautenbach & Nell 1990, Fenton et al. 1996, Schoeman & Jacobs 2003, Chapter 4). Thus, bats that emit echolocation frequencies > 60 kHz, frequently form the most significant component of the total selection pressure acting on the hearing sensitivities of African moths (Fullard 1990).

A consideration of these results and those of Bogdanowicz, Fenton & Daleszczyk (1999), Jacobs (2000), and Schoeman & Jacobs (2003) suggests that echolocation is the major constraint on the dietary niche of coexisting insectivorous bats. The constraining influence of size and wing morphology (Aldridge & Rautenbach 1987, Norberg & Rayner 1987) thus appears to be mediated by the constraints of echolocation strategies.

CONCLUSIONS

Evidence for competition was only found in instances of high species richness and then only in the form of a reduction in the variance associated with dietary overlap, not in dietary overlap itself. Evidence for coevolution in the form of the AFH, on the other hand, was more ubiquitous. It thus appears that where bat diversity was low, prey defences exerted the major influence on bat trophic structure. However, where species richness was high (especially if species were closely related and ecologically similar) competition had also exerted some, albeit limited, influence.

Chapter 7

PATTERNS OF SPECIES COMPOSITION DO NOT SUPPORT COMPETITION HYPOTHESES

INTRODUCTION

There are assembly rules that predict the presence or absence of particular species in ensembles, irrespective of the phenotypic and trophic niches of the species involved. I used null models based on such assembly rules to investigate the influence of the biotic filter, competition, on patterns of species composition in ensembles and functional groups.

COMPETITION BETWEEN SPECIES

The influence of competition on the structure of species composition can be tested using models that simulate Diamond's assembly rules. Diamond's (1975) study of the coexisting bird species of the Bismarck Archipelago popularized the idea of using "assembly rules" based on competitive interactions between species to interpret species composition patterns. Consequently, these assembly rules have been at the center of intense theoretical and statistical scrutiny (Gotelli & Graves 1996). Diamond proposed the following seven rules through which species composition is structured by interspecific competition in ensembles.

(i) only certain combinations of related species can coexist in nature;
(ii) permissible combinations prevent invasions from species that would transform them into forbidden combinations;
(iii) combinations stable on large or species-rich islands may be unstable on small or species-poor islands;
(iv) combinations on small or species-poor islands may resist invaders that would be incorporated on large and species-rich islands;
(v) some species combinations never exist,
(vi) some pairs of species may form unstable combinations by themselves but form part of a larger combination that is stable; and
(vii) combinations composed entirely of stable sub-combinations may themselves be unstable.

Species composition patterns can be investigated using Q-mode and R-mode analyses (Gotelli & Graves 1996). The Q-mode of analysis assesses how similar ensembles or guilds are with respect to the species they contain, and has its roots in biogeographic studies of faunal similarities (McCoy & Heck 1987). Many different indices such as Jaccards's (1908) or Simpson's (1960) have been used to quantify ensemble or guild similarity (Jackson, Somers & Harvey 1989). However, the Q-mode analysis should be used as a biogeographic tool to group ensembles or guilds on the basis of similarity of species composition, not to infer species interactions on the basis of similarity (Gotelli & Graves 1996). If the question under investigation involves the influence of competition *per se* on species composition patterns, the R-mode analysis is more appropriate (Gotelli & Graves 1996). The R-mode of analysis assesses how similar species combinations are in sets of ensembles or guilds.

Powerful R-mode null model analyses of species composition patterns have been developed during the last two decades (Wilson 1987, Manly 1991, Stone & Roberts 1990, 1992, Gotelli & Graves 1996, Gotelli, Buckley & Wiens 1997, Gotelli 2000). However, these advances are also reflected in the wide range of indices and algorithms available to researchers to simulate species composition patterns. For example, the standard Co-occurrence module of Ecosim null model software (version 7.7, Gotelli & Entsminger 2004) has four indices of species combinations and nine simulation algorithms, totaling 36 randomization procedures. To simplify matters, therefore, Gotelli (2000) conducted a series of trials to investigate the probability of Type 1 (false positives hence incorrectly rejecting the null hypothesis) and Type 2 (false negatives hence incorrectly accepting the null hypothesis) errors using these 36 randomization procedures. Three indices, C-score, number of species combinations, and V-ratio, when combined with an appropriate simulation algorithm, consistently performed well, i.e. there was a low risk of Type 1 or Type 2 error.

The C-score (Stone & Roberts 1990) and number of species combinations (Pielou & Pielou 1968) test different predictions of Diamond's assembly rules (Feeley 2003). The number of species combinations index tests Diamond's first and second assembly rules: there should be significantly fewer unique species-pair combinations among ensembles than expected by the null model. The C-score index tests Diamond's fifth assembly rule: there should be significantly more species-pair combinations among ensembles that never co-occur (also called checkerboard pairs) than expected by chance, if competition structured species composition.

In contrast to the indices testing Diamond's assembly rules, the V-ratio (Schluter 1984) provides an index of the variance of species richness among sites (Gotelli & Entsminger 2004), and tests the theory of ecological limiting similarity (MacArthur & Levins 1967). The V-ratio tests the prediction that the variance of species richness among sites should be significantly small if competition structured species composition (Wilson, Gitay & Agnew 1987, Gotelli & Entsminger 2004).

COMPETITION BETWEEN GROUPS OF SPECIES

Competition may structure ensembles at the level of species groups, defined as species utilizing resources in a similar way (Fox 1989, Wilson 1989, Gotelli & Graves 1993). Assembly rules are then defined as restrictions on the presence of species that are based on the presence of one or several other species, or types of species, belonging to the same group (Graves & Gotelli 1993). For example, using the indices described above, the Guild Proportionality hypothesis predicts similar non-random patterns of species groups among sites rather than of individual species among sites (Wilson 1989, Gotelli and Graves 1993, 1996, Gotelli & Entsminger 2004). Fox's Favoured States model (Fox 1987) is a stricter form of the Guild Proportionality hypothesis where the composition of species groups is predicted to be nonrandom across and within ensembles. Ensembles are considered to be in "favoured states" if their species groups are as equally represented as possible given the number of species present. If competition influenced species group structure, there should more favoured states than the number expected by the null model (Fox 1987).

In this chapter, the influence of competition on species composition of seven insectivorous bat ensembles is investigated using R-type null models based on predictions from Diamond's assembly rules and the niche limitation hypothesis. I also investigate the influence of competition at the species group level based on predictions from Guild Proportionality and Fox's Favoured States hypotheses. Species composition is quantified as: (i) the number of checkerboard pairs (C-score, Stone and Roberts 1990), (ii) the number of species combinations (Pielou and Pielou 1968), and (iii) the variance of species richness (V-ratio, Schluter 1984). Observed scores are compared with expected (chance) scores generated by appropriate randomization procedures of the original data matrices.

METHODS

Presence-absence data of the bat species caught in seven ensembles of southern Africa were collected between 2001 and 2004 (Chapter 4). The sites are described in detail in Chapter 3. To ensure relatively accurate species inventories, ensembles were surveyed during wet and dry seasons using a combination of techniques. In addition, species inventories of ensembles were verified with statistical methods (Chapter 4).

Using the census data, I created one presence-absence matrix of all the insectivorous bat species caught at ensembles, and three separate matrices of the species classified to functional groups, open-air, clutter-edge, and clutter foragers (Chapter 3, Table 5.1). In addition to the functional groups, I also classified bat species to two groups based on their roosting habits and distributional range (Arita 1997).

SPECIES GROUPS

Roost group

I classified bat species to three roost groups based on their roosting requirements, based on the physical characteristics and distribution of roosts, with special emphasis on their use of human built structures. Associations between bats and their roosts range from obligatory to opportunistic, with selection of particular roosts often dependent on availability (Kunz & Lumden 2004). Bats that primarily roost in rock crevices, caves or abandoned mines during the day were allotted to the "Cave" class. These roosts offer the advantages of relative permanency, thermal stability, and protection from climatic extremes (Kunz 1982). However, they may be patchy in distribution. Bats with more flexible roosting habits, i.e. species that use mines, but also other human-built structures such as bridges, houses, or tunnels, were allotted to the "General" class. For example, *Rhinolophus clivosus* uses caves and mines as roosts, but also tunnels, road culverts, and roofs of houses and barns (pers. observation), hence the species was classified under the General class. Similarly, *Tadarida aegyptiaca* was classified under this class because it roosts in rock crevices and frequently in roofs of houses. These human-built roosts may offer similar advantages as caves and rock crevices, but offer less thermal stability and protection from climatic extremes. However, they are more available at an increasing rate. Bat species able to utilize such structures may negatively influence resident species not able to utilize them (Arlettaz, Godat & Meyer 2002). Bats that do not utilize caves, mines, or other human built structures as roosts were allotted to the "Non-Cave" class. More than half of all bat species use trees or plants exclusively or opportunistically as roosts (Kunz & Lumsden 2004). Although non-cave roosts such as spaces beneath bark and foliage are more ephemeral and subject to environmental change, they are often relatively abundant (Kunz 1982). Data on the roosting requirements of the bats were based on personal observation and published records (Skinner & Smithers 1990, Friedmann & Daly 2004, Jacobs, Schoeman & Barclay 2005).

Distribution range group

I also classified bats into three distribution range groups based on their distribution range. I quantified distribution range using a point scale, because this gives a better resolution than a simple binary classification of widespread versus restricted (Arita 1997). Based on distribution maps from Skinner & Smithers (1990) and Friedmann & Daly (2004), bats scored points if their distribution ranges overlapped the following biomes: (i) fynbos (1 point), (ii) forest (1 point), (iii) Nama-Karoo (1 point), (vi) Succulent Karoo (1 point), (v) Desert (1 point), (vi) grassland (1 point), and (vii) savanna (1 - 3 points). In the savanna biome, bats scored three points if distribution range covered most of the savanna biome of the African continent, two points if distribution range covered approximately 50% of the savanna biome, and 1 point if distribution records were rare and scattered. Based on total points scored, species were allotted to three distribution range groups: short-range (1 to 3 points), medium-range (4 to 6 points), and long-range (> 6 points).

STATISTICAL ANALYSES

Diamond's assembly rules

Using the Co-occurrence module of Ecosim software (version 7.7, Gotelli & Entsminger 2004), I calculated the number of checkerboard units (C-score) for each species pair as:

$$\text{C-score} = (R_i - S)\,(R_j - S),$$

where, R_i and R_j are the number of occurrences for species *i* and *j* and S is the number of co-occurrences of species *i* with *j* (Gotelli & Entsminger 2004).

A checkerboard pair is any submatrix of the form:

$$\begin{matrix}10\\01\end{matrix}$$

$$\text{or,}\ \begin{matrix}01\\10\end{matrix}$$

where, 0 represents absence of a species, and 1 presence of a species in an ensemble or functional group. A large C-score indicated that there were fewer checkerboard pairs than the number expected by chance (Stone and Roberts 1990, Gotelli & Entsminger 2004).

I calculated the number of species combinations index as the number of unique species combinations that were present in ensembles (Gotelli & Entsminger 2004). For an ensemble or functional group of *n* species, there are 2^n possible species combinations, including the combination of no species present (Pielou & Pielou 1968). Because the number of sites (columns) was less than the number of species, there was an upper bound to the observed and expected number of species combinations that could be found in matrices (Gotelli & Entsminger 2004).

I used Monte Carlo randomizations of the original presence-absence matrix to calculate the probability that the observed values of the two indices were significantly different from those expected by chance. The Sim9 algorithm (Gotelli & Entsminger 2004) was used to randomize the original matrix, i.e. row and column totals were fixed. An earlier version of this simulation procedure (Connor & Simberloff 1979) was widely criticized. In particular, so much structure is built into the null model that little ever differs from it (Diamond and Gilpin 1982).

However, the algorithm used in Ecosim null model software has a good Type 1 error rate, and is powerful in detecting non-random patterns even in noisy data sets, especially when used with the C-score (Gotelli & Entsminger 2004). First, original matrices were randomized 5000 times to remove any pattern in the data (Feeley 2003, Gotelli & Entsminger 2004). Expected indices were calculated for 1000 simulations of ensemble or functional group matrices. If the observed values of the C-score and the number of species combinations were significantly different from 95% of the expected values, I concluded that non-random patterns existed in the original data (Manly 1991).

Niche limitation hypothesis

Using the Co-occurrence module of Ecosim software (version 7.7, Gotelli & Entsminger 2004), I calculated the V-ratio as the ratio of the variance of the column sums to the sum of the row variances. In other words, the V-ratio was the ratio of the variance in species richness to the sum of the variance in species occurrence (Gotelli & Entsminger 2004). If the species were distributed randomly and the probability of them occurring at a site was equal, the V-ratio was 1. If species occurred together at few sites, i.e. there was a strong negative covariance between species pairs, the V-ratio was < 1. Conversely, if species occurred together at many sites, i.e. there was a strong positive covariance, the V-ratio was > 1.

I used Monte Carlo randomizations of the original presence-absence matrix to calculate the probability that the observed V-ratio was significantly different from expected by chance. The Sim8 algorithm (Gotelli & Entsminger 2004) was used to randomize the original matrix. In this simulation procedure, rows were filled randomly, but the likelihood of a particular row being "hit" was proportional to the row total. Similarly, columns were filled randomly, but the probability of a particular column being "hit" was proportional to the column total (Gotelli & Entsminger 2004). Hence, the rank order of species selected in the null model depended on the rank order of the species in the original matrix. First, original matrices were randomized 5000 times to remove any pattern in the data (Feeley 2003, Gotelli & Entsminger 2004). Expected V-ratios were calculated for 1000 simulations of ensemble or functional group matrices. If the observed values were significantly different from 95% of the values expected by the null model, I concluded that non-random patterns existed in the original data (Manly 1991).

Guild Proportionality

Using the Guild module of Ecosim software (version 7.7, Gotelli & Entsminger 2004), I calculated the C-score, number of species combination, and V-ratio indices (see above) for functional, roosting and distribution range groups.

I used Monte Carlo randomizations of the original presence-absence matrix to calculate the probability that the observed values of the C-score, number of species combinations, and V-ratio indices were significantly different from those expected by chance. The Sim9 algorithm was used for the first two indices, and the Sim8 algorithm for the latter index, to randomize matrices (see above, Gotelli & Entsminger 2004). Expected values of indices were calculated for 1000 simulations of ensemble or functional group matrices. If the observed values were different from 95% of the values expected by the null model, I concluded that non-random patterns existed in the original data (Manly 1991).

Fox's Favoured States

Using the Guild module of Ecosim software (version 7.7, Gotelli & Entsminger 2004), I calculated the number of favoured states of the species groups among sites.

I used Monte Carlo randomizations of the original presence-absence matrix to calculate the probability that the observed number of favoured states was significantly greater than expected by chance. Matrices were randomized by reshuffling functional group or guild labels while keeping row-column totals fixed (Gotelli & Entsminger 2004). Expected number of favoured states were calculated for 1000 simulations of ensemble or functional group matrices. If the observed number of favoured states were more than 95% of the expected values, I concluded that non-random patterns existed in the original data (Manly 1991).

In addition, experiment-wise error of the significance tests (i.e. *p* values) was held constant at five percent for ensembles separately from functional groups at each site by application of Bonferroni sequential adjustments (Rice 1989).

RESULTS

SPECIES COMPOSITION OF ENSEMBLES AND SPECIES GROUPS

Twenty-seven insectivorous bat species were recorded in the seven ensembles. Rarefaction and species richness estimators indicated that species inventories of the fynbos, forest, and savanna ensembles were complete (Chapter 4). The vespertilionid, *Neoromicia capensis,* the miniopterid, *Miniopterus natalensis*, the molossid, *Tadarida aegyptiaca*, and the rhinolophid, *Rhinolophus clivosus*, were the only species represented in each of the seven ensembles. These four species represented the three functional groups: clutter-edge (*N. capensis* and *M. natalensis*), clutter (*R. clivosus*), and open-air (*T. aegyptiaca*).

Frequency distribution of species in the different classes of the functional and roost groups (Table 7.1) differed significantly among the ensembles (Chi-square; average observed = 2.4, average simulation = 19.9, $p < 0.001$, and average observed = 9.4, average simulation = 20.1,

$p < 0.01$, respectively; Standard Module, Ecosim version 7.7, Gotelli & Entsminger 2004). However, the frequency distribution of species in classes of the distribution range group did not differ significantly among ensembles (Chi square; average observed = 15.8, average simulation = 20.1, $p = 0.27$; Table 7.1). Species of functional, roost and distribution range groups were represented at all ensembles. Except at the De Hoop, Die Hel, and Koegelbeen ensembles where species of the non-cave roost group were absent (Table 7.1).

NON-RANDOM COMPOSITION PATTERNS OF ENSEMBLES

Null model analyses of the presence-absence matrix of bat species captured in ensembles found some support for Diamond's assembly rules. The observed C-score was significantly higher than expected by the null model (Table 7.2). However, when the data matrix was reanalyzed without the species-rich sub-tropical savanna ensemble (Sudwala), the observed C-score was not significantly greater than the expected score (0.88 and 0.84, respectively; $p = 0.16$). Furthermore, the number of species combinations was not significantly different from expected by chance (Table 7.2). There was also no support for the niche limitation hypothesis. In contrast to predictions, the observed V-ratio was significantly higher than expected by the null model (Table 7.2). Thus, there was a significantly strong covariance between species among ensembles. However, in all cases significant differences between observed and expected values changed to not significant after Bonferroni sequential adjustments.

No evidence was found for the hypothesis that competition structured composition of ensembles at the species group level. Observed C-score, number of species combinations, and V-ratio scores were not significantly different from scores expected by chance (Table 7.3). Similarly, the number of observed favoured states of species groups among ensembles was not significantly more than expected by the null model (Table 7.3).

NON-RANDOM COMPOSITION PATTERNS OF FUNCTIONAL GROUPS

Clutter-edge functional group

Null model analyses of the clutter-edge species matrix found no support for predictions of Diamond's assembly rules or the niche limitation hypothesis. Observed C-score, number of species combinations, and V-ratio indices were not significantly different from those expected by chance (Table 7.2).

There was also no evidence that competition structured composition at the species group level. Observed C-score, number of species combinations, and V-ratio scores were not significantly different from those expected from chance (Table 7.3). Similarly, the number of observed favoured states was not significantly more than the number expected by chance (Table 7.3).

Table 7.1 Classification of 27 insectivorous bat species to three classes of functional groups (O = open-air, CE = clutter-edge, and C = clutter feeders), roost groups (C = cave, G = general, and NC = non-cave), and distribution range groups (S = short-range, M = medium-range, and L = long-range). See text for more detail on classification principles applied.

Species	Functional group	Roost group	Distr. Range group	Ensembles						
				Algeria	Die Hel	De Hoop	Knysna	Goodhouse	Koegelbeen	Sudwala
Chaerephon pumilus	O	G	M	0	0	0	0	0	0	1
Cistugo lesueuri	CE	NC	S	1	0	0	0	0	0	0
Cistugo seabrai	CE	NC	S	0	0	0	0	1	0	0
Cloeotis percivali	C	C	S	0	0	0	0	0	0	1
Eptesicus hottentotus	CE	NC	L	1	0	0	0	1	0	0
Hipposideros caffer	C	C	L	0	0	0	0	1	0	1
Laephotus wintoni	CE	NC	S	1	0	0	0	0	0	0
Miniopterus fraterculus	CE	C	S	0	1	0	1	0	0	0
Miniopterus natalensis	CE	C	L	1	1	1	1	1	1	1
Mops condylurus	O	G	M	0	0	0	0	0	0	1
Myotis tricolor	CE	C	M	1	1	1	0	0	0	1
Neoromicia africanus	CE	NC	L	0	0	0	0	0	0	1
Neoromicia capensis	CE	G	L	1	1	1	1	1	1	1
Neoromicia zuluensis	CE	NC	S	0	0	0	0	0	0	1
Nycteris thebaica	C	G	L	1	0	1	0	1	1	1
Pipistrellus anchietai	CE	NC	S	0	0	0	0	0	0	1
Pipistrellus hesperidus	CE	NC	S	0	0	0	1	0	0	0
Rhinolophus blasii	C	C	M	0	0	0	0	0	0	1
Rhinolophus capensis	C	C	S	1	1	1	1	0	0	0
Rhinolophus clivosus	C	G	L	1	1	1	1	1	1	1
Rhinolophus darlingi	C	C	M	0	0	0	0	1	1	1
Rhinolophus denti	C	C	S	0	0	0	0	0	1	0
Rhinolophus hildebrandti	C	C	L	0	0	0	0	0	0	1
Rhinolophus simulator	C	C	L	0	0	0	0	0	0	1
Sauromys petrophilus	O	NC	M	1	0	0	0	1	0	0
Scotophilus dinganii	CE	G	M	0	0	0	0	0	0	1
Tadarida aegyptiaca	O	G	L	1	1	1	1	1	1	1
Taphozous mauritianus	O	G	L	0	0	0	0	0	0	1

Table 7.2 Observed and expected C-score, number of species combination, and V-ratio indices of ensembles and functional groups. Indices with significant different ($p < 0.05$) scores from those expected by the null model are in bold print.

	Diamond's Assembly Rules				Niche limitation	
	C-score		No. spp comb.		V-ratio	
Matrix	Obs	Exp	Obs	Exp	Obs	Exp
Ensemble	0.84	**0.74**	7	7	4.5	**2.2**
Clutter-edge	0.83	0.81	7	7	1.4	1
Clutter	1.13	0.95	6	6.7	2.1	**1**
Open-air	0.6	0.44	3	3.8	1.8	0.9

Note: Not significant after Bonferroni sequential adjustments (Rice 1989)

Table 7.3 Observed and expected C-score, number of species combination, V-ratio, and number of favoured states indices of functional groups (FG) and guilds among ensembles and functional groups. The first three indices tested predictions of the Guild Proportionality hypothesis, and the fourth index, predictions of the Fox's Favoured States (FFS) hypothesis. Indices with significant different ($p < 0.05$) scores from scores expected by the null model are in bold print.

		Guild Proportionality						FFS	
		C-score		No. Spp comb		V-ratio		Fav states	
FG and spp group	Matrix	Obs	Exp	Obs	Exp	Obs	Exp	Obs	Exp
FG	Ensemble	0.84	0.87	5	5.1	1.8	1.8	0	1.4
Roost-group	Ensemble	0.86	0.86	4.7	5.4	1.6	1.9	4.3	1.8
	Clutter-edge	0.82	0.8	4	3.4	0.76	0.75	4	2.5
	Clutter	0.89	1.1	4	4	1.3	1.3	7	**2.4**
	Open	0	0.5	1.5	1.8	1	0.5	2	2.1
Distr. range-group	Ensemble	0.84	0.86	5.7	5.3	1.8	1.9	0	1.4
	Clutter-edge	0.49	0.82	3.3	3.4	0.66	0.8	2	2.9
	Clutter	0.57	1.1	3.3	3.1	1	0.98	3	3.2
	Open	1	0.5	2	1.8	0.5	0.5	3	2

Note: Not significant after Bonferroni sequential adjustments (Rice 1989)

Clutter functional group

Null model analyses of the clutter species matrix found no support for predictions of Diamond's assembly rules. Observed C-score and number of species combinations were not significantly different from expected values (Table 7.2). In contrast to predictions from the niche limitation hypothesis, the observed V-ratio was significantly high (Table 7.2).

There was no evidence that competition structured composition of ensembles at the species group level. Observed C-score, number of species combinations, and V-ratio values were not significantly different from those expected by chance (Table 7.3). On the other hand, the number of favoured states in the roost group was significantly more than expected by the null model (Table 7.3). However, the roost group was represented by two classes only: Cave and General bats, and the test not significant after sequential Bonferroni adjustments.

Open-air functional group

Null model analyses of the open-air species matrix found no support for predictions of Diamond's assembly rules or the niche limitation hypothesis. Observed C-score, number of species combinations, and V-ratio indices were not significantly different from scores expected by chance (Table 7.2).

There was no evidence that competition structured ensembles at the species group level. Observed C-score, number of species combinations, V-ratio and number of favoured states were not significantly different from those expected by chance (Table 7.3).

DISCUSSION

DIAMOND'S ASSEMBLY RULES

I found little support for Diamond's (1975) assembly rules. If Diamond's assembly rules are valid, ensembles structured by competition should exhibit fewer species combinations and higher C-scores than expected by chance (Gotelli & McCabe 2002). Only the C-score was significantly large, thus fewer unique species pairs co-occurred in ensembles than the number expected by the null model. However, forces other than interspecific competition may have produced these non-random species composition patterns. For example, habitat heterogeneity and differences in habitat affinities of species can create checkerboard patterns similar to those produced by interspecific competition (Gotelli & McCabe 2002). When I tested this hypothesis by excluding the sub-tropical savanna ensemble from the data matrix, the observed C-score for the fynbos, forest, and Nama-Karoo ensembles was not significantly different from expected by chance.

I also found no evidence for the prediction that competitive patterns should be more apparent among species of functional groups, i.e. among species with similar resource requirements (Diamond & Gilpin 1982). Similarly, Feeley (2003) found some support for Diamond's assembly rules in species composition patterns of the forest-interior bird species of a Scandinavian archipelago, but no support was found in the species composition patterns of dietary guilds (insectivores/omnivores and exclusive insectivores) of the forest-interior bird assemblage.

NICHE LIMITATION HYPOTHESIS

I found no support for the niche limitation hypothesis. Contrary to predictions, the variance of species richness among ensembles was significantly higher than expected by the null model. If a limit to niche similarity affects the number of coexisting species, the variance in species richness among ensembles should be significantly low (Wilson, Gitay & Agnew 1987, Gotelli & Entsminger 2004). High variance of species richness indicates a strong positive covariance between species among ensembles (Gotelli & Entsminger 2004). This was linked to the four species recorded at every ensemble: the vespertilionid, *Neoromicia capensis*, the miniopterid, *Miniopterus natalensis*, the molossid, *Tadarida aegyptiaca*, and the rhinolophid, *Rhinolophus clivosus* (Chapter 4). Because the niche requirements of bat families are ecologically very different from each other (e.g. the four species belonged to three functional feeding groups), it is unlikely that these common species were affected by strong competitive interactions between them.

GUILD PROPORTIONALITY AND FOX'S FAVOURED STATES

Competition may structure ensembles at the species group level rather than at the individual species level (Fox 1989, Wilson 1989, Wilson & Whitaker 1995). However, I found no evidence that strongly supports this hypothesis. Composition patterns of species groups were not different from patterns expected by chance. Similarly, there was little support for Fox's Favoured State model (Fox 1987). The number of favoured states was in general not significantly more than the number expected by chance. However, the strict demands of the Fox's Favoured States model may be unrealistic for most data sets (Feeley 2003).

Researchers cannot be sure in advance on which species groups competitive processes are most likely operating on (Wilson & Roxburgh 1994, Wilson & Whitaker 1995). Thus, I may have found stronger support for the Guild Proportionality or Fox's Favoured States hypotheses using an alternative classification system (Mikkelson 1993). For example, Fox & Brown (1993) used a taxonomic classification system (genus) of rodent ensembles and found strong support for the Fox's Favoured State model. However, it was not possible to analyse composition patterns based on a taxonomic classification, because species group null models require at least two species allotted to each class, but only three genera comprised more than one species in this study (*Rhinolophus*, *Miniopterus*, *Neoromicia*).

Classes of species groups were represented by bat species at every ensemble, except the Non-cave roost group. Non-cave species were not recorded at two fynbos ensembles (De Hoop and Die Hel), and one Nama-Karoo ensemble (Koegelbeen). Vegetation in the fynbos can be characterised as hard-leafed, evergreen, and fire-prone shrubs that thrive on the Cape Floristic Kingdom's rocky or sandy nutrient-poor soils (Cowling, Richardson & Mustard 1997). Similarly, vegetation of the Nama-Karoo biome consists primarily of structurally sparse arid grassland and dwarf shrubs (Palmer & Hoffman 1997). Consequently, non-cave roosts such as tree cavities and spaces beneath bark may be relatively scarce in the fynbos and Nama-Karoo biomes. Furthermore, distribution range of southern African bat species such as *Neoromicia africanus* and *Myotis bocagei* that roost in the furled up leaves of wild bananas (*Musa* or *Strelitzia* spp.) may primarily depend on the distribution range of their tropical plant hosts (Kunz & Lumden 2004). Thus, abiotic factors such as roost availability may be a key factor that structured species composition of ensembles.

Three of the four common species (see above) were classified to the General roost class. The fourth, *Miniopterus natalensis*, was classified to the Cave class, but this species may also use roosts such as road culverts (pers. comm. S. Stoffberg). These human built structures offer less thermal stability and protection from climatic extremes than caves, but may be more abundant. Thus, the relative flexible roosting habits of the common species may have assisted them to occur in ensembles across the southern African landscape.

Indeed, these four species belonged to the long-range class of the distribution range group. If distributional range is a measure of the dispersal ability of a species (Graves & Gotelli 1983), then a good dispersal ability may be another reason why these four species were present at every ensemble. However, area of distribution and local abundance are correlated in most animals (Gaston & Blackburn 2000), including bats (Arita 1993). Thus, if the four bat species were more abundant than other bats on a regional scale, then their presence at local ensembles may have been due to proportional sampling from the regional source pool (Willig, Patterson, and Stevens 2004). Alternatively, widespread species might have large distributional ranges because they are superior competitors, able to displace other species in changing landscapes (Arlettaz, Wrazen & Burnett 2000).

CONCLUSIONS

Little evidence was found that competition influenced species composition patterns of ensembles and functional groups based on the predictions of Diamond's Assembly Rules or the niche limitation hypothesis. I also found little evidence that competition influenced composition at the species group level. No support was found for the predictions of the Guild Proportionality hypothesis, and very limited support for Fox's Favoured States model. Basic species composition structure of ensembles consisted of four bat species representing four families. These species were probably dissimilar enough ecologically to avoid competitive interactions between them. Large-scale abiotic factors such as roost availability or distribution range may have had a strong influence on species composition patterns of ensembles. A combination of traits, for example excellent dispersal ability and/or flexible roosting habitats may have allowed some bats to pass through these abiotic filters and to become established in their respective ensembles.

Chapter 8

GENERAL SUMMARY AND CONCLUSIONS

Biotic filters are more likely to structure communities of stable systems than unstable systems (Lawton 2000, Jackson, Peres-Neto & Olden 2001). Specifically, biotic filters rather than abiotic filters should influence the community structure of insectivorous bats with life histories characterized by low fecundity, low predation risk, long life expectancy, and stable populations (Findley 1993). As hypothesised, competition and coevolution filters strongly influenced parameters that define bat community structure. There is evidence that both biotic filters influenced the phenotypic and trophic niche structures of communities, but in different ways and at specific scales. However, patterns of species composition were not different from patterns expected by chance (Chapter 7).

THE INFLUENCE OF COEVOLUTION

I found strong evidence for coevolution influencing the trophic niche structure - based on the Allotonic Frequency Hypothesis (Chapter 6). Specifically, peak echolocation frequency was significantly correlated with the proportion of moths in the diet of sympatric bats, and was the best overall predictor of diet. This is consistent with evidence that echolocation is the major constraint on the dietary niche of bats (Bogdanowicz, Fenton & Daleszczyk 1999, Jacobs 2000, Schoeman & Jacobs 2003). Furthermore, consistent with predictions from coevolution theory, phenotypic patterns of echolocation parameters among sympatric bat species were more similar than expected by chance in four ensembles (Chapter 5). The strong relationship between echolocation and diet is probably because, if bats and their insect prey coevolved, there would have been stronger and more direct interaction, over evolutionary time, between insect hearing and bat echolocation than between insect hearing and the body size or wing morphology of bats. Bats and insects have coexisted for at least 50 million years, and the radiation of bats during the early Tertiary period probably resulted in strong selective pressure favouring insects that can detect the echolocation calls of bats and take evasive action (Waters 2000, Jones & Rydell 2004). Insects evolve faster than bats because they have shorter generation times and possess a diverse range of morphological, behavioural and physiological defences against bats (Waters 2000, Jones & Rydell 2004). Thus, insect defence against bat predation is probably one of the most important factors determining what coexisting bats are able to catch and eat, and therefore, how their trophic and phenotypic niches are structured. For this reason, considering the influence of insect defences is essential for a proper understanding of the community ecology of insectivorous bats at a local and regional scale.

THE INFLUENCE OF COMPETITION

Interspecific competition appears to influence the trophic structure and to a lesser extent the phenotypic niche structure of relatively species-rich bat communities, comprising many closely related, and ecologically and morphologically similar species (Chapters 5 and 6). A large number of species with similar resource requirements must partition the resources of their environment - if the environment is assumed to be stable and its resources limited - until interspecific competition becomes, overall, less significant than intraspecific competition (Hutchinson 1957, Giller 1984, Begon, Harper & Townsend 1990). Generally, competition did not lead to larger differences between niches of bat species than expected from chance. Instead, differences between niches of coexisting species were less variable than expected from chance. This may be because of the exclusion and/or displacement of bats that exceed the limit of similarity (MacArthur and Levins 1967), but my data do not test between these hypotheses.

Nevertheless, stochastic (abiotic) factors are less likely to override competitive interactions if the size of the community is relatively large (Orrock & Fletcher 2005). When the community size shrinks, superior competitors are less likely to experience a positive growth rate when rare, making them highly susceptible to loss from the community due to stochastic forces (Orrock & Fletcher 2005). Thus, I found evidence for interspecific competition influencing the structure of relatively species rich bat communities such as the Sudwala ensemble in the savanna biome or the Algeria ensemble in the Cape Floristic Kingdom (Chapters 4, 5 and 6).

What is more difficult to understand, however, is why body size patterns at a local scale showed evidence of having been influenced by competition, irrespective of the ensemble's species richness (Chapter 5). Body size is a useful predictor of interspecific differences in metabolic range, energy use, distribution range, population density, and growth rate of species, and therefore expected to exhibit deterministic patterns if competition influences community structure (Brown, Marquet & Taper 1993, Brown 1995, Stevens, Willig & Strauss 2006). However, body size is also significantly correlated with wing morphology and echolocation of insectivorous bat species (Jones 1994, 1996, Bogdanowicz, Fenton & Daleszczyk 1999, Chapter 5), and combined, they are part of the same adaptive complex (Fenton 1990, Arita & Fenton 1997). Indeed, it is unlikely that competition influenced body size *per se*. It is more likely that competition influenced a combination of flight, echolocation, and/or life history parameters that are significantly correlated with body size. Moreover, it is not certain that competition *per se* was responsible for the nonrandom spacing of body size in ensembles. Abiotic filters may have played significant roles in producing these body size patterns (Brown & Nicoletto 1991, Brown, Marquet & Taper 1993, Chapter 5).

THE INFLUENCE OF ABIOTIC FILTERS

Contrary to what I hypothesized, there was some evidence for abiotic filters driving bat community structure. Firstly, the non-random patterns of body size at a local scale may have been the result of abiotic processes operating at a regional scale, in particular, the higher extinction risk of small-bodied and large-bodied bat species with small distribution ranges (Chapter 5). Secondly, non-random niche patterns may have been - directly or indirectly - the result of the severe constraints imposed by the physics of flight and echolocation enabling insectivorous bats to capture small, volant insect prey (Chapters 5 and 6). Thirdly, the distribution ranges of certain southern African bat species may depend primarily on the flexibility of their roosting habits, or the distribution range of their tropical plant hosts (Chapter 7). Fourthly, the low insect diversity and abundance of the Cape Floristic Kingdom (Gilliomee 2003) may restrict insectivorous bat species richness at a local and regional scale in this region (Chapter 4). Jointly these factors may have resulted in low numbers of species in the Cape Floristic Kingdom and, more importantly, low numbers of similar species, thus precluding competition. However, these abiotic processes are not mutually exclusive, and may operate independently, or interact with biotic filters, at different scales (Angermeier & Winston 1998).

CONCLUSIONS

I investigated the relative influence of biotic filters on various parameters that define bat community structure, based on predictions from competition and coevolution hypotheses. Each of the competing hypotheses was considered from a number of different perspectives to provide multiple opportunities from which to uncover the mechanism that could result in non-random patterns of community structure. My results show that the phenotypic and trophic community structure of insectivorous bats at a local scale exhibit non-random patterns consistent with competition and coevolution hypotheses. Except for an even body size distribution, non-random patterns are not ubiquitous across ensembles. This is linked to multiple causations of competition and coevolution filters operating at a local scale (Fig. 8.1).

There is evidence that interspecific competitive interactions influence body size distribution in ensembles. In addition, competition also drives local echolocation and dietary patterns if species richness or abundance is relatively high. (Fig. 8.1). At the same time, coevolution filters - mediated by prey defence - strongly influence dietary niche patterns, and to a lesser degree, echolocation patterns (Fig. 8.1). Thus, the non-random phenotypic and trophic patterns of ensembles across southern Africa reflect competition and coevolution filters operating in tandem, or separately, at a local scale.

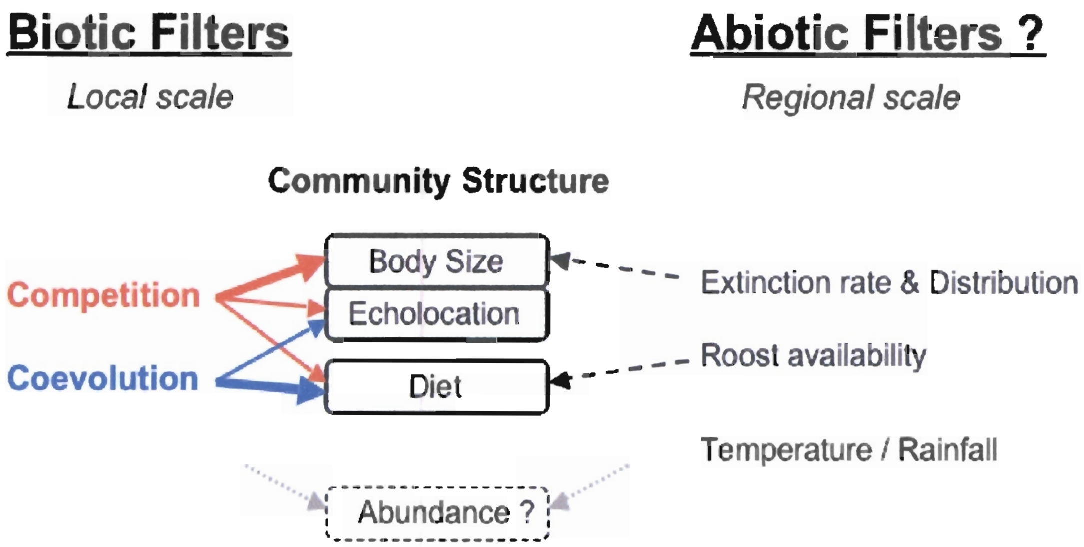

Fig. 8.1 Shows how biotic filters interact at a local scale to influence parameters that define community structure of insectivorous bat species in southern Africa. Competitive interactions strongly influence body size, and to a lesser degree echolocation and diet. Coevolution mediated by prey defence strongly influences diet, and to a lesser degree echolocation (solid arrows, thickness denotes strength of filter). However, abiotic filters (e.g. extinction rate and roost availability) may operate independently or jointly at a regional scale, and/or interact with biotic filters on a local scale to influence phenotypic and trophic niche structure (broken black arrows). In addition, biotic filters may operate variably along abiotic gradients such as temperature or rainfall. Biotic and abiotic filters may also influence community structure parameters that were not investigated in this study, such as abundance (broken box line and arrows).

To complicate matters, however, abiotic filters mediated by geographic distribution range of small and large-bodied bat species and their extinction risk, probably interact at regional and continental scales to also influence the phenotypic structure, in particular body size, of ensembles (Fig. 8.1). Similarly, abiotic filters such as roost availability may alter the trophic structure of sympatric bat species. For example, a quarter million *Miniopterus natalensis* bats roost in one cave at De Hoop during the summer months, consuming approximately 100 tons of insects (McDonald, Rautenbach & Nell 1990, Taylor 2000). Thus, resource utilization and trophic niche patterns of the other sympatric bat species are probably severely affected. Moreover, data characterizing insectivorous bat ensembles come from locations across southern Africa. These ensembles not only represent different biomes, but lie along extensive gradients of temperature, rainfall and productivity. The degree of variability in non-random patterns of community structure may reflect the tendency of biotic filters to structure insectivorous bat ensembles along any or all of these environmental gradients. Future research should decouple the relative influence of abiotic filters from biotic filters on patterns of phenotypic and trophic niches, and how these filters operate at multiple spatial scales and environmental gradients.

Biotic and/or abiotic filters may influence alternative parameters that define community structure (Fig. 8.1). In particular, biotic filters such as competition are density-dependent phenomenon, and may therefore have a strong effect on the abundance structure of sympatric species (Giller 1984, Begon, Harper & Townsend 1990, Lawton 2000). For example, competition may not be strong enough to drive competitors to local extinction, but cause a reduction in their abundance (Stevens and Willig 2000), called density compensation (Root 1973). Future research should test predictions from such theory on the abundance structure of southern African insectivorous bat ensembles as an additional approach for characterising the influence of interspecific competition (or other filter) on community structure.

In conclusion, the macroecological and multidimensional approach taken in this study can be a powerful tool in understanding community structure at a local scale. Furthermore, a pluralistic analytical approach is always better than relying on a single technique to tease apart the relative influence of abiotic and biotic filters on different parameters that define community structure. In this way, nonrandom patterns are revealed that may contribute significantly to future community ecology studies.

REFERENCES

Abele, L.G. (1984). Biogeography, colonization and experimental community structure of coral-associated crustaceans. In *Ecological Communities* (eds D.R. Strong, D. Simberloff, L.G. Abele & A.B. Thistle), pp. 123-137. Princeton University Press, Princeton.

Abramsky, Z. & Sellah, C. (1982) Competition and the role of habitat selection in Gerbillus allenbyi and Meriones tristrami: a removal experiment. *Ecology*, **63**, 1242-1247.

Acharya, L. & Fenton, M.B. (1999) Bat attacks and moth defensive behaviour around street lights. *Canadian Journal of zoology*, **77**, 27-33.

Aldridge, H.D.J.N. & Rautenbach, I.L. (1987) Morphology, echolocation and resource partitioning in insectivorous bats. *Journal of Animal Ecology*, **56**, 763-778.

Angermeier, P.L. & Winston, M.R. (1998) Local vs. regional influences on local diversity in stream fish communities of Virginia. *Ecology*, **79**, 911-927.

Anthony, E.L.P. (1988). Age determination in bats. In *Ecological and Behavioural Methods for the Study of Bats* (ed T.H. Kunz), pp. 47-58. Smithsonian Institution Press, Washington DC.

Appleton, B.R., McKenzie, J.A., & Christidis, L. (2004) Molecular systematics and biogeography of the bent-wing bat complex *Miniopterus schreibersii* (Kuhl, 1817) (Chiroptera: Vespertilionidae). *Molecular Phylogenetics and Evolution*, **31**, 431-439.

Arita, H.T. (1993) Rarity in Neotropical bats: correlations with phylogeny, diet, and body mass. *Ecological Applications*, **3**, 506-517.

Arita, H.T. (1997) Species composition and morphological structure of the bat fauna of Yucatan, Mexico. *Journal of Animal Ecology*, **66**, 83-97.

Arita, H.T. & Fenton, M.B. (1997) Flight and echolocation in the ecology and evolution of bats. *TREE*, **12**, 53-58.

Arita, H.T. & Figueroa, F. (1999) Geographic patterns of body-mass diversity in Mexican mammals. *Oikos*, **85**, 310-319.

Arita, H.T. & Rodriguez, P. (2004) Local-regional relationships and the geographical distribution of species. *Global Ecology and Biogeography*, **13**, 15-21.

Arlettaz, R. (1999) Habitat selection as a major resource partitioning mechanism between two sympatric sibling bat species *Myotis myotis* and *Myotis blythii*. *Journal of Animal Ecology*, **68**, 460-471.

Arlettaz, R., Godat, S., & Meyer, H. (2000) Competition for food by expanding pipistrelle bat populations (*Pipistrellus pipistrellus*) might contribute to the decline of the lesser horseshoe bats (*Rhinolophus hipposideros*). *Biological Conservation*, **93**, 55-60.

Arlettaz, R., Perrin, N., & Hausser, J. (1997) Trophic resource partitioning and competition between the two sibling bat species *Myotis myotis* and *Myotis blythii*. *Journal of Animal Ecology*, **66**, 897-911.

Barclay, R.M.R. (1985) Long- versus short-range foraging strategies of hoary (*Lasiurus cinereus*) and silver-haired (*Lasionycteris noctivagans*) bats and the consequences for prey selection. *Canadian Journal of zoology*, **63**, 2507-2515.

Barclay, R.M.R. (1994) Constraints on reproduction by flying vertebrates: energy and calcium. *American Naturalist*, **144**, 1021-1031.

Barclay, R.M.R. (1995) Does energy or calcium availability constrain reproduction by bats? *Symposia of the Zoological Society of London*, **67**, 245-258.

Barclay, R.M.R. (1999) Bats are not birds - a cautionary note on using echolocation calls to identify bats: a comment. *Journal of Mammalogy*, **80**, 290-296.

Barclay, R.M.R. & Brigham, R.M. (1991) Prey detection, dietary niche breadth, and body size in bats. Why are aerial insectivorous bats so small? *The American Naturalist*, **137**, 693-703.

Barclay, R.M.R. & Harder, L.D. (2004). Life Histories. In *Bat Ecology* (eds T.H. Kunz & M.B. Fenton), pp. 209-253. University of University Press, Chicago.

Begon, M., Harper, J.H., & Townsend, C.R. (1990) *Ecology: Individuals, Populations and Communities*. Blackwell Scientific Publications, Oxford.

Bell, G.P. (1982) Behavioral and ecological aspects of gleaning by a desert insectivorous bat, *Antrozous pallidus* (Chiropetra: Vespertilionidae). *Behav Ecol Sociobiol*, **10**, 217-223.

Bengtsson, J., Baillie, S.R., & Lawton, J.H. (1997) Community variability increases with time. *Oikos*, **78**, 249-256.

Bernard, E. & Fenton, M.B. (2002) Species diversity of bats (Mammalia: Chiroptera) in forest fragments, primary forests, and savannas in central Amazonia, Brazil. *Canadian Journal of zoology*, **80**, 1124-1140.

Bigalke, R.C. (1979). Aspects of vertebrate life in fynbos, South Africa. In *Heathlands and Related Shrublands of the World* (ed R.L. Specht), Vol. 9A, pp. 81-95. Elsevier Scientific Publishing, Amsterdam.

Biscardi, S., Orprecio, J., Fenton, M.B., Tsoar, A., & Ratcliffe, J.M. (2004) Recognition of species by their echolocation calls. *Acta Chiropterologica*, **6**, 347-363.

Black, H.L. (1974) A north temperate bat community: structure and prey populations. *Journal of Mammalogy*, **55**, 138-157.

Blomberg, S.P., Garland Jnr, T., & Ives, A. (2003) Testing for phylogenetic signal in comparative data: behavioural traits are more labile. *Evolution*, **57**, 717-745.

Bogdanowicz, W., Fenton, M.B., & Daleszczyk, K. (1999) The relationship between echolocation calls, morphology and diet in insectivorous bats. *Journal of Zoology, London*, **247**, 381-393.

Bohning-Gause, K., Taper, K.M.L., & Brown, J.H. (1994) Avian community dynamics are discodant in space and time. *Oikos*, **70**, 121-126.

Bolnick, D.I. (2001) Intraspecific competition favours niche width expansion in *Drosophila melanogaster. Nature*, **410**, 463-466.

Bond, P. & Goldblatt, P. (1984) Plants of the Cape flora. A descriptive catalogue. *J. S. Afr. Bot. Suppl.*, **13**, 1-455.

Bowers, M.A. & Brown, J.H. (1982) Body size and coexistence in desert rodents: chance or community structure? *Ecology*, **63**, 391-400.

Bradley, R.A. & Bradley, D.W. (1985) Do non-random patterns of species in niche space imply competition? *Oikos*, **45**, 443-445.

Brigham, R.M., Aldridge, H.D.J.N., & Mackay, R.L. (1992) Variation in habitat use and prey selection by Yuma bats, *Myotis yumanensis. Journal of Mammalogy*, **73**, 640-645.

Brosset, A., Charles-Dominique, P., Cockle, A., Cosson, J., & Massson, D. (1996) Bat communities and deforestation in French Guiana. *Canadian Journal of zoology*, **74**, 1974-1982.

Brown, J.H. (1975). Geographical ecology of desert rodents. In *Ecology and Evolution of Communities*. (eds M.L. Cody & J.M. Diamond). Belknap Press, Cambridge.

Brown, J.H. (1987). Variation in desert rodent guilds: patterns, processes, and scales. In *Organization of Communities Past and Present* (eds J.H.R. Gee & P.S. Giller), pp. 185-203. Blackwell Scientific, Oxford.

Brown, J.H. (1995) *Macroecology*. University of Chicago Press, Chicago.

Brown, J.H. & Bowers, M.A. (1985) Community organization in hummingbirds: relationships between morphology and ecology. *Auk*, **102**, 251-269.

Brown, J.H., Marquet, P.A., & Taper, M.L. (1993) Evolution of body size: consequences of an energetic definition of fitness. *The American Naturalist*, **142**, 574-584.

Brown, J.H. & Maurer, B.A. (1987) Evolution of species assemblages: effects of energetic constraints and species dynamics on the diversification of the American avifauna. *American Naturalist*, **130**, 1-17.

Brown, J.H. & Maurer, B.A. (1989) Macroecology: the division of food and space mong species on continents. *Science*, **243**, 1145-1150.

Brown, J.H. & Nicoletto, P.F. (1991) Spatial scaling of species composition: body masses of North American land mammals. *The American Naturalist*, **138**, 1478-1512.

Brown, J.H., Taper, K.M.L., & Marquet, P.A. (1996) Darwinian fitness and reproductive power: reply to Kozlowski. *American Naturalist*, **147**, 1092-1097.

Brown, J.H., Valone, T.J., & Curtin, C.G. (1997) Reorganisation of an arid ecosystem in response to recent climate change. *PNAS*, **94**, 9729-9733.

Brown, W.L. & Wilson, E.O. (1956) Character displacement. *Systematic Zoology*, **7**, 49-64.

Bruno, J.F., Stachowicz, J.J., & Bertness, M.D. (2003) Inclusion of facilitation into ecological theory. *TREE*, **18**, 119-125.

Burnham, K.P. & Overton, W.S. (1978) Estimation of the size of a closed population when capture probabilities vary among mammals. *Biometrika*, **65**, 623-633.

Calder, W.A. (1984) *Size, Function and Life History* Harvard University Press, Cambridge, Massachusetts.

Case, T.J. (1983) Niche overlap and the assembly of island lizard communities. *Oikos*, **41**, 427-433.

Case, T.J. & Sidell, R. (1983) Pattern and chance in the structure of the model and natural communities. *Nature*, **37**, 832-849.

Chao, A. (1989) Estimating population size for sparse data in capture-recapture experiments. *Biometrics*, **45**, 427-438.

Clarke, F.M. & Downie, J.R. (2001) A bat (Chiroptera) survey of Mora rainforest in Trinidad's Victoria-Mayaro Forest Reserve. *Biodiversity and Conservation*, **10**, 725-736.

Colwell, R.K. (2004) EstimateS: Statistical estimation of species richness and shared species from samples. Version 7. Persistant URL <purl.oclc.org/estimates>.

Colwell, R.K. & Coddington, J.A. (1994) Estimating terrestial biodiversity through extrapolation. *Phil. Trans. R. Soc. Lond. B.*, **345**, 101-118.

Colwell, R.K. & Futuyma, D.J. (1971) On the measurement of niche breadth and overlap. *Ecology*, **52**, 567-576.

Colwell, R.K. & Lees, D.C. (2000) The mid-domein effect: geometric constraints on the geography of species richness. *TREE*, **15**, 70-76.

Colwell, R.K. & Winkler, D.W. (1984). A null model for null models in biogeography. In *Ecological Communities: Conceptual Issues and the Evidence*. (eds D.R. Strong, D. Simberloff, L.G. Abele & A.B. Thistle), pp. 344-359. Princeton University Press, Princeton.

Colwell, R.K., Xuan Mao, C., & Chang, J. (2004) Interpolating, extrapolating, and comparing incidence-based species accumulation curves. *Ecology*, **85**, 2717-2727.

Connell, J.H. (1975). Some mechanisms producing structure in natural communities: a model and evidence from field experiments. In *Ecology and Evolution of Communities*. (eds M.L. Cody & J.M. Diamond), pp. 460-490. Harvard University Press, Cambridge.

Connell, J.H. (1980) Diversity and the coevolution of competitors, or the ghost of competition past. *Oikos*, **35**, 131-138.

Connell, J.H. (1983) On the prevalence and relative importance of interspecific competition: evidence from field experiments. *American Naturalist*, **122**, 661-696.

Connor, E.F. & Simberloff, D. (1978) Species number and compositional similarity of the Galapagos flora and avifauna. *Ecological Monographs*, **48**, 219-248.

Connor, E.F. & Simberloff, D. (1979) The assembly of species communities: chance or competition? *Ecology*, **60**, 1132-1140.

Connor, E.F. & Simberloff, D. (1983) Interspecific competition and species co-occurrence patterns on islands: null models and the evaluation of evidence. *Oikos*, **41**, 455-465.

Connor, E.F. & Simberloff, D. (1986) Competition, scientific method, and null models in ecology. *American Naturalist*, **74**, 155-162.

Connor, W.E. (1999) 'Un chant d'appel amoureaux': acoustic communication in moths. *Journal of Experimental Biology*, **202**, 1711-1723.

Corbet, G.B. & Harris, S. (1991) *Handbook of British Mammals* Blackwell Scientific Publications, Oxford.

Cornell, H.V. (1999) Unsaturation and regional influences on species richness in ecological communities: a review of the evidence. *Ecoscience*, **6**, 1-13.

Cornell, H.V. & Lawton, J.H. (1992) Species interactions, local and regional processes, and limits to the richness of ecological communities: a theoretical perspective. *Journal of Animal Ecology*, **61**, 1-12.

Cowling, R.M. & Holmes, P.M. (1992). Flora and Vegetation. In *The Ecology of the Fynbos. Nutrients Fire and Diversity*. (ed R.M. Cowling), pp. 23-61. Oxford University Press, Cape Town.

Cowling, R.M., Richardson, D.M., & Mustard, P.J. (1997). Fynbos. In *Vegetation of Southern Africa* (eds R.M. Cowling, D.M. Richardson & G.J. Pierce), pp. 99-130. Cambridge University Press, Cambridge.

Crome, F.H.J. & Richards, G.C. (1988) Bats and gaps: microchiropteran community structure in a Queensland rain forest. *Ecology*, **69**, 1960-1969.

Csorba, G., Ujhelyi, P., & Thomas, N. (2003) *Horseshoe Bats of the World (Chiroptera: Rhinolophidae* Alana Books, Shrewsbury, Shropshire.

Cumming, G.S. & Bernard, R.T.F. (1997) Rainfall, food abundance and timing of parturition in African bats. *Oecologia*, **111**, 309-317.

Darwin, C. (1859) *The Origin of Species*. Wordsworth Editions Limited, Hertfordshire.

Davis, W.H. & Hitchcock, H.B. (1995) A new longevity record for the bat *Myotis lucifugus*. *Bat Research News*, **36**, 6.

Dayan, T. & Simberloff, D. (1994) Character displacement, sexual dimorphism, and morphological variation among British and Irish mustilids. *Ecology*, **75**, 1063-1073.

Dayan, T. & Simberloff, D. (1998) Size patterns among competitors: ecological character displacement and character release in mammals, with special reference to island populations. *Mammalian Review*, **28**, 99-124.

Dayan, T., Simberloff, D., Tchernov, E., & Yom-Tov, Y. (1989) Inter- and intraspecific character displacement in mustelids. *Ecology*, **70**, 1526-1539.

Dayan, T., Simberloff, D., Tchernov, E., & Yom-Tov, Y. (1990) Feline canines: community wide character displacement among the small cats of Israel. *American Naturalist*, **136**, 39-60.

de Jong, J. (1994) Habitat use, home range and activity pattern of the northern bat, *Eptesicus nilssoni*, in a hemiboreal forest. *Mammalia*, **58**, 535-548.

Diamond, J.M. (1975). Assembly of species communities. In *Ecology and Evolution of Communities* (eds M.L. Cody & J.M. Diamond), pp. 342-444. Cambridge University Press, Cambridge.

Diamond, J.M. (1986). Overview: laboratory experiments, field experiments, and natural experiments. In *Community Ecology*. (eds T.J. Case & J.M. Diamond), pp. 3-22. Harper and Row, New York.

Diamond, J.M. & Gilpin, M.E. (1982) Examination of the "null" model of Connor and Simberloff for species co-occurrences on islands. *Oecologia*, **52**, 64-74.

Diamond, J.M., Pimm, S.L., Gilpin, M.E., & LeCroy, M. (1989) Rapid evolution of character displacement in myzomelid honeyeaters. *American Naturalist*, **134**, 675-708.

Dumont, E.R. (2004). Bats and Fruit. In *Bat Ecology*. (eds T.H. Kunz & M.B. Fenton), pp. 398-429. The University of Chicago Press, Chicago.

Eichstadt, H. (1997) Ressourcennutzung und Nischebgestaltung einer Fledermausgemeinschaft im Nordosten Brandenburgs. *Saugetierkundliche Mitteilungen*, **40**, 3-171.

Eick, G.N., Jacobs, D.S., & Matthee, C.A. (2005) A nuclear DNA phylogenetic perspective on the evolution of echolocation and historic biogeography of extant bats (Chiroptera). *Molecular Biology and Evolution*, **22**, 1868-1886.

Elton, C. (1927) *Animal Ecology*. Sidgwick and Jackson, London.

Faure, P.A., Fullard, J.H., & Barclay, R.M.R. (1990) The response of tympanate moths to the echolocation calls of a substrate gleaning bat, *Myotis evotis*. *Journal of Comparative Physiology A*, **166**, 843-849.

Fauth, J.E., Bernardo, J., Camara, M., Resetarits Jnr, W.J., Van Buskirk, J., & McCollum, S.A. (1996) Simplifying the jargon of community ecology: a conceptual approach. *American Naturalist*, **147**, 282-286.

Feeley, K. (2003) Analysis of avian communities in Lake Guri, Venezuela, using multiple assembly rule models. *Oecologia*, **137**, 104-113.

Feinsinger, P., Spears, E.E., & Poole, R.W. (1981) A simple measure of niche breadth. *Ecology*, **62**, 27-32.

Felsenstein, J. (1985) Phylogenies and the comparative method. *The American Naturalist*, **125**, 1-15.

Fenton, M.B. (1972) The structure of aerial-feeding bat faunas as indicated by ears and wing elements. *Canadian Journal of zoology*, **50**, 287-296.

Fenton, M.B. (1982). Echolocation calls, insect hearing, and the feeding ecology of insectivorous bats. In *Ecology of Bats*. (ed T.H. Kunz), pp. 261-285. Plenum Press, New York.

Fenton, M.B. (1984) Echolocation: implications for ecology and evolution of bats. *Quarterly Review of Biology*, **59**, 33-53.

Fenton, M.B. (1990) The foraging ecology of animal-eating bats. *Canadian Journal of zoology*, **68**, 411-422.

Fenton, M.B. (1995) Constraints and flexibility - bats as predators, bats as prey. *Symp. zool. Soc. Lond.*, **67**, 277-289.

Fenton, M.B., Acharya, L., Audet, D., Hickey, M.B.C., Merriman, C.B., Obrist, M.K., & Syme, D.M. (1992) Phyllostomid bats (Chiroptera: Phyllostomidae) as indicators of habitat destruction in the Neotropics. *Biotropica*, **24**, 440-446.

Fenton, M.B., Audet, D., Obrist, M.K., & Rydell, J. (1995) Signal strength, timing, and self-deafening: the evolution of echolocation in bats. *Paleobiology*, **21**, 229-242.

Fenton, M.B. & Bell, G.P. (1981) Recognition of species of insectivorous bats by their echolocation calls. *Journal of Mammalogy*, **62**, 233-243.

Fenton, M.B., Bouchard, S., Vonhof, M.J., & Zigouris, J. (2001) Time-expansion and zero-crossing period meter systems present significantly different views of echolocation calls of bats. *Journal of Mammalogy*, **82**, 721-727.

Fenton, M.B., Cumming, D.H.M., Rautenbach, I.L., Cumming, G.S., Cumming, M.S., Ford, G., Taylor, R.D., Dunlop, J., Hovorka, M.D., Johnston, D.S., Portfors, C.V., Kalcounis, M.C., & Mahlanga, Z. (1998a) Bats and the loss of tree canopy in African woodlands. *Conservation Biology*, **12**, 399-407.

Fenton, M.B. & Fullard, J.H. (1979) The influence of moth hearing on bat echolocation strategies. *Journal of Comparative Physiology A*, **132**, 77-86.

Fenton, M.B., Gaudet, C.L., & Leonard, M.L. (1983) Feeding behaviour of the bats *Nycteris grandis* and *Nycteris thebaica* (Nycteridae) in captivity. *J. Zool. Lond*, **200**, 347-354.

Fenton, M.B., Jacobs, D.S., Richardson, E.J., Tayler, P.J., & White, W. (2004) Individual signatures in frequency-modulated sweep calls of African long-eared, free-tailed bats, *Otomops martiensseni* (Chiroptera: Molossidae). *Journal of Zoology, London*, **262**, 11-19.

Fenton, M.B. & Morris, D. (1976) Opportunistic feeding by desert bats (*Myotis* spp.). *Canadian Journal of zoology*, **54**, 526-530.

Fenton, M.B., Portfors, C.V., Rautenbach, I.L., & Waterman, J.M. (1998b) Compromises: sound frequencies used in echolocation by aerial-feeding bats. *Canadian Journal of zoology*, **76**, 1174-1182.

Fenton, M.B., Rautenbach, I.L., Smith, S.E., Swanepoel, C.M., Grosell, J., & van Jaarsveld, J. (1994) Raptors and bats: threats and opportunities. *Animal Behavior*, **48**, 9-18.

Fernandez, M.H. & Vrba, E.S. (2005) Rapoport effect and biomic specialization in African mammals: revisiting the climatic variability hypothesis. *Journal of Biogeography*, **32**, 903-918.

Findley, J.S. (1976) The structure of bat communities. *The American Naturalist*, **110**, 129-139.

Findley, J.S. (1993) *Bats. A Community Perspective.* Cambridge University Press, Cambridge.

Findley, J.S. & Black, H. (1983) Morphological and dietary structuring of a Zambian insectivorous bat community. *Ecology*, **64**, 625-630.

Fleming, T.H. (1988) *The short-tailed fruitbat: a study of plant-animal interaction* Chicago University Press, Chicago.

Fleming, T.H. (1993) Plant-visiting bats. *American Scientist*, **81**, 460-467.

Fleming, T.H., Hooper, E.T., & Wilson, D.E. (1972) Three central American bat communities: structure, reproductive cycles and movement patterns. *Ecology*, **53**, 555-569.

Fox, B.J. (1987) Species assembly and the evolution of community structure. *Evolutionary Ecology*, **1**, 201-213.

Fox, B.J. (1989). Small-mammal community pattern in Australian heathland: a taxonomically based rule for species assembly. In *Patterns in the Structure of Mammalian Communities.* (eds D.W. Morris, Z. Abramsky, B.J. Fox & M.R. Willig). Special Publication 28 of the Museum, Texas Tech University, Lubbock.

Fox, B.J. & Brown, J.H. (1993a) Assembly rules for functional groups in North American desert rodent communities. *Oikos*, **67**, 538-370.

Fox, B.J. & Brown, J.H. (1993b) Assembly rules for functional groups in North American desert rodent communities. *Oikos*, **67**, 358-370.

Francis, C.M. (1990) Trophic structure of bat communities in the understorey of lowland dipterocarp rain forest in Malaysia. *Journal of Tropical Ecology*, **10**, 523-530.

Friedman, Y. & Daly, B., eds. (2004) *Red Data Book of the Mammals of South Africa: A Conservation Assessment: CBSG Southern Africa, Conservation Breeding Specialist Group (SSC/IUCN), Endangered Wildlife Trust. South Africa.*

Fullard, F.H., Koehler, C., Surlykke, A., & McKenzie, N.L. (1991) Echolocation Ecology and Flight Morphology of Insectivorous Bats (Chiroptera) of south -western Australlia. *Aust. J. Zool*, **39**, 427-438.

Fullard, J.H. (1982) Echolocation assemblages and their effects on moth auditory systems. *Canadian Journal of zoology*, **60**, 2572-2576.

Fullard, J.H. (1987). Sensory ecology and neuroethology of moths and bats: interactions in a global perspective. In *Recent Advances in the Study of Bats*. (eds M.B. Fenton, P.A. Racey & J.M.V. Rayner), pp. 244-272. Cambridge University Press, Cambridge.

Fullard, J.H. (1988) The tuning of moth ears. *Experientia*, **44**, 423-428.

Fullard, J.H. (1990). The sensory ecology of moths and bats: global lessons in staying alive. In *Insect Defences: Adaptive Mechanisms and Strategies of Prey and Predators* (eds D.L. Evans & J.O. Schmidt), pp. 203-226. State University of New York Press, Albany.

Fullard, J.H. (1994) Auditory changes in noctuid moths endemic to a bat-free habitat. *Journal of Evolutionary Biology*, **7**, 435-445.

Fullard, J.H., Dawson, J.W., & Jacobs, D.S. (2003) Auditory encoding during the last moment of a moth's life. *The Journal of Experimental Biology*, **206**, 281-294.

Fullard, J.H., Dawson, J.W., Otero, L.D., & Surlykke, A. (1997) Bat-deafness in day-flying moths (Lepidoptera, Notodontidae, Dioptinae). *Journal of Comparative Physiology A*, **181**, 477-483.

Fullard, J.H. & Thomas, D.W. (1981) Detection of certain African, insectivorous bats by sympatric, tympanate moths. *Journal of Comparative Physiology A*, **143**, 363-368.

Fullard, J.H. & Yack, J.E. (1993) The evolutionary biology of insect hearing. *TREE*, **8**, 248-252.

Futuyma, D.J. & Slatkin, M. (1983) *Coevolution*. Sinauer, Massachusetts.

Gaisler, J. (1979). Ecology of bats. In *Ecology of Small Mammals* (ed D.M. Stoddart), pp. 281-342. Chapman and Hall, London.

Garland Jnr, T.P., Harvey, P.H., & Ives, A.R. (1992) Procedures for the analysis of comparative data using phylogenetically independent contrasts. *Systematic Biology*, **41**, 8-32.

Gaston, K.J. (1988) The intrinsic rate of increase of insects of different body sizes. *Ecological Entomology*, **14**, 399-409.

Gaston, K.J. & Blackburn, T.M. (2000) *Patterns and Process in Macroecology*. Blackwell Science Ltd, Cambridge.

Gaston, K.J., Blackburn, T.M., & Lawton, J.H. (1997) Interspecific abundance-range size relationships: an appraisal of mechanisms. *Journal of Animal Ecology*, **66**, 579-601.

Gaston, K.L. (1990) Patterns in the geographical ranges of species. *Biological Review*, **65**, 105-129.

Gelderblom, C.M., Bronner, G.N., Lombard, A.T., & Taylor, P.J. (1995) Patterns of distribution and current protection status of the Carnivora, Chiroptera and Insectivora *South African Journal of Zoology*, **30**, 103-114.

Giannini, N.P. & Kalko, E.K. (2004) Trophic structure in a large assemblage of phyllostomid bats in Panama. *Oikos*, **105**, 209-220.

Giller, P.S. (1984) *Community Structure and the Niche*. Chapman and Hall, London.

Giller, P.S. & Gee, J.H.R. (1987). The analysis of community organization: the influence of equilibrium, scale and terminology. In *Organization of Communities Past and Present*. (eds J.H.R. Gee & P.S. Giller), pp. 519-542. Blackwell Scientific, Oxford.

Gilliomee, J.H. (2003) Insect diversity in the Cape Floristic Region. *South African Journal of Ecology*, **41**, 237-244.

Gopfert, M.C. & Wasserthal, L.T. (1999) Hearing with the mouthparts: behavioural responses and the structural basis of ultrasound perception in Acherontine hawkmoths. *The Journal of Experimental Biology*, **202**, 909-918.

Gotelli, N.J. (2000) Null model analysis of species co-occurrence patterns. *Ecology*, **81**, 2606-2621.

Gotelli, N.J. (2001) Research frontiers in null model analysis. *Global Ecology and Biogeography*, **10**, 337-343.

Gotelli, N.J. (2004) A taxonomic wish-list for community ecology. *Phil. Trans. R. Soc. Lond. B.*, **359**, 585-597.

Gotelli, N.J., Buckley, N.J., & Wiens, J.A. (1997) Co-occurrence of Australian land birds: Diamond's assembly rules revisited. *Oikos*, **80**, 311-324.

Gotelli, N.J. & Colwell, R.K. (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters*, **4**, 379-391.

Gotelli, N.J. & Entsminger, G.L. (2004) EcoSim: null models software for ecology Version 7.7. Kesey-Bear.

Gotelli, N.J. & Graves, G.R. (1990) Body size and the occurrence of avian species on land-bridge islands. *Journal of Biogeography*, **17**, 315-325.

Gotelli, N.J. & Graves, G.R. (1993) A general model of metapopulation dynamics. *Oikos*, **68**, 36-44.

Gotelli, N.J. & Graves, G.R. (1996) *Null Models in Ecology*. Smithsonian Institution Press, Washington.

Gotelli, N.J. & McCabe, D.J. (2002) Species co-occurrences: a meta-analysis of J.M. Diamond's assembly rule model. *Ecology*, **83**, 2091-2096.

Grafen, A. (1989) The phylogenetic regression. *Phil. Trans. R. Soc. Lond. B.*, **326**, 119-157.

Grant, P.R. (1972) Interspecific competition among rodents. *Annual Review of Ecology and Systematics*, **3**, 79-106.

Graves, G.R. & Gotelli, N.J. (1983) Neotropical land-bridge avifaunas: new approaches to null hypotheses in biogeography. *Oikos*, **41**, 322-333.

Griffin, D.R. & Galambos, R. (1941) The sensory basis of obstacle avoidance by flying bats. *Journal of Experimental Zoology*, **86**, 481-506.

Haefner, J.W. (1988) Assembly rules for Greater Antillean Anolis lizards. Competition and random models compared. *Oecologia*, **74**, 551-565.

Hanski, I. (1998) Metapopulation dynamics. *Nature*, **396**, 41-49.

Hanski, I., Kouki, J., & Halkka, A. (1993). Three explanations of the positive relationship between the distribution and abundance of species. In *Species diversity in ecological Communities*. (eds R.E. Ricklefs & D. Schluter), pp. 108-116. University of Chicago Press, Chicago.

Hardin, G. (1960) The competitive exclusion principle. *Science*, **131**, 1292-1297.

Harvey, P.H., Colwell, R.K., Silvertown, J.W., & May, R.M. (1983) Null models in ecology. *Annual Review of Ecology and Systematics*, **14**, 189-211.

Harvey, P.H. & Pagel, M.D. (1991) *The Comparative Method in Evolutionary Biology*. Oxford University Press, Oxford.

Hayman, R.W. & Hill, J.E. (1971). Order Chiroptera, Part2. In *The Mammals of Africa: an Identification Manual*. (eds J. Meester & H.W. Setzer), pp. 1-73. Smithsonian Institution Press, Washington DC.

Heller, K.-G. & v. Helversen, O. (1989) Resource partitioning of sonar frequency bands in rhinolophoid bats. *Oecologia*, **80**, 178-186.

Heller, K.-G. & Volleth, M. (1995) Community structure and the evolution of insectivorous bats in the Paleotropics and Neotropics. *Journal of Tropical Ecology*, **11**, 429-442.

Herselman, J.C. & Norton, P.M. (1985) The distribution and status of bats (Mammalia: Chiroptera) in the Cape Province. *Annals of the Cape Provincial Museums*, **16**, 73-126.

Hickey, M.B.C., Acharya, L., & Pennington, S. (1996) Resource partitioning by two species of vespertilionid bats (*Lasiurus cinereus* and *Lasiurus borealis*) feeding around street lights. *Journal of Mammalogy*, **77**, 325-334.

Hillebrandt, H. & Blenckner, T. (2002) Regional and local impact on species diversity - from pattern to process. *Oecologia*, **132**, 479-491.

Holmes, D.J. & Austad, S.N. (1994) Fly now, die later: life-history correlates of gliding and flying in mammals. *Journal of Mammalogy*, **75**, 224-226.

Holt, R.D. (1993). Ecology at the mesoscale: the influence of regional processes on local communities. In *Species Diversity in Ecological Communities* (eds R.E. Ricklefs & D. Schluter), pp. 77-88. University of Chicago Press, Chicago.

Husar, S.L. (1976) Behavioral character displacement, evidence of food partitioning in insectivorous bats. *Journal of Mammalogy*, **57**, 331-338.

Hutcheon, J.M. & Kirsch, J.A.W. (2004) Camping in a different tree: Results of molecular systematic studies of bats using DNA-DNA hybridization. *Journal of Mammalian Evolution*, **11**, 17-34.

Hutchinson, G.E. (1957) Concluding remarks. *Cold Spring Harbour Symposia in Quantitative Biology*, **22**, 415-427.

Hutchinson, G.E. (1959) Homage to Santa Rosalia, or why are there so many kinds of animals? *American Naturalist*, **93**, 145-159.

Hutchinson, G.E. & MacArthur, R.H. (1959) A theoretical ecological model of size distribution among species of animals. *American Naturalist*, **93**, 117-125.

Hutson, A.M., Mickleburgh, S.P., & Racey, P.A. (1993) *Global Action Plan for Michrochiropteran bats*. IUCN, Gland, Switzerland.

Jaccard, P. (1908) Nouvelles recherches sur la distribution florale. *Bulletijn de la Soeciete Vaudoise de la science naturelle*, **44**, 223-276.

Jackson, D.A., Peres-Neto, P.R., & Olden, J.D. (2001) What controls who is where in freshwater fish communities - the roles of biotic, abiotic and spatial factors? *Can. J. Fish. Aquat. Sci.*, **58**, 157-170.

Jackson, D.A., Somers, K.M., & Harvey, H.H. (1989) Similarity coefficients: measures of co-occurrence and association or simply measures of occurrences? *American Naturalist*, **133**, 436-453.

Jacobs, D.S. (1999) Intraspecific variation in wingspan and echolocation call flexibility might explain the use of different habitats by the insectivorous bat, *Miniopterus schreibersii* (Vespertilionidae: Miniopterinae). *Acta Chiropterologica*, **1**, 93-103.

Jacobs, D.S. (2000) Community level support for the allotonic frequency hypothesis. *Acta Chiropterologica*, **2**, 197-207.

Jacobs, D.S., Eick, G.N., Schoeman, M.C., & Matthee, C.A. (in press) Cryptic species in an insectivorous bat, Scotophilus dinganii. *Journal of Mammalogy*.

Jacobs, D.S. & Fenton, M.B. (2001) It is *Sauromys petrophilus* not *Chaerephon pumilus* (Chroptera: Molossidae) in the western Cape province of South Africa. *African Journal of Zoology*, **36**.

Jacobs, D.S., Schoeman, M.C., & Barclay, R.M.R. (2005) Foraging and roosting ecology of a rare insectivorous bat species, *Laephotus wintoni* (thomas, 1901), Vespertilionidae. *Acta Chiropterologica*, **7**, 101-109.

Janzen, D.H. (1980) When is it coevolution? *Evolution*, **34**, 611-612.

Jones, G. (1992). Bats vs moths: studies on the diets of rhinolophid and hipposiderid bats support the allotonic frequency hypothesis. In *Prague Studies in Mammalogy* (eds I. Horácek & V. Vohralik), pp. 87-92. Charles University Press, Prague.

Jones, G. (1994) Scaling of wingbeat and echolocation pulse emission rates in bats: why are aerial insectivorous bats so small? *Functional Ecology*, **8**, 450-457.

Jones, G. (1996) Does echolocation constrain the evolution of body size in bats? *Symposia of the Zoological Society of London*, **69**, 111-128.

Jones, G. & Rydell, J. (2004). Bat-Insect Interactions. In *Bat Ecology* (eds T.H. Kunz & M.B. Fenton), pp. 301-345. University of Chicago Press, Chicago.

Jones, G., Vaughan, N., & Parsons, S. (2000) Acoustic identification of bats from directly sampled and time expanded recordings of vocalizations. *Acta Chiropterologica*, **2**, 155-170.

Jones, G. & Waters, D.A. (2000) Moth hearing in response to bat echolocation calls manipulated independently in time and frequency. *Proc. R. Soc. Lond. B*, **267**, 1627-1632.

Jones, K.E. & MacLarnon, A. (2001) Bat life histories: testing models of mammalian life-history evolution. *Evolutionary Ecology Research*, **3**, 465-476.

Jones, K.E. & Purvis, A. (1997) An optimum body size for mammals? Comparative evidence from bats. *Functional Ecology*, **11**, 751-756.

Jones, K.E., Purvis, A., & Gittleman, J.L. (2003) Biological correlates of extinction risk in bats. *American Naturalist*, **161**, 601-614.

Kalko, E.K.V. (1995). Echolocation signal design, foraging habitats and guild structure in six Neotropical sheath-tailed bats (Emballonuridae). In *Ecology, evolution and behaviour of bats*. (eds P.A. Racey & S.M. Swift), pp. 259-273. The Zoological Society of London, Oxford.

Kalko, E.K.V., Friemel, D., Handley Jnr, C.O., & Schnitzler, H.-U. (1999) Roosting and foraging behavior of two Neotropical gleaning bats, *Tonatia silvicola* and *Trachops cirrhosus*. *Biotropica*, **31**, 344-353.

Kalko, E.K.V., Handley, C.O., & Handley, D. (1996). Organization, diversity and long-term dynamics of a Neotropical bat community. In *Long-term Studies of Vertebrate Communities* (eds M.L. Cody & J.A. Smallwood), pp. 503-553. Academic Press, San Diego.

Kalko, E.K.V. & Schnitzler, H.-U. (1993) Plasticity in echolocation signals of European pipistrelle bats in search flight - implications for habitat use and prey detection. *Behavioral Ecology and Sociobiology*, **33**, 415-428.

Keddy, P. & Weiher, E. (1999). The scope and goals of research on assembly rules. In *Ecological Assembly Rules: Perspectives, Advances, Retreats*. (eds E. Weiher & P. Keddy), pp. 1-20. Cambridge University Press, Cambridge.

Keeler, J.O. & Studier, E.H. (1992) Nutrition in pregnant brown bats (*Eptesicus fuscus*) feeding on June beetles. *Journal of Mammalogy*, **73**, 426-430.

Kelt, D.A., Brown, J.H., Heske, E.J., Marquet, P.A., Morton, S.R., Reid, J.R.W., Rogovin, K.A., & Shenbrot, G. (1996) Community structure of desert small mammals: comparisons across four continents. *Ecology*, **77**, 746-761.

Kick, S.A. (1982) Target detection by the echolocating bat, *Eptesicus fuscus*. *J. Comp. Phys. A* 145, 431-435

Kingston, T., Jones, G., Zubaid, A., & Kunz, T.H. (2000) Resource partitioning in rhinolophoid bats revisited. *Oecologia*, **124**, 332-342.

Kober, R. & Schnitzler, H.-U. (1980) Information in sonar echoes of fluttering insects available for echolocating bats. *Journal of the Acoustical Society of America*, **87**, 882-896.

Koopman, K.F. (1994) *Chiroptera: Systematics*. Walter de Gruyter, New York.

Kozlowski, J. (1996) Energetic definition of fitness? Yes, but not that one. *American Naturalist*, **147**, 1087-1091.

Kunin, W.E. & Lawton, J.H. (1996). Does biodiversity matter? Evaluating the case for conserving species. In *Biodiversity. A Biology of Numbers and Difference*. (ed K.J. Gaston), pp. 283-308. Blackwell Science, Oxford.

Kunz, T.H. (1982). Roosting ecology of bats. In *Ecology of Bats*. (ed T.H. Kunz), pp. 1-55. Plenum Press, New York.

Kunz, T.H. & Lumsden, L.F. (2004). Roosting Ecology. In *Bat Ecology*. (eds T.H. Kunz & M.B. Fenton), pp. 3-89. University of Chicago Press, Chicago.

Kunz, T.H. & Pierson, E.D. (1994). Bats of the world - an introduction. In *Bats of the World* (ed R.W. Novak). John Hopkins University Press, Baltimore.

Kunz, T.H. & Whitaker, J.O. (1983) An evaluation of fecal analysis for determining food habits of insectivorous bats. *Canadian Journal of zoology*, **61**, 1317-1321.

Kunz, T.H., Wrazen, J.A., & Burnett, C.D. (1998) Changes in body mass and fat reserves in pre-hibernating little brown bats (*Myotis lucifugus*). *Ecoscience*, **5**, 8-17.

Kurta, A. & Kunz, T.H. (1987) Size of bats at birth and maternal investment during pregnancy. *Symposia of the Zoological Society of London*, **57**, 79-106.

Lack, D.L. (1947) *Darwin's Finches*. Cambridge University Press, Cambridge.

Lawlor, L.R. (1980) Overlap, similarity, and competition coefficients. *Ecology*, **61**, 245-251.

Lawrence, B.D. & Simmons, J.A. (1982) Measurements of atmospheric attenuation at ultrasonic frequencies and the significance for echolocation by bats. *J. Acoust. Soc. Am.*, **71**, 585-590.

Lawton, J.H. (1999) Are there general laws in ecology? *Oikos*, **84**, 177-192.

Lawton, J.H. (2000) *Community Ecology in a Changing World*. Ecology Institute, Oldendorf/Luhe.

Lawton, J.H. & May, R.B. (1995) *Extinction rates*. Oxford University Press, Oxford.

Loreau, M. (2000) are communities saturated? On the relationship between a, b and y diversity. *Ecology Letters*, **3**, 73-76.

Losos, J.B. (1990) A phylogenetic analysis of character displacement in Caribbean Anolis lizards. *Evolution*, **44**, 558-569.

Lotka, A.J. (1925) *Elements of Physical Biology*. Williams and Wilkens, Baltimore.

Lovegrove, B.A. & Haines, L. (2004) The evolution of placental mammal body sizes: evolutionary history, form, and function. *Oecologia*, **138**, 13-27.

MacArthur, R.H. (1958) population ecology of some warblers of norteastern coniferous forests. *Ecology*, **39**, 599-619.

MacArthur, R.H. (1972) *Geographical Ecology*. Harper and Row, New York.

MacArthur, R.H. & Levins, R. (1967) The limiting similarity, convergence and divergence of coexisting species. *American Naturalist*, **101**, 377-385.

MacArthur, R.H. & Wilson, O.E. (1967) *The theory of Island Biogeography*. Princeton University Press, Princeton.

Maclean, G.L. (1985) *Roberts' Birds of Southern Africa* The John Voelcker Bird Book Fund, Cape Town.

Maddison, W.P. & Maddison, D.R. (2004) Mesquite: a modular system for evolutionary analyses. Version 1.05. http://mesquiteproject.org/mesquite/.

Magurran, A.E. (1988) *Ecological diversity and Its Measurement*. Princeton University Press, Princeton.

Manly, B.F.J. (1991) *Randomization and Monte Carlo Methods in Biology*. University of Chicago Press, Chicago.

Martin, E.P. & Garland Jnr, T. (1991) Phylogenetic analyses of the correlate evolution of continuous characters: a simulation study. *Evolution*, **45**, 534-557.

Maurer, B.A. (1999) *Untangling Ecological Diversity*. University of Chicago Press, Chicago.

May, R.M. (1974) Ecosystem patterns in randomly fluctuating environments. *Progress in Theoretical Ecology*, **3**, 1-50.

May, R.M. (1986) The search for patterns in the balance of nature: advances and retreats. *Ecology*, **67**, 1115-1126.

May, R.M. (1988) How many species are there on earth? *Science*, **241**, 1441-1448.

McCoy, E.D. & Heck, K.L. (1987) Some observations on the use of taxonomic similarity in large-scale biogeography. *Journal of Biogeography*, **14**, 79-87.

McDonald, J.T., Rautenbach, I.L., & Nel, J.A.J. (1990) Foraging ecology of bats observed at De Hoop Nature Reserve, southern Cape Province. *S. Afr. J. Wildl. Res.*, **20**, 133-144.

McIntosh, R.P. (1967) An index of diversity and the relation to certain concepts to diversity.

Ecology, **48**, 392-404.

McKenna, M.C. & Bell, S.K. (1997) *Classification of Mammals above the Species Level.* Columbia University Press, Ney York.

McKenzie, N.L. & Rolfe, J.K. (1986) Structure of bat guilds in the Kimberley mangroves, Australia. *Journal of Animal Ecology*, **55**, 401-420.

Meyers, P. (1978) Sexual dimorphism in size of vespertilionid bats. *American Naturalist*, **112**, 701-711.

Midford, P.E., Garland Jnr, T., & Maddison, W.P. (2004) PDAP: PDTREE package for Mesquite Version 1.00. http://mesquiteproject.org/mesquite/pdap/.

Midgley, J.J., Cowling, R.M., Seydack, A.H.W., & van Wyk, G.F. (1997). Forest. In *Vegetation of Southern Africa* (eds R.M. Cowling, D.M. Richardson & G.J. Pierce), pp. 278-299. Cambridge University Press, Cambridge.

Mikkelson, G.M. (1993) How do food webs fall apart? A study of changes in trophic structure during relaxation on habitat fragments. *Oikos*, **67**, 1993.

Miller, L.A. & Surlykke, A. (2001) How some insects detect and avoid being eaten by bats: tactics and countertactics of prey and predator. *BioScience*, **51**, 570-581.

Miller-Butterworth, C.M., Jacobs, D.S., & Harley, E.H. (2003) Strong population substructure is correlated with morphology and ecology in a migratory bat. *Nature*, **424**.

Moreno, C.E. & Halffter, G. (2000) Assessing the completeness of bat biodiversity inventories using species accumulation curves. *Journal of Applied Ecology*, **37**, 149-158.

Morin, P.J. (1999) *Community Ecology*. Blackwell Science, Malden.

Moss, C.F. & Schnitzler, H.-U. (1995). Behavioural studies of auditory information processing. In *Springer Handbook of Auditory Research*. (eds A.N. Popper & R.R. Fay), pp. 87-145. Springer-Verlag, New York.

Moss, C.F. & Zagaeski, M. (1994) Acoustic information available to bats using frequency mudualted echolocation sounds for the perception of insect prey. *Journal of the Acoustical Society of America*, **95**, 2745-2756.

Moulton, M.P. & Pimm, S.L. (1986). The extent of competition in shaping an introduced avifauna. In *Community Ecology* (eds T.J. Case & J. Diamond), pp. 80-97. Harper and Row, New York.

Moulton, M.P. & Pimm, S.L. (1987) Morphological assortment in introduced Hawaiian passerines. *Evolutionary Ecology*, **1**, 113-124.

Neuweiler, G. (1990) Auditory adaptations for prey capture in echolocating bats. *Physiological Reviews*, **70**, 615-641.

Neuweiler, G. (2000) *The Biology of Bats*. Oxford University Press, Oxford.

Neuweiler, G. (2003) Evolutionary aspects of bat echolocation. *J Comp Physiol*, **189**, 245-256.

Norberg, U.M. (1998). Morphological adaptations for flight in bats. In *Bat Biology and Conservation* (eds T.H. Kunz & P.A. Racey), pp. 93-108. Smithsonian Institution Press, Washington DC.

Norberg, U.M. & Rayner, J.M.V. (1987) Ecological morphology and flight in bats (Mammalia: Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. *Phil. Trans. R. Soc. Lond. B*, **316**, 335-427.

Norman, A.P. & Jones, G. (2000) Size, peripheral auditory tuning and target strength in noctuid moths. *Physiological Entomology*, **25**, 346-353.

Novick, A. (1977). Acoustic orientation. In *Biology of Bats. Vol. III.* (ed W.A. Wimsatt), pp. 73-287. Academic Press, New York.

O'Farrell, M.J. & Miller, B.W. (1997) A new examination of echolocation calls of some neotropical bats (Emballonuridae and Mormoopidae). *Journal of Mammalogy*, **78**, 954-963.

O'Farrell, M.J. & Miller, B.W. (1999) Use of vocal signitures for the inventory of free-flying neotropical bats. *Biotropica*, **31**, 507-516.

O'Farrell, M.J., Miller, B.W., & Gannon, W.L. (1999) Qualitative identification of free-flying bats using the Anabat detector. *Journal of Mammalogy*, **80**, 11-23.

O'Shea, T.J. & Vaughan, T.A. (1980) Ecological observations on an East African bat community. *Mammalia*, **44**, 485-496.

Obrist, M.K. (1995) Flexible bat echolocation: the influence of individual, habitat and conspecifics on sonar signal design. *Behavioral Ecology and Sociobiology*, **36**, 207-219.

Ochoa, J., O'Farrell, M.J., & Miller, B.W. (2000) Contribution of acoustic methods to the study of insectivorous bat diversity in protected areas from northern Venezuela. *Acta Chiropterologica*, **2**, 171-183.

Oliver, I. & Beattie, A.J. (1993) A possible method for the rapid assessment of biodiversity. *Conservation Biology*, **7**, 562-568.

Oliver, I. & Beattie, A.J. (1996) Invertebrate morphospecies as surrogates for species: a case study. *Conservation Biology*, **10**, 99-109.

Palmer, A.R. & Hoffman, M.T. (1997). Nama-Karoo. In *Vegetation of Southern Africa*. (eds R.M. Cowling, D.M. Richardson & G.J. Pierce), pp. 167-188. Cambridge University Press, Cambridge.

Parsons, S. & Jones, G. (2000) Acoustic identification of 12 species of echolocating bats by discriminant function analysis and artificial neural networks. *Journal of Experimental Biology*, **203**, 2641-2656.

Patterson, B.D., Willig, M.R., & Stevens, R.D. (2004). Ecological Diversity of Bats. In *Bat Ecology* (eds T.H. Kunz & M.B. Fenton), pp. 536-579. The University of Chicago Press, Chicago.

Pavey, C.R. & Burwell, C.J. (1998) Bat predation on eared moths: a test of the allotonic frequency hypothesis. *Oikos*, **81**, 143-151.

Peet, R.K. (1975) Relative diversity indices. *Ecology*, **5**, 285-307.

Peres-Neto, P.R. & Olden, J.D. (2001) Assessing the robustness of randomization tests: examples from behavioural studies. *Animal Behaviour*, **61**, 79-86.

Peters, P.H. (1991) *A Critique for Ecology*. Cambridge University Press, Cambridge.

Peters, R.H. (1983) *The Ecological Implications of Body Size* Cambridge University Press, Cambridge.

Pianka, E.R. (1973) The structure of lizard communities. *Annual Review of Ecology and Systematics*, **4**, 53-74.

Pianka, E.R. (1974) Niche overlap and diffuse competition. *Proceedings of the National Academy of Sciences USA*, **71**, 2141-2145.

Pianka, E.R. (1980) Guild structure in desert lizards. *Oikos*, **35**, 194-201.

Pianka, E.R. (1986) *Ecology and Natural History of Desert Lizards* Princeton University Press, Princeton.

Pielou, D.P. & Pielou, E.C. (1968) Associations among species of infrequent occurrence: the insect and spider fauna of Polyporus betulinus (Bulliard) Fries. *Journal of Theoretical Biology*, **21**, 202-216.

Pomeroy, D. (1990) Why fly? The possible benefits for lower mortality. *Biological Journal of the Linnean Society*, **40**, 53-65.

Pool, R.W. & Rathcke, B. (1979) Regularity, randomness, and aggregation in flowering phenologies. *Science*, **203**, 470-471.

Pulliam, H.R. (2000) On the relationship between niche and distribution. *Ecology Letters*, **3**, 349-361.

Pye, J.D. (1980) Adaptiveness of echolocation signals in bats: Flexibility in behaviour and evolution. *Trends in Neuroscience*, **3**, 232-235.

Pye, J.D. (1993) Is fidelity futile? the "true" signal is illusionary, especially with ultrasound. *Bioacoustics*, **4**, 271-286.

Rabinowitz, A.R. & Tuttle, M.D. (1982) A test of the validity of two currently used methods of determining bat prey preferences. *Acta Theriologica*, **27**, 283-293.

Racey, P.A. & Entwistle, A.C. (2000). Life history and reproductive strategies of bats. In *Reproductive Biology of Bats* (eds E.C. Crichton & P.H. Krutzsch), pp. 363-414. Academic Press, San Diego.

Racey, P.A. & Entwistle, A.C. (2004). Conservation Ecology of Bats. In *Bat Ecology* (eds T.H. Kunz & M.B. Fenton), pp. 680-743. Chicago University Press, Chicago.

Randsome, R. (1995) Earlier breeding shortens life in female greater horseshoe bats. *Phil. Trans. R. Soc. Lond. B* 350, 153-161

Rathcke, B. (1984). Patterns of flowering phenologies: testability and causal inference using a random model. In *Ecological Communities: Conceptual Issues and the Evidence* (eds D.R. Strong, D. Simberloff, L.G. Abele & A.B. Thistle), pp. 383-396. Princeton University Press, Princeton.

Rautenbach, I.L. (1986) Karyotypic variation in southern African Rhinolophidae (Chiroptera) and nongeographic variation in *Rhinolophus denti* Thomas, 1904. *Cimbebasia Series A*, **8**, 129-139.

Rautenbach, I.L., Bronner, G.N., & Schlitter, D.A. (1993) Karyotypic data and attendant systematic implications for the bats of southern Africa. *Koedoe*, **36**, 87-104.

Rautenbach, I.L., Fenton, M.B., & Whiting, M. (1996) Bats in riverine forests and woodlands: a latitudinal transect in southern Africa. *Canadian Journal of zoology*.

Rautenbach, I.L., Kemp, A.C., & Scholtz, C.H. (1988) Fluctuations in the availability of arthropods correlated with microchiropteran and avian predator activities. *Koedoe*, **31**, 77-90.

Rautenbach, I.L. & Nel, J.A.J. (1978) Three species of microchiropteran bats recorded for the first time from the South-western Cape biotic zone. *Annals of the Transvaal Museum*, **31**.

Reich, P.B. (2001) Body size, geometry, longevity and metabolism: do plant leaves behave like animal bodies? *TREE*, **16**, 674-680.

Ricklefs, R.E. (1987) Community diversity: relative roles of local and regional processes. *Science*, **235**, 167-171.

Rice, W. R. (1989) Analyzing tables of statistical tests. *Evolution* 43, 223-225

Roberts, K.S. (1951) *The Mammals of South Africa* Central News Agency, Cape Town.

Roeder, K.D. (1967) Turning tendency of moths exposed to ultrasound while in stationary flight. *Journal of Insect Physiology*, **13**, 873-888.

Roeder, K.D. (1975) Neural factors and evitibility in insect behaviours. *Journal of Experimental Zoology*, **194**, 75-88.

Roeder, K.D. & Treat, A.E. (1957) Ultrasonic reception by the tympanic organ of noctuid moths. *Journal of Experimental Biology*, **134**, 127-158.

Root, R.B. (1973) The niche exploitation of the blue-gray gnatcatcher. *Ecological Monographs*, **37**, 317-350.

Roughgarden, J. (1983) Competition and theory in community ecology. *American Naturalist*, **122**, 583-601.

Russo, D. & Jones, G. (2002) Identification of twenty-two bat species (Mammalia: Chiroptera) from Italy by analysis of time-expanded recordings of echolocation calls. *Journal of Zoology, London*, **258**, 91-103.

Rutherford, M.C. (1997). Categorization of biomes. In *Vegetation of Southern Africa*. (eds R.M. Cowling, D.M. Richardson & S.M. Pierce), pp. 91-98. Cambridge University

Press, Cambridge.

Rutherford, M.C. & Westfall, R.H. (1986) Biomes of southern Africa - an objective categorization. *Mem. Bot. Surv. S. Afr.*, **54**, 1-98.

Rydell, J. (1992) Exploitation of insects around streetlamps by bats in Sweden. *Functional Ecology*, **6**, 744-750.

Rydell, J., Jones, G., & Waters, D.A. (1995) Echolocating bats and hearing moths: who are the winners? *Oikos*, **73**, 419-424.

Rydell, J. & Lancaster, W.C. (2000) Flight and thermoregulation in moths were shaped by predation from bats. *Oikos*, **88**, 13-18.

Saunders, M.B. & Barclay, R.M.R. (1992) Ecomorphology of insectivorous bats: a test of predictions using two morphologically similar species. *Ecology*, **73**, 1335-1345.

Schluter, D. (1984) A variance test for detecting species associations, with some example applications. *Ecology*, **65**, 998-1005.

Schluter, D. & McPhail, J.D. (1992) Ecological character displacement and speciation in sticklebacks. *The American Naturalist*, **140**, 85-108.

Schluter, D., Price, T.D., & Grant, P.R. (1985) Ecological character displacement in Darwin's finches. *Science*, **227**, 1056-1059.

Schnitzler, H.-U. (1987). Echoes of fluttering insects: Information for echolocating bats. In *Recent Advances in the Study of Bats*. (eds M.B. Fenton, P.A. Racey & J.M.V. Rayner), pp. 226-243. Cambridge University Press, Cambridge.

Schnitzler, H.-U. & Kalko, E.K.V. (1998). How echolocating bats search and find food. In *Bat Biology and Conservation* (eds T.H. Kunz & P.A. Racey), pp. 183-196. Smithsonian Institution Press, Washington DC.

Schnitzler, H.-U. & Kalko, E.K.V. (2001) Echolocation by insect-eating bats. *BioScience*, **51**, 557-569.

Schoeman, M.C. & Jacobs, D.S. (2003) Support for the allotonic frequency hypothesis in an insectivorous bat community. *Oecologia*, **134**, 154-163.

Schoener, T.W. (1974) Resource partitioning in ecological communities. *Science*, **185**, 27-39.

Schoener, T.W. (1983) Field experiments on interspecific competition. *American Naturalist*, **122**, 240-285.

Schoener, T.W. (1984). Size differences among sympatric, bird-eating hawks: a world-wide survey. In *Ecological Communities: Conceptual Issues and the Evidence*. (eds D.R. Strong, D. Simberloff, L.G. Abele & A.B. Thistle), pp. 254-279. Princeton University Press, Princeton.

Schoener, T.W. (1986a). Overview: kinds of ecological communities - ecology becomes pluristic. In *Community Ecology*. (eds T.J. Case & J. Diamond), pp. 467-479. Harper and Row, New York.

Schoener, T.W. (1986b). Resource Partitioning. In *Community Ecology* (ed J. Kikkawa), pp. 91-125. Blackwell, Oxford.

Scholes, R.J. (1997). Savanna. In *Vegetation of Southern Africa*. (eds R.M. Cowling, D.M. Richardson & G.J. Pierce), pp. 258-277. Cambridge University Press, Cambridge.

Scholtz, C.H. & Holm, E., eds. (1985) *insects of Southern Africa*. University of Pretoria, Pretoria.

Schulze, R.E. (1997). Climate. In *Vegetation of Southern Africa*. (eds R.M. Cowling, D.M. Richardson & G.J. Pierce), pp. 21-42. Cambridge University Press, Cambridge.

Schum, M. (1984) Phenetic structure and species richness in North and Central American bat faunas. *Ecology*, **65**, 1315-1324.

Scoble, M.J. (1995) *The Lepidoptera: Form, Function and Diversity* Oxford University Press, Oxford.

Sedgeley, J.A. & O'Donnell, C.F.J. (1999) Factors influencing roost cavity selection by a temperate rainforest bat (*Chalinolobus tuberculatus*, Vespertilionidae) in New Zealand. *Journal of Zoology, London*, **249**, 437-446.

Siemers, B.M. & Schnitzler, H.-U. (2004) Echolocation signals reflect niche differentiation in five sympatric congeneric bat species. *Nature*, **429**, 657-661.

Simberloff, D. (1982) The status of competition theory in ecology. *Annales Zoologici Fennici*, **19**, 241-253.

Simmons, J.A. & Stein, R.A. (1980) Acoustic imaging in bat sonar: Echolocation signals and the evolution of echolocation. *Journal of Comparative Physiology A*, **135**, 61-84.

Simmons, N.B. (1998). A reappraisal of interfamilial relationships of bats. In *Bat Biology and Conservation*. (eds T.H. Kunz & P.A. Racey), pp. 3-26. Smithsonian University Press, Washington D.C.

Simmons, N.B. (2003). Order Chiroptera. In *Mammal Species of the World: A Taxonomic and Geographic Reference* (eds D.E. Wilson & D.M. Reeder). Smithsonian Institution Press, Wasgington D.C.

Simmons, N.B. & Conway, T.M. (2004). Evolution of Ecological Diversity. In *Bat Ecology*. (eds T.H. Kunz & M.B. Fenton), pp. 493-535. The University of Chicago Press, Chicago.

Simmons, N.B. & Geisler, J.H. (1998) Phylogenetic relationships of *Icaronycteris*, *Archaeonycteris*, *Hassianycteris*, and *Palaeochiropteryx* to extant bat lineages, with comments on the evolution of echolocation and foraging strategies in Microchiroptera. *Bulletin of the American Museum of Natural History*, **235**, 1-182.

Simmons, N.B. & Voss, R.S. (1998) The Mammals of Paracou, French Guiana: a Neotropical lowland rainforest fauna. 1. Bats. *Bulletin of the American Museum of Natural History*, **237**, 1-219.

Simpson, G.G. (1960) Notes on the measurement of faunal resemblance. *American Journal of Science*, **258**, 300-311.

Skinner, J.D. & Smithers, R.H.N. (1990) *The Mammals of the Southern African Subregion*, 2 edn. University of Pretoria, Pretoria.

Soberon, J.M. & Llorente, J.B. (1993) The use of species accumulation functions for the prediction of species richness. *Conservation Biology*, **7**, 480-488.

Spangler, H.G. (1988) Moth hearing, defense and communication. *Annual Review of Entomology*, **33**, 59-81.

Speakman, J.R. (1995) Chiropteran nocturnality. *Symposia of the Zoological Society of London*, **67**, 187-201.

Speakman, J.R., Rydell, J., Webb, P.I., Hayes, J.P., Hulbart, I.A.R., & McDevitt, R.M. (2001) Activity patterns of insectivorous bats and birds in northern Scandinavia (69 W) during continuous midsummer night. *Oikos*, **88**, 75-86.

Srivastrava, D.S. (1999) Using local-regional species richness plots to test for species saturation: pitfalls and potentials. *Journal of Animal Ecology*, **68**, 1-16.

Stadelmann, B., Jacobs, D.S., Schoeman, M.C., & Ruedi, M. (2004) Phylogeny of African Myotis bats (Chiroptera, Vespertilionidae) inferred from cytochrome b sequences. *Acta Chiropterologica*, **6**, 177-192.

Stevens, G.C. (1989) The latitudinal gradient in geographical range: how so many species coexist in the tropics. *American Naturalist*, **133**, 240-256.

Stevens, J. (1986) *Applied multivariate statistics for the social sciences*. Erlbaum, Hillsdale, NJ.

Stevens, R.D. & Willig, M.R. (1999) Size assortment in new world bat communities. *Journal of Mammalogy*, **80**, 644-658.

Stevens, R.D. & Willig, M.R. (2000) Density compensation in New World bat communities.

Oikos, **89**, 367-377.

Stevens, R.D., Willig, M.R., & Strauss, R.E. (2006) Latitudinal gradients in the phenetic diversity of New World bat communities. *Oikos*, **112**, 41-50.

Stone, L. & Roberts, A. (1990) Ther checkerboard score and species distributions. *Oecologia*, **85**, 74-79.

Stone, L. & Roberts, A. (1992) Competitive exclusion, or species aggregation? An aid in deciding. *Oecologia*, **91**, 419-424.

Strong, D.R., Simberloff, D., Abele, L.G., & Thistle, A.B. (1984) *Ecological Communities: Conceptual Issues and the Evidence*. Princeton University Press, Princeton.

Strong, D.R., Szyska, L.A., & Simberloff, D. (1979) Tests of community-wide character displacement against null hypotheses. *Evolution*, **33**, 897-913.

Studier, E.H. & Sevick, S.H. (1992) Live mass, water content, nitrogen and mineral levels in some insects from south-central lower Michigan. *Comparative Biochemistry and Physiology Part A*, **103**, 579-595.

Surlykke, A. (1988). Interaction between echolocating bats and their prey. In *Animal sonar: processes and performance* (eds P.E. Nachtigall & P.W.B. Moore), pp. 551-566. Plenum Press, New York.

Surlykke, A., Filskov, M., Fullard, J.H., & Forrest, E. (1999) Auditory relationships to size in Noctuid moths: bigger is better. *Naturwissenschaften*, **86**, 238-241.

Surlykke, A., Skals, N., Rydell, J., & Svensson, M.G.E. (1998) Sonic hearing in a diurnal geometric moth *Archiears parthenias* (L.) temporally isolated from bats. *Naturwissenschaften*, **85**, 36-37.

Swartz, S.M., Freeman, P.W., & Stockwell, E.F. (2004). Ecomorphology. In *Bat Ecology* (eds T.H. Kunz & M.B. Fenton), pp. 257-300. University of Chaicago Press, Chicago.

Swofford, D.L. (2002) PAUP - Phylogenetic Analysis using Parsimony (and Other Methods). Version 4. Sinauer Associates, Sunderland, Massachusetts.

Taper, K.M.L., Bohning-Gaese, K., & Brown, J.H. (1995) Individualistic responses of bird species to environmental change. *Oecologia*, **101**, 478-486.

Taylor, P.J. (1999) Problems with the identification of southern African *Chaerephon* (Molossidae) and the possibility of a cryptic species from South Africa and Swaziland. *Acta Chiropterologica*, **1**, 191-200.

Taylor, P.J. (2000) *Bats of Southern Africa*. University of Natal Press, Pietermaritzburg.

Teeling, E.C., Madsen, O., Van Den Bussche, R.A., de Jong, W.W., Stanhope, M.J., & Springer, M.S. (2002) Microbat paraphyly and the convergent evolution of a key innovation in Old World rhinolophoid microbats. *PNAS*, **99**, 1431-1436.

Teeling, E.C., Scally, M., Kao, D.J., Romagnoli, M.S., Springer, M.S., & Stanhope, M.J. (2000) Molecular evidence regarding the origin of echolocation and flight in bats. *Nature*, **403**, 188-192.

Thomas, S.P. (1987). The physiology of bat flight. In *Recent Advances in the Study of Bats* (eds M.B. Fenton, P.A. Racey & J.M.V. Rayner), pp. 75-99. Cambridge University Press, Cambridge.

Thompson, J.N. (1994) *The Coevolutionary Process*. University of Chicago Press, Chicago.

Treat, A.E. (1955) The response to sound in certain Lepidoptera. *Annals of the Entomological Society of America*, **48**, 272-284.

Tuttle, M.D. & Ryan, M.J. (1981) Bat predation and the evolution of frog vocalizations in the Neotropics. *Science*, **214**, 677-678.

Tuttle, M.D. & Stevenson, D. (1982). Growth and survival of bats. In *Ecology of Bats*. (ed T.H. Kunz), pp. 105-150. Plenum Press, New York.

Ugland, K.I., Gray, J.S., & Ellingsen, K.E. (2003) The species-accumulation curve and estimation of species richness. *Journal of Animal Ecology*, **72**, 888-897.

Van Den Bussche, R.A. & Hoofer, S.R. (2004) Phylogenetic relationships among recent chiropteran families and the importance of choosing appropriate out-group taxa. *Journal of Mammalogy*, **85**, 321-330.

Van Valen, L. (1965) Morphological variation and width of the ecological niche. *American Naturalist*, **94**, 377-390.

Volterra, V. (1926). Variations and fluctuations of the number of individuals of animal species living together. In *Animal Ecology* (ed R.N. Chapman). McGraw-Hill, New York.

von der Emde, G. & Menne, D. (1989) Discrimination of insect wingbeat-frequencies by the bat Rhinolophus ferrumequinum. *Journal of Comparative Physiology A*, **164**, 663-671.

von der Emde, G. & Schnitzler, H.-U. (1990) Classification of insects by echolocating greater horseshoe bats. *Journal of Comparative Physiology A*, **167**, 423-430.

Waters, D.A. (2003) Bats and moths: what is there left to learn? *Physiological Entomology*, **28**, 237-250.

Waters, D.A. & Jones, G. (1995) Echolocation call structure and intensity in five species of insectivorous bats. *Journal of Experimental Biology*, **198**, 475-489.

Waters, D.A. & Jones, G. (1996) The peripheral auditory characteristics of noctuid moths: nresponses to search-phase echolocation calls of bats. *Journal of Experimental Biology*, **199**, 857-868.

Waters, D.A., Rydell, J., & Jones, G. (1995) Echolocation call design and limits on prey size: a case study using the aerial-hawking bat *Nyctalus leisleri*. *Behav. Ecol. Sociobiol.*, **37**, 321-328.

Webb, C.O., Ackerly, D.D., McPeek, M.A., & Donoghue, M.J. (2002) Phylogenies and community ecology. *Ann. Rev. Ecol. Syst.*, **33**, 475-505.

West, G.B., Brown, J.H., & Enquist, B.J. (1997) A general model for the origin of allometric scaling laws in biology. *Science*, **276**, 122-126.

Whitaker, J.O. (1988). Food habits analysis of insectivorous bats. In *Ecological and Behavioral Methods for the Study of Bats* (ed T.H. Kunz), pp. 171-189. Smithsonian Institution Press, Washington DC.

Whitaker, J.O. (1994) Food availability and opportunistic versus selective feeding in insectivorous bats. *Bat Research News*, **35**, 75-77.

Whitaker, J.O. & Black, H.L. (1976) Food habits of cave bats from Zambia. *Journal of Mammalogy*, **57**, 199-205.

Whitaker, J.O., Suthakar, I.S., Marimuthu, G., & Kunz, T.H. (1999) Seasonal variation in the diet of the Indian pygmy bat, Pipistrellus mimus, in southern India. *Journal of Mammalogy*, **80**, 60-70.

White, F.B. (1877) Untitled communication. *Nature*, **15**, 293.

Wiens, J.A. (1981) Single-sample surveys of communities: are the revealed patterns real? *American Naturalist*, **117**, 90-98.

Wiens, J.A. (1989) *The Ecology of Bird Communities. Vol. 1. Foundations and Patterns* Cambridge University Press, Cambridge.

Wiens, J.A., Stenseth, N.C., Van Horne, B., & Ims, R.A. (1993) Ecological mechanisms and landscape ecology. *Oikos*, **66**, 369-380.

Williams, C.B. (1964) *Patterns in the Balance of Nature*. Academic Press, London.

Williamson, M.H. (1987). Are communities ever stable? In *Colonization, Succession, and Stability*. (eds A.J. Gray, M.J. Crawley & P.J. Edwards). Blackwell, Oxford.

Willig, M. & Moulton, M.P. (1989) The role of stochastic and deterministic processes in structuring Neotropical bat communities. *Journal of Mammalogy*, **70**, 323-329.

Willig, M.R. (1986) Bat community structure in South America: a tenaceous chimera. *Revista Chilena de Historia Natural*, **59**, 151-168.

Willig, M.R., Patterson, B.D., & Stevens, R.D. (2004). Range Size, Richness, and Body Size. In *Bat Ecology* (eds T.H. Kunz & M.B. Fenton), pp. 580-621. Chicago University Press, Chicago.

Wilson, E.O. (1992) *The Diversity of Life*. Penguin Books Ltd., London.

Wilson, J.B. (1987) Methods for detecting non-randomness in species co-occurrences: a contribution. *Oecologia*, **73**, 579-582.

Wilson, J.B. (1989) A null model of guild proportionality, applied to stratification of a New Zealand temperate rain forest. *Oecologia*, **80**, 263-267.

Wilson, J.B., Gitay, H., & Agnew, D.Q. (1987) Does niche limitation exist? *Functional Ecology*, **1**, 391-397.

Wilson, J.B. & Roxburgh, S.H. (1994) A demonstration of guild-based assembly rules for a plant community, and demonstration of intrinsic guilds. *Oikos*, **69**, 267-276.

Wilson, J.B. & Whittaker, R.J. (1995) Assembly rules demonstrated in a saltmarsh community. *Journal of Ecology*, **83**, 801-807.

Winemiller, K.O. & Pianka, E.R. (1990) Organization in natural assemblages of desert lizards and tropical fishes. *Ecological Monographs*, **60**, 27-55.

Zar, J.H. (1999) *Biostatistical analysis 4th edn*. Prentice-Hall, Englewood Cliffs, N. J.