Factors affecting the emergence times of seven sympatric insectivorous bat species

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In memory of Graham Barry Thomas (22-03-1959 to 02-11-2009)

A father no daughter could forget!

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Declaration

I, Alicia Jessica Thomas, know the meaning of plagiarism and declare that all of the work in the document, save for that which is properly acknowledged, is my own.

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Abstract

The onset of activity in animals restricted to being active for only part of the day, is one of the most fundamental aspects of their biology. Onset of activity is likely subject to several factors including presence/absence of predators and the vagaries of environmental conditions at the time of emergence. The aim of my study was to test several hypotheses accounting for differing emergence times amongst sympatric insectivorous bat species. I recorded the emergence times of seven species of bats (*Myotis tricolor, Rhinolophus capensis, Rhinolophus clivosus, Miniopterus natalensis, Neoromicia capensis, Nycteris thebaica, Tadarida aegyptiaca*) within the same community, by recording echolocation calls as they emerged. I also measured predation risk, food availability, and recorded weather conditions at the site during a single season (summer). As expected in nocturnal animals, peak emergence was correlated with sunset time and appeared to be a function of foraging strategy, diet and the risks posed by predators. Clutter foragers emerged earlier than clutter-edge and open foragers, suggesting that vegetative cover is important for bats trying to avoid predation. Bats feeding on Lepidoptera emerged earlier than bats feeding on Diptera. However, insect peak activity was highly variable and did not differ between orders or time of year. None of the weather variables I measured were correlated with emergence.

Chapter 1

INTRODUCTION

The terrestrial environment is subject to constant rhythmic changes including light intensity, temperature, humidity, day length and duration of twilight (Erkert 1982). Organisms have to adapt to these changing environmental conditions to survive and reproduce, usually by limiting their activity to parts of the day or night when conditions are most favourable (Erkert 1982). The evolution of circadian rhythms is therefore a key step in the adaptation of organisms to changing environments (Haeussler and Erkert 1978; Erkert 1982). Factors that influence these rhythms can be divided into extrinsic environmental factors (*e.g*. predation, food availability and weather conditions) and intrinsic factors (*e.g*. foraging strategy, diet and foraging habitat).

The most influential environmental factor affecting activity is probably time of day (or rather sunset and sunrise) and the activity of most animals can be broadly divided into diurnal activity (which include most animals *e.g.* most birds, lizards, some snakes, mongoose, monkeys and horses; Aschoff 1966; Berger 1977; Shine 1979; Uehara and Ihobe 1998; Blouin-Demers 2000; Cant *et al*. 2002; Stapley 2004) or nocturnal activity (*e.g.* bats, owls, hedgehogs, and jaguars; Haeussler and Erkert 1978; Erkert 1982; Rabinowitz and Nottingham 1986; Taylor 1994; Rondinini and Doncaster 2002). Of course there are always exceptions to the rule; crepuscular activity, which are animals that are active on the boarder of night and day (*i.e*. dusk or dawn), including spotted hyena, nightjars and Florida panther (Maehr 1997; Jetz *et al*.

2003; Kolowski *et al*. 2007; Mills 2008). The onset (*i.e*. emergence) of activity is typically initiated by environmental cues (Aschoff 1966; Haeussler and Erkert 1978; Erkert 1982) including; light intensity (day/night and lunar cycles; Mills 2008), precipitation (*e.g.* rainfall, snow, and hail), temperature, cloud cover, humidity (Aschoff 1966; Haeussler and Erkert 1978; Erkert 1982; Lacki 1984) and predation risk (Speakman 1991 a, b; Jones and Rydell 1994; Rydell and Speakman 1995; Rydell *et al.* 1996).

Environmental variables can influence several activities including the initiation of emergence or the reduction or cessation of activity. One of these variables is changing light levels associated with the lunar cycle and several nocturnal organisms are known to change their activity in response to the lunar cycle (Erkert 1982; Lang *et al*. 2006). A decrease in activity over periods of full moon (or high light intensity) has been suggested as an anti-predatory mechanism employed by many animals, known as lunar phobia, such as the woolly opossum, *Caluromys philander,* (Julien-Laferrière 1997), the grasshopper mouse, *Onychomys leucogaster breviauritus* (Jahoda 1973), the Galápagos fur seal, *Arctocephalus galapagoensis* (Trillmich and Mohren 1981; Horning and Trillmich 1999), and snowshoe hares, *Lepus americanus* (Gilbert and Boutin 1991).

The effect of weather (*i.e.* temperature, rainfall, cloud cover, and humidity) on the emergence and activity of animals depends on the cost-benefit ratio of emerging in unfavourable conditions (Erkert 1982) and might be expected to have a positive or a negative effect. In some cases precipitation (*e.g*. rainfall) can encourage emergence (*e.g.* spadefoot Toad, *Scaphiopus,* Dimmitt and

Ruibal 1980; and turtles, *Testudines*, Gibbons and Nelson 1978) while in others it can delay or prevent emergence (*e.g.* giant sand scorpion, *Paruroctonus mesaensis*, Polis 1980 and red foxes,*Vulpes fulva*, Ables 1969). The severity of rainfall may also influence activity patterns for example some rodents decrease their activity as rainfall increases (O'Farrell 1974).

Cloud cover generally favours emergence as light levels and therefore predation risk are decreased (*e.g*. masked shrew, *Sorex cinereus*, increased their activity on cloudy nights; Doucet and Bider 1974). Temperature extremes (*i.e*. cold or hot), on the other hand, tend to decrease or prevent emergence and activity (Erkert 1982) and animals will alter their emergence and activity patterns in response to temperature changes. Red foxes, *Vulpes fulva*, (Ables 1969) and greater kudu, *Tragelaphus strepsiceros*, (Owen-Smith 1998) increase activity as temperature decreases. Owl monkey's, *Aotus azarsi*, increase activity with warmer temperatures (Fernandez-Duque 2003), while raccoon dogs, *Nyctereutes procyonoides*, (Kauhala *et al*. 2007) become less active with decreasing temperatures.

Evaporative water loss can also be an important determinant of animal activity, particularly in small mammals (Vickery and Bider 1981; Baudinette *et al.* 2000) which have a high surface area to volume ratio and therefore have a larger relative area of body over which to lose water (Vickery and Bider 1981). As a result some of these mammals time their activity to occur during periods when evaporative water loss is at a minimum. For example, humidity negatively affects evaporative water loss in animals; southern red backed voles, *Clethrionomys gapperi,* increase activity with increased humidity when water loss is lower (Vickery and Bider 1981).

Risk of predation has also been suggested as a driving factor in determining an animal's activity levels (Lima 1998). The cost associated with emerging from a refuge must be outweighed by the benefit of emerging *i.e.* gaining foraging and reproductive opportunities (Gilliam and Fraser 1987; Sih 1992; Lima 1998). An animal would be expected to optimise its fitness by balancing the costs and benefits associated with the decision to emerge or not (Lima 1998). Animals use both direct and indirect cues for detecting predators (Thorson *et al*. 1998). Direct cues include those that are produced by the predator such as visual, olfactory, auditory and tactile cues (Thorson *et al.* 1998). Indirect cues are those not produced by the predator but are rather associated with the likelihood of encountering a predator. These include the type of substrate, presence of vegetation, diameter of vegetation and light level (Thorson *et al*. 1998). Alpine, *Lacerta monticola*, (Martín and López 1999; Martín *et al*. 2003) and scincid lizards, *Eumeces laticeps*, (Cooper 1998) both adjust emergence times (*i.e.* emerge later) due to the perceived presence of a predator.

In summary, the effect of environmental and predatory cues on emergence times is variable between species, affecting each species differently depending on life history and ecological traits. Furthermore, the emergence and activity patterns of some animals can be cryptic, making the study of such behaviour difficult. Some species (*e.g*. bats) are more amenable to studying factors influencing emergence times because their emergence is a predictable and conspicuous event (Erkert 1982; Speakman *et al*. 1999).

Bats (Order: Chiroptera) are the second largest order of mammals and occur in a variety of habitats (Thomas and Suthers 1972). They spend most of the day time in roosts which provide stable microclimates, protection from predators and unfavourable weather (Kunz 1982; Chruszcz and Barclay 2002; Jacobs *et al*. 2007). Bats are nocturnal, emerging from roosts at dusk and sometimes only returning to roosts near sunrise (Erkert 1978, 1982; Duvergé 2000; Kaňuch 2007). Some use night roosts between foraging bouts (Anthony *et al.* 1981; Speakman 1999). By avoiding diurnal activity bats not only avoid potential diurnal predators such as birds of prey (Erkert 1982; Speakman 1991 a; Rydell and Speakman 1995; Rydell *et al*. 1996) but also competition for food from diurnal animals (Jones and Rydell 1994). Many species emerge from roosts to forage before the sun has fully set to take advantage of the peak in insect activity which occurs at dusk (Pavey *et al*. 2001). Technically, this period, known as civil twilight, also called dusk or dawn, is defined as the time when the sun is either 6° below or above the horizon, respectively. For example, *Hipposideros speoris* forage during civil twilight making use of peak insect abundance during that time (Pavey *et al*. 2001).

The emergence times of bats are variable both within and between species and this variability has been attributed to a number of intrinsic and extrinsic factors. Intrinsic factors specifically suggested to be important for bats include foraging strategy (Anthony *et al*. 1981; Jones and Rydell 1994; Rydell *et al*. 1996; Clark *et al*. 2002), body size which is related to flight speed (Taake 1985; Jones and Rydell 1994; Rydell *et al*. 1996), age (Duvergé *et al*. 2000; Lee and McCracken 2001), sex (Kunz 1974) and reproductive status (Anthony *et al*. 1981; Rydell 1989; Lee and McCracken 2001; Clark *et al*. 2002). While the extrinsic factors include weather conditions (temperature, rain, cloud cover, humidity; DeCoursey and DeCoursey 1964; Lacki 1984; Kunz and Anthony 1996; O'donnell 2000; Erickson and West 2002; Weinbeer *et al.* 2006), predation risk (Speakman 1991 a, b; Jones and Rydell 1994; Rydell and Speakman 1995; Gannon and Willig 1996; Welbergen 2006), competition avoidance (with insectivorous birds; Jones and Rydell 1994), light levels (Aschoff 1966; Haeussler and Erkert 1978; Erkert 1982; Gannon and Willig 1996; Elangovan and Marimuthu 2001; Karlsson *et al*. 2002), food availability (Erkert 1982; Jones and Rydell 1994; O'Donnell 2000), noise (Shirley *et al*. 2001), colony size (Speakman *et al*. 1999) and seasonal variation (O'Donnell 2000; Clark *et al*. 2002). It has also been suggested that inter-specific differences in emergence times is related to predation risk, foraging strategy and dietary specialization (Rydell *et al*. 1996; Duvergé *et al*. 2000).

Although variable, emergence from roosts is nonetheless predictable and conspicuous because bats have to emerge to forage (Erkert 1982; Speakman *et al*. 1999). This predictability may encourage predators as it creates a reliable potential food source. Bats are hunted by a variety of predators including amphibians, reptiles, mammals, birds and fish (Speakman 1991 a). Predation events on bats by birds of prey, for example owls, appear to be opportunistic and in most situations do not constitute a major part of the birds' diet (Baker 1962; Vernon 1972; Morrison 1978 a; Ruprecht 1979; Speakman 1991 a). However, Speakman (1991 a) calculated that about 11% of the annual mortality of British bats results from avian predators, despite bats making up only a small percentage of the these birds' diet. The risk of predation (by birds) is estimated to be two orders of magnitude greater for bats that fly during the day (Speakman 1991 a). Predation risk may therefore be a significant factor selecting for nocturnal activity in bats (Erkert 1982; Speakman 1991 a; Rydell and Speakman 1995).

Information on the predation pressures on bats is mostly anecdotal (Twente 1954; Baker 1962; Speakman 1991 a; Swengel and Swengel 1992; Fenton *et al*. 1994; Sparks *et al*. 2003; Lang *et al*. 2006). It has been suggested that nocturnality (Speakman 1991 a, b), coloniality (Kunz 1982) and clustering (dilution effect; Duvèrge *et al*. 2000) act as mechanism of predator avoidance. The risk of predation likely increases with the light levels occurring during activity (Erkert 1982; Speakman 1991 a, b; Gannon and Willig 1997; Meyer *et al*. 2004; Lang *et al*. 2006). Baxter *et al*. (2006), using an artificial acoustic predator cue, simulating the presence of an owl, found that bats change foraging behaviour in response to a perceived predation risk. Fewer bats were recorded foraging in the vicinity of the acoustic cue playback stations than at the control stations. They acknowledge that the reaction could have resulted from disturbance caused by the noise from the cue and not actually perceived predation risk (Baxter *et al*. 2006). Conversely, Kalcounis and Brigham (1994) using a similar method found no effect on bat activity when presented with a predator model.

Measuring the effect of predation is difficult in bats due to the difficulty of making direct observations during darkness (Twente 1954; Baker 1962;

Sparks *et al.* 2003). Many birds of prey including owls regurgitate the bones of their prey (Dodson and Wexlar 1979). These pellets are often used by mammalogists to assess the small mammal community in a region (Dodson and Wexlar 1979; Avenant 2005; Avery *et al*. 2005). Regurgitated pellets have been used to determine diets of birds of prey (Vernon 1972; Marti 1974; Dodson and Wexlar 1979; Rupercht 1979; Avery *et al*. 1985; Swengel and Swengel 1992; Avenant 2005), but also to assess the impact of these birds on small mammal populations (Vernon 1972; Ruprecht 1979; Speakman 1991 a; Swengel and Swengel 1992; Avenant 2005). Unlike many other birds of prey (*e.g*. hawks*; Accipitridae*, Smith and Richmond 1972; Taylor 1994) the pH of an owls stomach is relatively high (less acidic), making pellets ideal for dietary studies because bones of prey remain undigested (Taylor 1994). Therefore the bones found in pellets closely matches that of the prey consumed (Dodson and Wexlar 1979). The remains of even the most delicate animals have been found in undamaged pellets, allowing for relatively easy identification (Taylor 1994). This allows for an assessment of the predation level they exert on different species. It may therefore be a mechanism though which predation pressure could be estimated.

Light intensity has been linked to the risk of predation (Gannon and Willig 1997; Meyer *et al*. 2004; Lang *et al*. 2006). The higher the light intensity, the greater the risk of predation by visually orienting predators (*e.g.* birds of prey; Meyer *et al*. 2004).The effect of the lunar light levels (as part of the monthly cycle) on animal behaviour is dependent on whether the animal is a predator, prey or both (Lang *et al*. 2006). Predators relying on vision to detect and catch their prey will benefit from bright moonlight as their prey will be easier to detect (Lang *et al*. 2006). Prey on the other hand should try to avoid periods of bright light in an attempt to elude predators (Lang *et al*. 2006). Animals that are both predators and prey must balance the risk of being predated with the benefit of foraging (Lima 1998; Lang *et al*. 2006).

Light sampling is employed by many bats apparently to assess light levels outside before they emerge to begin foraging (Twente 1955). It involves one or two bats flying into the light zone and turning around and flying back into their roost. As light levels decreased bats fly farther and farther from the entrance (Twente 1955). This behaviour continues until just before the onset of full emergence (Twente 1955). This behaviour may synchronize daily and seasonal activity with changing sunset time, serving as an external cue that entrains the internal time-keeping system of organisms (DeCoursey and DeCoursey 1964; Aschoff 1966; Clark *et al*. 2002).

The avoidance of high light intensities (*i.e.* full moon) has been suggested to decrease predation risk and is known as lunar phobia (Morrison1978 a, b; Erkert 1982; Jones and Rydell 1994; Rydell and Speakman 1995; Lang *et al*. 2006). Lunar phobia has been reported in frugivorous bats such as *Cynopterus sphinx* (Elangovan and Marimuthu 2001), *Artibeus jamaicensis* (Morrison 1978 a, b), *Artibeus lituratus* and *Phyllostomus discolour* (Haeussler and Erkert 1978) and *Stenoderma rufum* (Gannon and Willig 1997) and vampire bats, *Desmodus rotundus.* Vampire bats are only active during true night (the point where there is no longer any sunlight only lunar light) and decrease activity during bright periods near full moon (Wimsatt 1969; Crespo *et al*. 1972). Insectivorous bats which exhibit lunar phobia include *Eptesicus nilssonii*, *Rhinolophus ferrumequinum* and *R. hipposideros* (Duvergé *et al*. 2000), *Myotis yumanensis* (Reith 1982), *Lophostoma silvicolum* (Land *et al.* 2006), *Nyctalus leisleri* (Shiel and Fairley 1999), *Scotophilus viridus, Eptesicus capensis and Nycticeius schlieffeni* (Fenton *et al*. 1977). On the other hand some species do not exhibit an obvious reaction to moonlight and changes to activity during full moon are related to factors other than light level. Such species include *Myotis lucifugus* (Negraeff and Brigham *et al*. 1995; Hecker and Brigham 1999), *M. californicus, M. evotis, M. keenii, M. yumanensis, M, volans, Lasiurus cinereus, Lasionycteris noctivagans, Corynorhinus townsendii* and *Eptesicus fuscus* (Hecker and Brigham 1999) *Carollia castanea* (Thies *et al.* 2006), and *Corynorhinus townsendii ingens* (Clark *et al*. 1999).

The behavioural responses of bats to light intensity may not be associated with predation but due to the effect of light on prey (Brown 1968; Rydell *et al*. 1996; Lang *et al*. 2006). Emergence times of insectivorous bats would be expected to coincide with the timing of insect flights. Thus, inter-specific variation in emergence times may be the result of variation in prey selection and availability (Rydell *et al*. 1996). Moon phase and weather influence insect density which in turn should mediate bat activity (Anthony *et al*. 1981; O'Donnell 2000). An example of this would be the interaction between *Lophostoma silvicolum* and their main prey, katydids, both are more active during dark periods associated with new moon (Lang *et al*. 2006). There are however, instances where no relationship occurs between numbers of insects and the lunar cycle (Williams *et al*. 1956).

Insect activity changes seasonally (Rautenbach *et al*. 1988; Wolda 1988). Temperature and rainfall influence insect density and activity (Rautenbach *et al*. 1988; Rydell 1989). Insect activity often decreases once the temperature reaches a threshold point of around 6-10°C, but this may be site specific (Rydell 1989). High temperatures and humidity create suitable conditions for peak arthropod activity at dusk. Bats have likely been selected to take advantage of this dusk peak in insect activity (Rautenbach *et al*. 1988). There is also evidence to suggest that the emergence of aquatic insects is the most important factor affecting the activity of riparian-foraging bats (Fukui *et al*. 2006). Taken together, these points of evidence suggest that bat activity is related to insect activity which may be related to both light intensity and weather conditions.

Bats are small endotherms and therefore spend considerable energy devoted to maintaining normothermic (condition of normal body temperature) body temperatures when not in torpor (Erickson and West 2002). Torpor is a mechanism by which bats reduce energy consumption during periods of inactivity (*i.e.* while roosting). It involves decreasing metabolic rates which as a consequence leads to a decline in body temperature (Bartels *et al*. 1998). Unfavourable weather conditions add additional energetic costs for thermoregulation when there is decreased food availability (Erickson and West 2002). This leads to the expectation that activity will change with changes in weather conditions (O'Donnell 2000; Clark *et al*. 2002). Weather variables that could possibly account for variation in activity include temperature, rainfall, humidity, cloud cover, wind and drought (Herreid and Davis 1966; O'Donnell 2000; Lee and McCracken 2001; Petrželková and Zulkal 2001; Clark *et al*. 2002; Erickson and West 2002).

The emergence times of some bats are directly affected by prevailing weather conditions such as rainfall (*Nyctalus leisleri*; Shiel and Fairly 1999), humidity (*Myotis luc*ifugus; Lacki 1984), cloud cover (*Tadarida brasiliensis mexicana*; Herreid and Davis 1966, *Nyctalus leisleri*; Shiel and Fairly 1999), temperature (*Myotis lucifugus*; Anthony *et al*. 1981, *Myotis lucifugus*; Negraeff and Brigham *et al*. 1995, *Rhinolophus ferrumequinum*; Park *et al*. 1999) and drought (*Tadarida brasiliensis mexicana*; Lee and McCracken 2001). However, for other species or in other circumstances, there is no evidence for variation in emergence due to weather; cloud cover (*Corynorhinus townsendii ingens*, Clark *et al*. 2002*),* wind and rain *(Pipistrellus pipistrellus* and *Carollia castanea*, Maier 1992; Thies *et al*. 2006). Weather induced changes to activity varies among studies and may be species and site specific (Hayes 1997; O'Donnell 2000).

The foraging strategy employed by different bat species reflects flight abilities, ability to forage in particular habitats and ability to avoid predators. Clutter foragers are defined as bats that are adapted (slow and manoeuvrable) to forage in highly cluttered environments close to and in between the vegetation and ground (*e.g*. in a forest; Norberg and Rayner 1987; Schoeman and

Jacobs 2008; 2010). Clutter-edge foragers are bats that are adapted to forage on the edge of vegetation (*e.g*. forest edges and gaps), while open air foragers are bats that forage in the open and are adapted for fast agile flight (Norberg and Rayner 1987; Schoeman and Jacobs 2008; 2010). The different kinds of habitat thus provide different degrees of protection from predators and foraging strategy may therefore influence activity periods (Norberg and Rayner 1987; Jones and Rydell 1994).

The foraging strategy used by bats is also related to both echolocation call structure and morphology (Norberg and Rayner 1987). This allows one to predict which habitat they are likely to use (Norberg and Rayner 1987). For example, bats with high wing loading (ratio of weight to wing area: Mg/S(Nm^{-2}) and long narrow wings (and therefore high aspect ratios) are constrained to flying fast in open habitats, while bats with low wing loading and short wings (and low aspect ratio) should be able to fly slower in cluttered habitats (Norberg and Rayner 1987).

Flight performance is also affected by body size; as body size increase so does wing loading which results in bats needing to fly faster to generate enough lift. This in turn reduces manoeuvrability (Norberg and Rayner 1987). So larger bats fly faster and may therefore be less prone to predation than slow (*i.e.* small) bats (Jones and Rydell 1994; Rydell *et al*. 1996). All else being equal slower less manoeuvrable bats will be more prone to predation. Bats that forage in cluttered habitats need to be more manoeuvrable and less agile and therefore slower than open air foragers (Norberg and Rayner 1987).

Jones and Rydell (1994) reported that fast flying (larger; high wing loading) bats emerge earlier than slow flying bats in brighter light conditions. They also found that gleaners (bats that locate and capture stationery prey from substrate; Norberg and Rayner 1987) emerge later than aerial-hawkers (bats that capture insects in flight; Norberg and Rayner 1987).

Although many studies have investigated factors affecting the emergence times of a single species within a single- or multi-species colony, few have compared emergence by different species living in the same roost or within the same community (Jones and Rydell 1994; Rydell *et al*. 1996; Lee and McCracken 2004). Exceptions include Jones and Rydell (1994) who summarised data on a number of different species across Europe and the tropics as well as Lee and McCraken (2006) and Rydell *et al*. (1996) who each studied three different sympatric species. The purpose of my study was to assess the influence of internal and external factors on the emergence of seven species of bats within the same community: *Myotis tricolor* (mass=13.1 g), *Rhinolophus capensis* (mass= 11.1 g), *Rhinolophus clivosus* (mass= 18 g), *Miniopterus natalensis* (mass= 10.6 g), *Neoromicia capensis* (mass= 7.9 g), *Tadarida aegyptiaca* (mass=16 g) and *Nycteris thebaica* (mass= 12.6 g).

Hypotheses and predictions

(1) Predation

Predation risk affects the emergence times of bats and is influenced by lunar cycle and foraging strategy (Erkert 1982; Jones and Rydell 1994). The two components to consider when dealing with foraging strategy namely foraging habitat and flight speed. Bats flying in cluttered habitats are generally slow and manoeuvrable (typical of smaller bats) while bats foraging in the open are generally fast and agile (typical of larger bats, Norberg and Rayner 1987; Barclay and Brigham 1991; Jones and Rydell 1994). Considering flight speed alone, bats that forage in clutter should be more susceptible to predation than bats foraging in open habitat and should emerge later to avoid visually oriented predators. In this case, based on the flight categories assigned to these species by Norberg and Rayner (1987), the order of emergence should be *Tadarida aegyptiaca* (open) followed by *Miniopterus natalensis*, *Myotis tricolor*, *Neoromicia capensis*, *Rhinolophus clivosus*, *Rhinolophus capensis* and then finally *Nycteris thebaica*. However, foraging in vegetation would give bats' foraging in cluttered habitats more cover from predation (through the protection granted by the surrounding bush as well as the decreased light level within the bush compared to the open). If so, bats foraging in clutter should emerge earlier despite their slower flight and the order of emergence should therefore be *Nycteris thebaica* (clutter), *Rhinolophus capensis* (clutter and clutter-edge) *Rhinolophus clivosus* (clutter and clutter-edge), *Miniopterus natalensis* (capable of both clutter and open air foraging), *Myotis tricolor* (clutter-edge), *Neoromicia* *capensis* (clutter-edge) and *Tadarida aegyptiaca* (open). I also predicted that bats emerging from caves (*M. natalensis, My. tricolor, R. clivosus, R. capensis* and *N. thebaica*) where emergence is clustered (*i.e*. dilution effect) would emerge earlier than bats roosting in houses (*N. capensis* and *T. aegyptiaca*) which tend to emerge one at a time.

(2) Insect activity

Insect activity should affect the emergence times of bats provided prey abundance is limiting and it is energetically profitable to forage only during peak insect activity. This hypothesis predicts that the emergence times of the different species of bats will reflect the activity of their preferred prey items. Bats specializing on insects active only during complete darkness (*e.g*. moths) should delay emergence until true night and on bright moonlight nights to coincide their activity with periods when prey are active. In contrast, bats hunting crepuscular insects should not alter emergence time with lunar condition and should therefore emerge the same time on moonlight nights as on dark nights, during the period of peak insect activity. I therefore expected that bats feeding on Lepidoptera (moths; *R. capensis, R. clivosus* and *N. thebaica*) would emerge later than bats feeding on Diptera (flies; *T. aegyptiaca*), Hemiptera (bugs; *M. natalensis*) or Coleoptera (beetles; *N. capensis, My. tricolor* and *R. clivosus*, Schoeman and Jacobs 2010). However if there is no relationship between insect activity and bat emergence there should be no difference in the emergence times.

If nocturnal insects initiate activity later on moonlight nights then it is logical to expect that the bats should emerge to coincide with prey availability but it does not negate the possible effect of predation as a factor also affecting the bats emergence. If however the insects are not active later on moonlight nights but the bats are then it is consistent with the predation hypothesis.

(3) Weather conditions

Differences in emergence times may be related to prevailing weather conditions (O'Donnell 2000; Clark *et al*. 2002). Bats should emerge later on evenings with unfavourable weather conditions (for example if it's raining, windy or cold) regardless of the timing of dusk (which will change through the year). If however there is no effect of weather, bats should emerge every night at the same time relative to sunset regardless of the weather.

In summary, the predation hypothesis predicts that bats who forage near or in clutter should emerge earlier in general but particularly on moonlit nights than bats that hunt in the open as they are afforded more protection from the vegetation. All else being equal, all species should emerge later on moonlit nights. In contrast, the foraging hypothesis, predicts that bats that eat Lepidoptera will emerge later than bats that eat Diptera or Coleoptera. The weather hypothesis predicts that emergence times will be the same for all species (*i.e.* if unaffected by predation, foraging strategy or habitat, and diet) but should be delayed during unfavourable weather

Chapter 2

METHODS

2.1. Study site

My study was done in the De Hoop Nature Reserve (Fig. 2.1, 34°26′S, 20°25′ E) approximately 50 km east of Bredasdorp on the southern coast of the Western Cape Province of South Africa. The region has a Mediterranean climate with hot, dry summers and wet winters (McDonald *et al*. 1990). Along the western boundary of the reserve is a 16 km freshwater vlei, which is a shallow seasonal or intermittent lake. The water level fluctuates with season, typically with more water in the rainy season (*i.e*. winter, McDonald *et al*. 1990).

The main colony of bats within the De Hoop Nature Reserve roosts in the De Hoop Guano Cave (34°25,269´S, 20°21,532´E). Guano Cave is situated at the northern end of the reserve on the banks of the vlei in a limestone cliff (Jacobs *et al*. 2007). Five of the seven species of bats within the De Hoop Nature Reserve use it as a roost; *Miniopterus natalensis, Rhinolophus clivosus, Rhinolophus capensis, Myotis tricolor* and *Nycteris thebaica*. Around the cave the dominant vegetation is coastal fynbos mostly made up of restios; *Chondropetalum spp*. and milkwood trees; *Sideroxylon inerme* (Stoffberg and Jacobs 2004). I recorded emergence times of these five species from Guano Cave as well as two species (*Neoromicia capensis* and *Tadarida aegyptiaca*) which used the roofs of buildings in the reserve (I recorded from the research house; 34° 27.376'S, 20° 24.393'E) about 5.84 km from Guano Cave. The data were collected over three periods representing early (14 November to 2 December 2009), middle (14 – 28 February 2010) and late summer (30 March to 14 April 2010) to determine within season variation in emergence time in response to change in time of sunset.

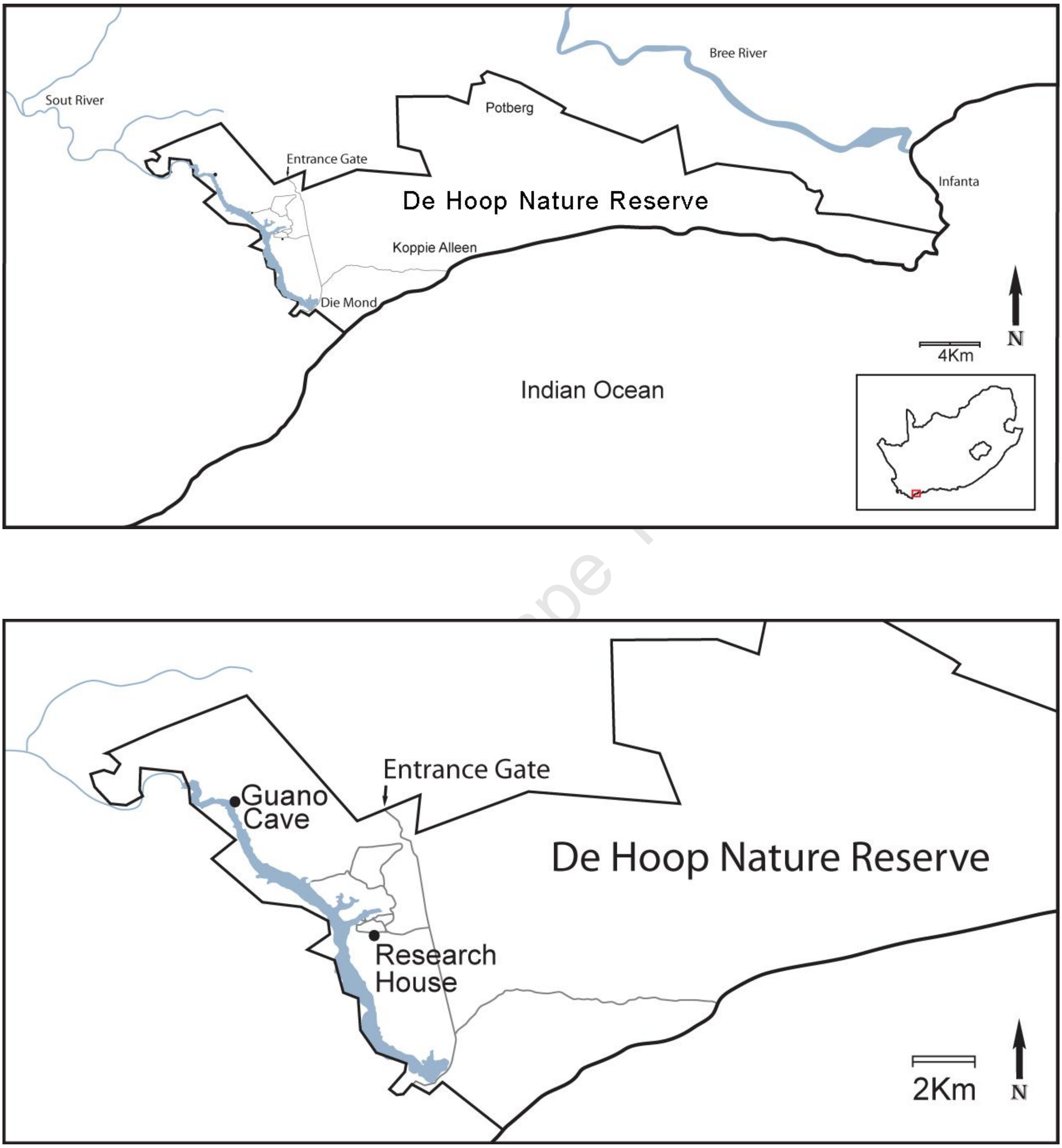


Figure 2.1: Location of the two colonies; Guano Cave and the research house within the De Hoop Nature Reserve, South Africa.

2.2. Study species

All seven species known to summer and reproduce within the De Hoop Nature Reserve were included in my study: *My. tricolor*, *N. capensis* (Family: Vespertiliondae), *R. capensis* and *R. clivosus* (Family: Rhinolophidae), *M. natalensis* (Family: Miniopteridae), *T. aegyptiaca* (Family: Molossidae) and *N. thebaica* (Family: Nycteridae). All species roost in caves except for *N. capensis* and *T. aegyptiaca* which use anthropogenic structures and use the roof spaces of most buildings within the reserve.

Nycteris thebaica (common slit-faced bat) are nasal echolocators whose nose leaf plays an important role in echolocation. They forage in dense clutter (Taylor 2000; Monadjem *et al*. 2010). *Nycteris thebaica* are extremely manoeuvrable and are reported to glean (method through which foraging bats locate and capture stationery prey from substrate; Monadjem *et al*. 2010) prey both from the ground and foliage (clutter foragers, Norberg and Rayner 1987; Monadjem *et al*. 2010). They have echolocation calls dominated by a FM (frequency modulated) component (Fig. 2.2) with a peak frequency of 77.5 kHz (Schoeman and Jacobs 2008). They occur in Fynbos, open savanna woodland, dense coastal forest and commonly roost in buildings (Taylor 2000; Monadjem *et al*. 2010). The diet is dominated by Lepidoptera but they also eat Coleoptera, Orthoptera and Hemiptera (Schoeman and Jacobs 2010).

Rhinolophus capensis (Cape horseshoe bat) is endemic to the Cape Floristic Region of south-western South Africa (Herselman and Norton 1985;

Monadjem *et al*. 2010). Their echolocation calls are dominated by a constant frequency (CF) component (i.e. most of the sound is concentrated in a very narrow frequency band, Fig. 2.2) with a peak frequency of 84.60 kHz (Odendaal and Jacobs 2010). They are predominantly found in the Fynbos and succulent karoo biomes (Monadjem *et al*. 2010). They employ slow manoeuvrable flight (Norberg and Rayner 1987) and feed on the wing while flying in dense vegetation, either by slow aerial foraging or by perch-hunting (clutter forager, Norberg and Rayner 1987; Taylor 2000; Monadjem *et al*. 2010). They eat mainly Lepidoptera, but also consume some Coleoptera and Hemiptera (Jacobs *et al*. 2007; Schoeman and Jacobs 2010).

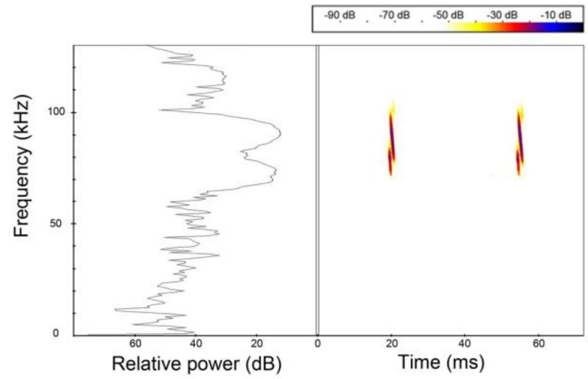
Rhinolophus capensis (*Rhinolophidae*) is morphological similar to *Rhinolophus clivosus* (Geoffory's horseshoe bat). These species can be distinguished by the presence of an anterior premolar separating the canine and the posterior premolar in *R. capensis* (Taylor 2000; Monadjem *et al*. 2010). *Rhinolophus clivosus* is also slightly bigger than *R. capensis* (Taylor 2000; Monadjem *et al*. 2010; Schoeman and Jacobs 2010). *Rhinolophus clivosus* is widely distributed throughout Africa and occurs in Fynbos, savanna, woodland and riparian forest (Taylor 2000; Monadjem *et al*. 2010). Their wing morphology and therefore foraging strategy is similar to *R. capensis* (clutter foragers, Norberg and Rayner 1987; Jacobs *et al.* 2007; Monadjem *et al*. 2010). They have echolocation calls dominated by a CF (Fig. 2.2) component with a peak frequency of 92.1 kHz (Jacobs *et al.* 2007). They eat mostly Coleoptera and some Lepidoptera (Jacobs *et al*. 2007; Schoeman and Jacobs 2010).

Miniopterus all have the second phalanges of their third digit elongated (more than 3x longer than the first) which gives their wings a narrow, pointed, swallow-like shape (Taylor 2000; Monadjem *et al*. 2010). This adaptation allows for fast flight in open areas and likely long distance migration (Taylor 2000). *Miniopterus natalensis* (Natal long-fingered bat) occupies a range of habitats including coastal, savannas, grasslands and Fynbos (Taylor 2000; Monadjem *et al*. 2010). Their wing morphology coupled with intermediate wing loading suggests a range of flight patterns from slow, manoeuvrable flight in clutter to hawking (a method of catching insects in flight) in semi-open areas (clutter-edge foragers, Norberg and Rayner 1987; Jacobs 1999; Monadjem *et al*. 2010). Norberg and Rayner (1987) also propose that they forage using high-altitude hawking due to their ability to fly swiftly. *Miniopterus natalensis* have steep FM (Fig. 2.2) calls with a peak frequency of 51.4 kHz (Schoeman and Jacobs 2008). They feed on Hemiptera but also eat some Diptera, Lepidoptera, and Coleoptera (Schoeman and Jacobs 2010).

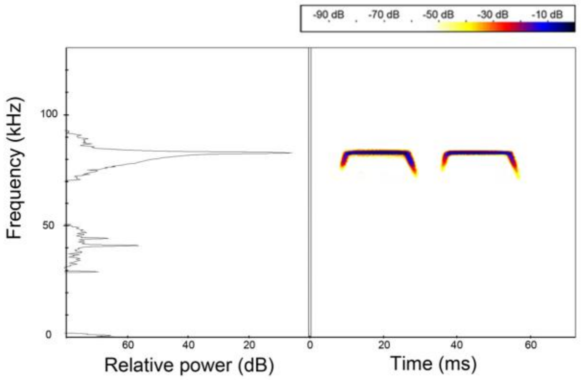
Myotis tricolor (Temminck's hairy bat) occurs in Fynbos, savanna woodland and arid and mountain regions where there are suitable roosts (*i.e*. caves; Taylor 2000; Monadjem *et al*. 2010). These bats migrate each year between summer maternity roosts and winter hibernation caves (Taylor 2000). Their morphology and slow agile flight suggest they can fly on the edge of clutter but rarely within it (clutter-edge forager, Norberg and Rayner 1987; Monadjem *et al*. 2010). They use FM echolocation calls (Fig. 2.2) with a peak frequency of 47.8 kHz (Schoeman and Jacobs 2008). They mainly feed on hard-bodied prey such as Coleoptera with some Hemiptera and Diptera (Schoeman and Jacobs 2010; Stoffberg and Jacobs 2004).

Neoromicia capensis (Cape serotine) have broad habitat tolerances and occur in habitats ranging from forests to deserts throughout South Africa (Taylor 2000; Monadjem *et al*. 2010). They often use the roofs of houses as roosts. This species is an aerial woodland edge feeder (clutter-edge forager, Taylor 2000; Monadjem *et al*. 2010). Their echolocation calls have a steep FM structure (Fig. 2.2) with a peak frequency of 39.4 kHz (Schoeman and Jacobs 2008). *Neoromicia capensis* mostly feeds on Hemiptera and some Coleoptera and Diptera (Schoeman and Jacobs 2010).

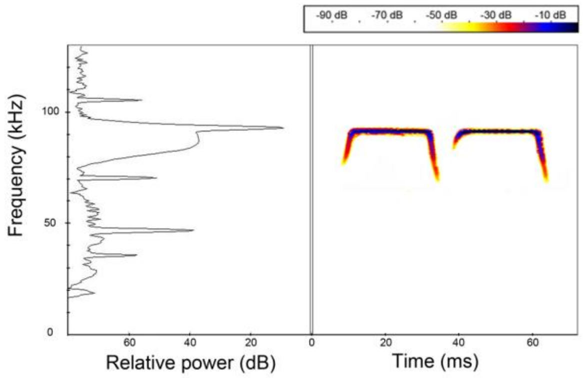
Molossidae (free-tailed bats) are characterized by their tail which extends beyond the margin of the tail membrane (Taylor 2000). Their morphology allows fast flight in open spaces (Norberg and Rayner 1987; Taylor 2000) and they are therefore specialized for hawking high-flying insects in open air (Norberg and Rayner 1987). *Tadarida aegyptiaca* (Egyptian free-tailed bat) is widespread throughout southern Africa and they occur in most vegetation except forests because they prefer open habitats (Taylor 2000). It flies slower than other molossids but are nevertheless confined to open spaces (open air foragers, Taylor 2000; Monadjem *et al*. 2010). Their peak echolocation (Fig. 2.2) frequency is 22.7 kHz (Schoeman and Jacobs 2008). Their diet mostly constitutes Diptera but they also eat Hemiptera and Coleoptera (Schoeman and Jacobs 2010).



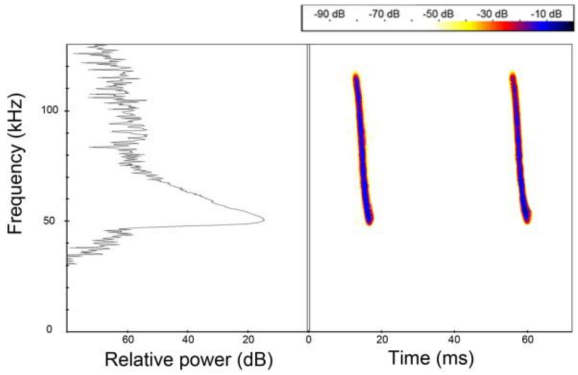
Nycteris thebaica



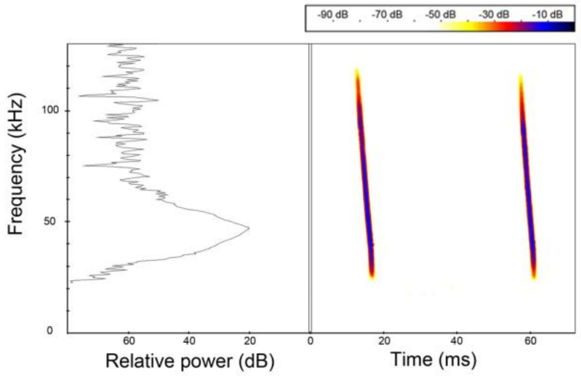
Rhinolophus capensis



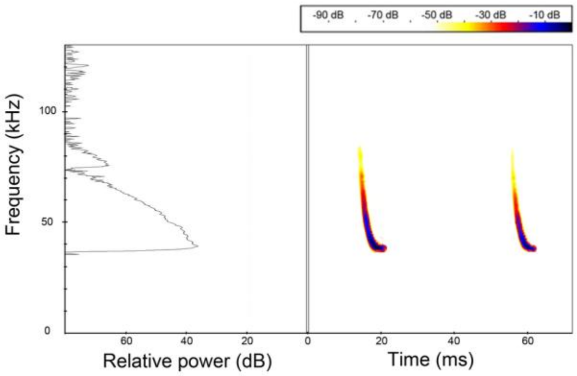
Rhinolophus clivosus



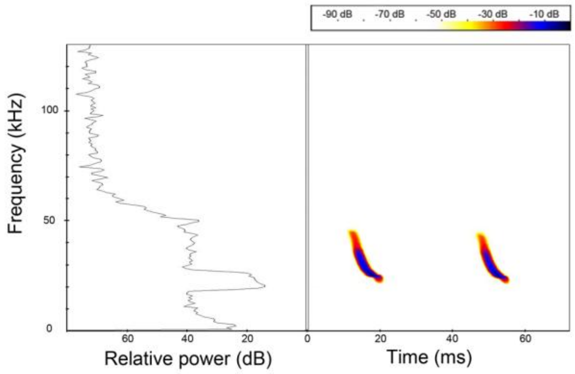
Miniopterus natalensis



Myotis tricolor



Neoromicia capensis



Tadarida aegyptiaca

Figure 2.2: Echolocation calls with associated power spectra (to the left of spectrograms) for all seven species found within De Hoop Nature Reserve, South Africa.

2.3. Emergence times

I determined emergence times by recording echolocation calls as bats emerged from roosts using D240x (Pettersson Elektronik AB, Uppsala, Sweden) ultrasound detectors connected to wave/MP3 recorders (R – 09HR, Edirol by Roland corporation, 2036-1Nakagawa, Hosoe-cho, Kitaku, Hamamatsu, Shizuoka 431-1304, Japan). Detectors were placed in front of the main and a side entrance to the Guano cave (34°25,269´S, 20°21,532´E) and research house (34° 27.376'S, 20° 24.393'E) roosts. They were deployed 15 - 30 minutes before sunset and set to record for three hours. Since there was never a clear end to emergence, as bats continued to enter and exit for most of the night, I recorded for a set amount of time each night to minimize interference from returning bats, but for long enough to record peak bat activity. Preliminary visual observations suggested that 3 hrs after sunset was long enough to determine the time of peak emergence. Emergence seemed to decrease about 2 hr after sunset. Time of peak emergence was recorded in minutes after sunset and determined as the time when the highest number of calls for each species was recorded. Sunset was defined as the time at which the sun was 6° below the horizon (*i.e*. civil twilight). This corresponded to the time when illumination (in fine weather) was good enough to be able to distinguish terrestrial objects.

Recorded calls were transferred from the recorder to a notebook computer and analysed using BatSound Pro software (version 3.20, Pettersson Elektronik AB, Uppsala, Sweden). Calls recorded each night were split into smaller files using Slice Audio File Splitter (version 2.00, © NCH Software, Greenwood village CO, USA). Due to the large number of calls recorded at Guano cave, I counted the number of calls during one minute for each 5 minutes of recording for each species. For the side cave and the research house all the calls were counted during the 3h period.

Calls were allocated to species by their bandwidth, duration, lowest, highest and peak frequency and shape. The power spectrum was used to measure peak frequency for both constant frequency (CF) and frequency modulated (FM) calls. Call duration for both CF and FM bats were measured using the oscillogram. For CF calls, the lowest frequency was measured from the spectrogram at the lowest point of the calls tail. Bandwidth was taken as the difference between peak and lowest frequency for high-duty cycle calls. For low duty-cycle calls bandwidth was taken at ±20dB below peak frequency. I identified species by comparing call parameters to those from a reference collection (compiled by David Jacobs).

2.4. Predators

I assessed predation risk by noting the presence or absence of all potential predators within or around Guano Cave and the research house at emergence and for every 30 min thereafter. I used visual and auditory cues to determine the presence or absence of a potential predator.

2.5. Insect activity

Insect activity was measured for each hour of the 3 hour echolocation recording session using a 22 w battery operated circle-line black-light trap (BioQuip Products, Rancho Dominguez, CA 90220, USA). I deployed a light trap close to the vlei near Guano cave where most species foraged (McDonald *et al.* 1990) and another near the research house roost. Insects were emptied from the traps every 60 min after the recording period started and stored in alcohol. Insects were identified to order using a key (Scholtz 1985; Picker *et al.* 2004), counted and then dried at 60 °C to a constant mass. After drying, insects were weighed and I calculated mean biomass for each order per hour per night.

2.6. Bat Diets

Data on the diets of each species were taken from the literature (McDonald *et al.*1990; Jacobs *et al.*2007; Schoeman and Jacobs 2010).

2.7. Weather

A weather station was set up next to the vlei to record continuous data near to where bats foraged. Temperature (˚C), rainfall (mm.s^{-1}), humidity, wind speed (m.s^{-1}), and atmospheric pressure (inHg) were recorded every 30 min.

2.8. Light levels

I used moon phase as a relative measure of light intensity. Data were collected from full moon until new moon over the course of the three sampling periods within summer. The moon phase and the time of sunset were taken from a moon phase calendar calculated for Bredasdorp (www.kwathaabeng.co.za). Cloud cover was assessed every 30 min using the standard Okta scale which ranges from 0 to 8 (where 0 is clear sky and 8 fully overcast; O'Connor *et al.* 2009).

2.9. Statistical analysis

Data on peak emergence times (mins after sunset) did not meet the assumptions of normality and were therefore log transformed. The data was analyzed across all sampling periods as well as separately to account for changes in sunset time between trips as within trips there was very little difference between days in sunset time but across sampling periods there were significant differences. Also we wanted to be able to compare moon phase within and between the three sampling periods. I used analysis of variance (ANOVA) to assess whether peak emergence times were significantly different between sampling periods and species. I used GLMs (general linear models) to determine the effect of environmental variables (including weather variables) on emergence times over all sampling periods and within sampling periods. I used principal components analysis (PCA) to extract uncorrelated weather variables (over all sampling periods and within each sampling period) from the 5 weather variables (temperature (˚C), rainfall ($m.s^{-1}$), humidity, wind speed ($m.s^{-1}$), and atmospheric pressure). Prior to a PCA, multicollineartiy between these variables made their use together in a GLM inappropriate.

To assess the relationship (over all sampling periods) between peak emergence time, weather variables, presence of a predator and sampling period, I used a general linear model (GLM) with peak emergence time as the dependent variable. Since life history traits do not change over sampling periods, we compared peak emergence time within sampling periods but not across. ANOVA was used to compare peak emergence time as a function of foraging strategy and diet. The relationship between body mass (data from Jacobs *et al*. 2007; Schoeman and Jacobs 2008) and peak emergence time was determined using linear regression.

I employed a t-test to determine whether there was a significant difference between peak insect activity (mins after sunset) for count vs. mass data at the cave and the house. Similarly, I used a t-test to determine if there was a significant difference between insect peak activity at the cave and house. To determine if insect peak activity was significantly different between sampling periods and species I used an ANOVA. To evaluate the relationship between insect peak activity, weather variables, species, sampling period and sunset, a general linear model (GLM) was used with insect peak activity as the dependent variable. Linear regression was used to determine if bat peak emergence and insect peak activity were correlated. All statistical analyses employed an alpha value of 0.05 and were carried out using Statistica (StatSoft Inc. 2009, version 9.0).

Chapter 3

RESULTS

3.1. Predators and predation events during the sampling period

No successful predation events were observed during my sampling periods at either Guano cave or the research house. However, two attempts to catch bats by an owl (Cape Eagle-Owl; *Bubo capensis*) were witnessed at the house, one during early (~19:44) and one during mid-summer (~19:40). Owls (*Tyto alba* and *Bubo capensis*) were frequently observed around the research house during early and mid-summer (a total of 14) but none in late summer. At Guano cave, owls (*Tyto alba* and *Bubo capensis*) were seen four times during mid and late summer. There was however, a genet (*Genetta genetta*) that was noted six times near the cave and surrounding trees during mid and late summer and seemed to live around the cave.

3.2. Timing of emergence over all three sampling periods

Sunset was significantly different between all sampling periods (ANOVA, $F_{2,\,255}$= 3689, p< 0.001). The mean time of sunset was earlier (18:27±00:06) in late summer than in early and mid-summer (19:31±00:04 and 19:26±00:05, respectively). Similarly, sunset was earlier in mid-summer than in early summer (Tukey's test, all p's< 0.001).

Peak emergence time (minutes after sunset) varied between sampling periods (Fig. 3.1; ANOVA $F_{2, 200}$= 9.11, $p< 0.005$) and between species (Fig. 3.2, $F_{6, 200}$= 25.87, $p< 0.001$, respectively). Peak emergence in early summer when the sun set latest was significantly later than in mid and late summer (Fig. 3.1, Tukey's test $p< 0.005$ and $p< 0.0005$, respectively) but there was no difference in peak emergence time between mid and late summer (Fig. 3.1, Tukey's test, $p= 0.31$). In all three sampling periods *R. clivosus* emerged earlier than all the other species (Fig. 3.2, Tukey's test, all p's< 0.05), followed by *M. natalensis, R. capensis, N. thebaica* and *My. tricolor* (Fig. 3.2, Tukey's test, all p's< 0.05). The two roof-roosting species, *N. capensis* and *T. aegyptiaca* emerged the latest (Fig. 3.2, Tukey's test, all p's < 0.05).

I found a significant interaction between sampling period and species (Fig. 3.3, ANOVA $F_{12, 200}$= 2.84, $p< 0.005$). *Miniopterus natalensis* and *R. capensis* emerged significantly later during early summer than they did in late summer (Fig. 3.3, Tukey's test, $p< 0.001$ and $p< 0.01$, respectively). There was no significant difference in the peak emergence time of *R. clivosus* and *My. tricolor* relative to sunset over the three sampling periods (Fig. 3.3, Tukey's test, p's> 0.39 and p's> 0.999). *Nycteris thebaica* emerged significantly earlier during mid-summer than during early and late summer (Fig. 3.3, Tukey's test, $p< 0.05$). There was no significant difference in peak emergence time of *N. capensis* and *T. aegyptiaca* between the three sampling periods (Fig. 3.3, Tukey's test, p's> 0.625).

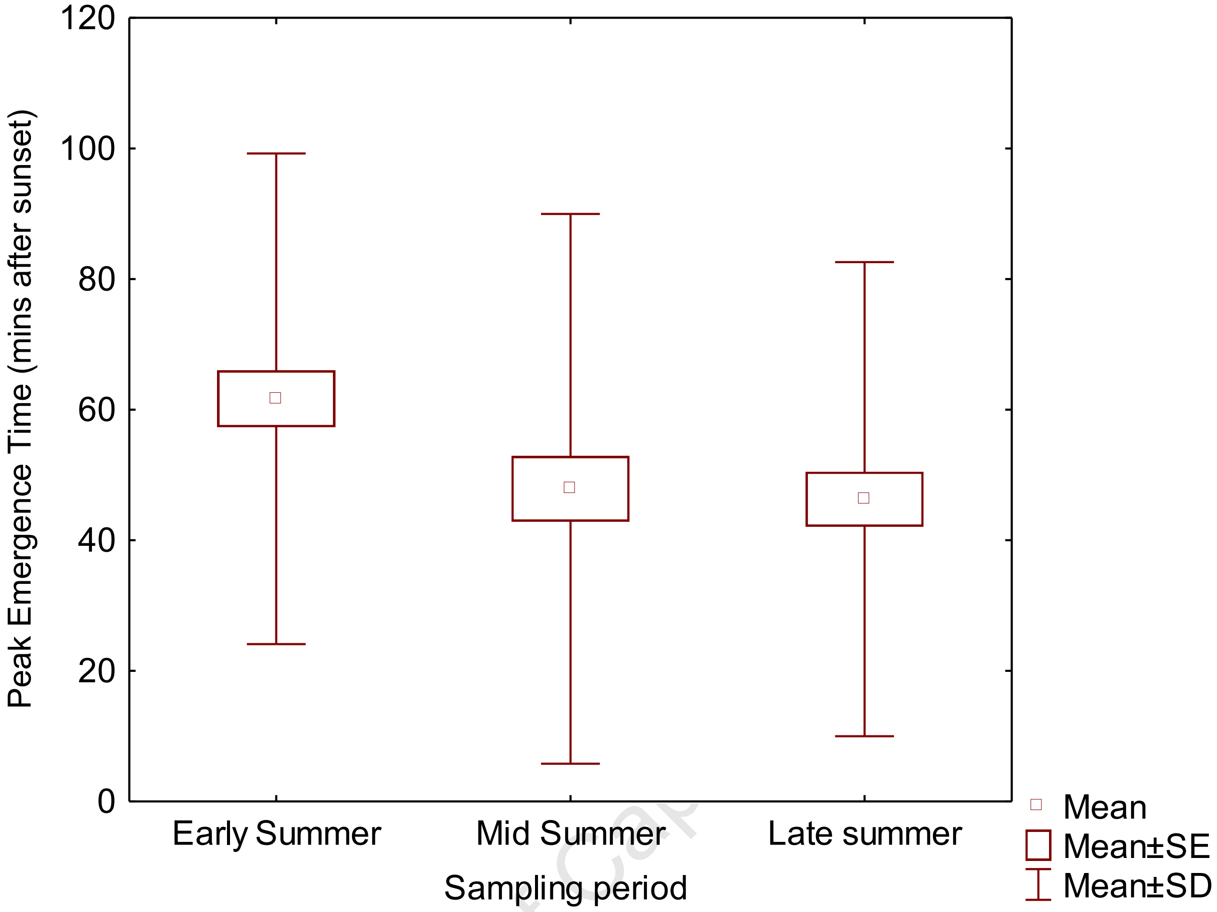


Figure 3.1: Mean peak emergence time (mins after sunset) of all bats over the three sampling periods.

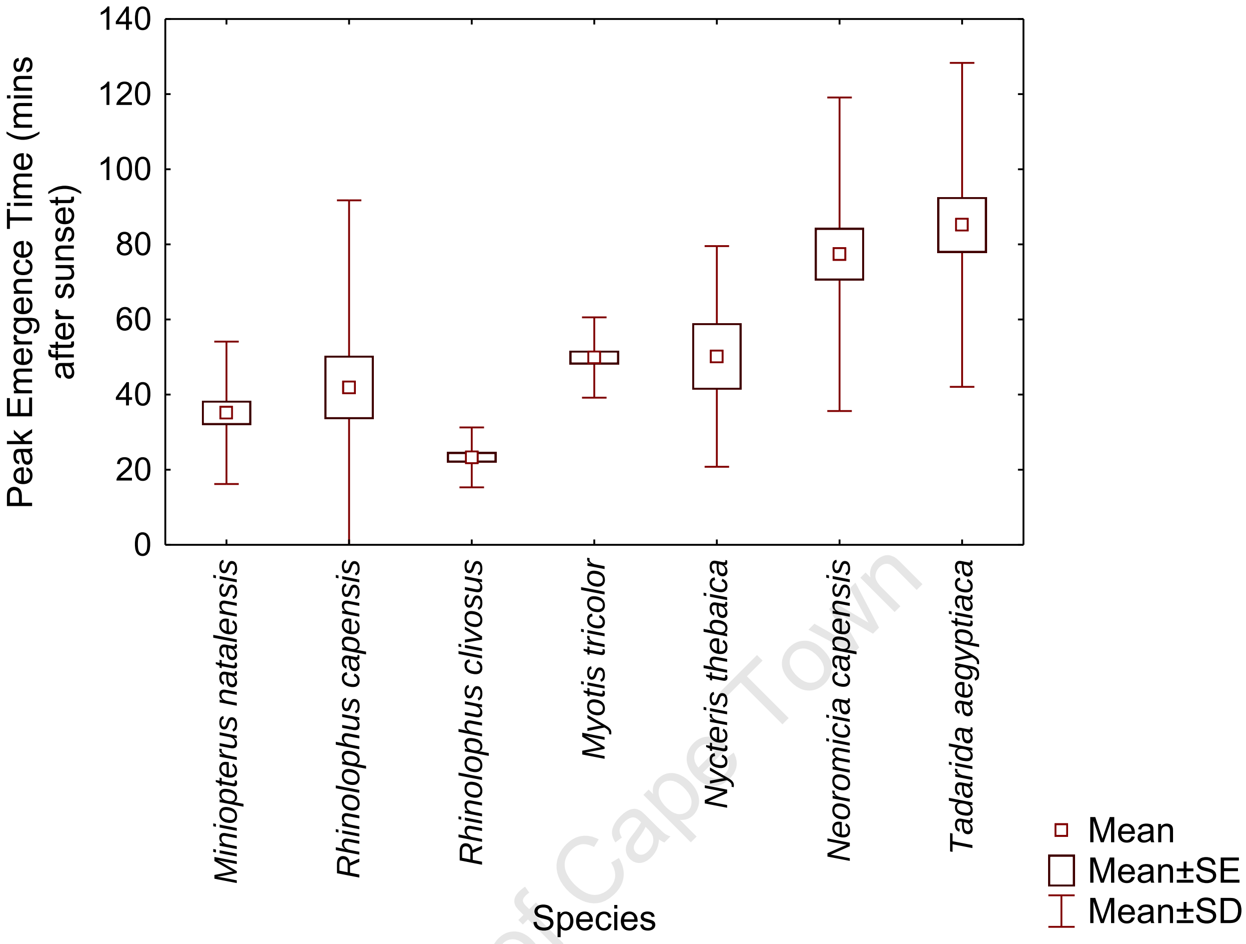


Figure 3.2: Mean peak emergence time (mins after sunset) for each species of bat over all three sampling periods.

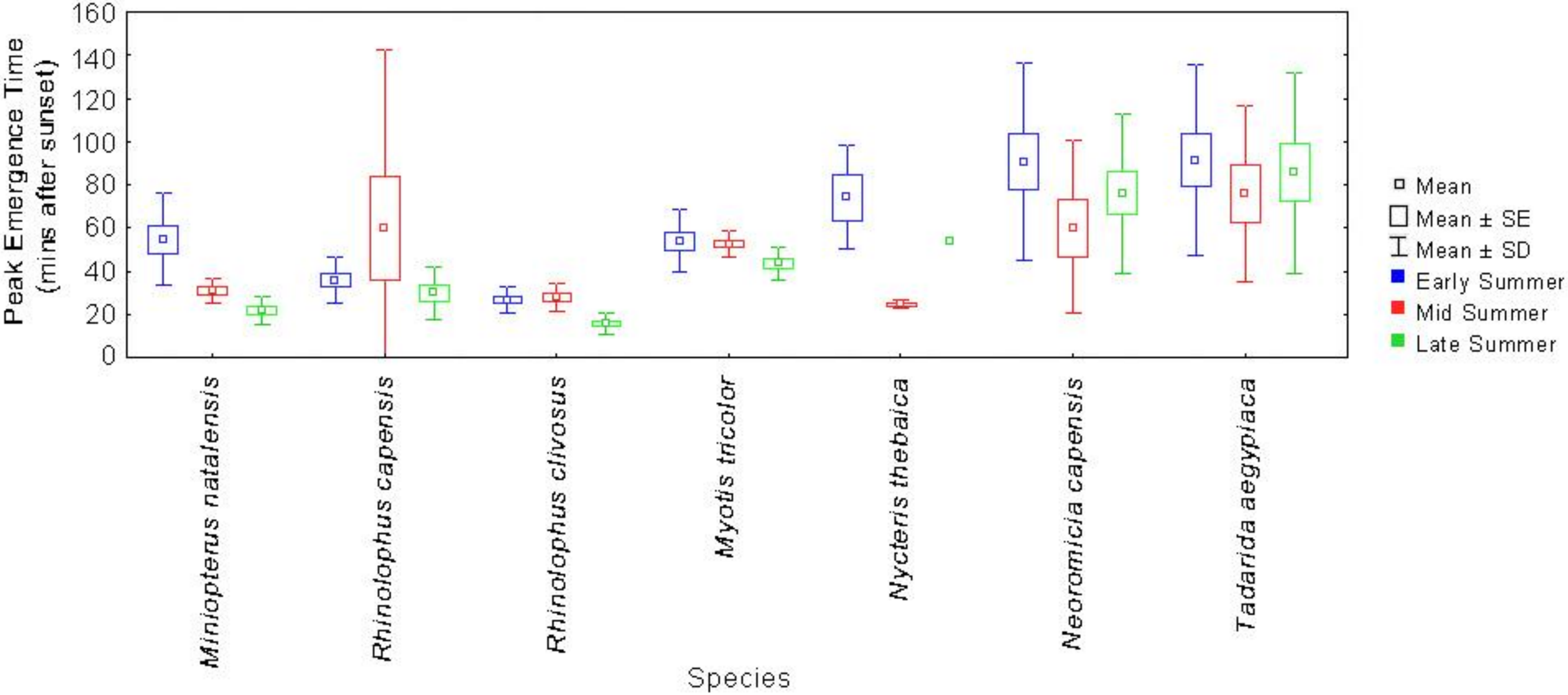


Figure 3.3: A comparison of the mean peak emergence time (mins after sunset) for each species of bat within each sampling period.

3.2.1. Timing of peak emergence: weather variables, sunset, sampling period and presence of a predator

The first four components extracted by the PCA (with eigenvalues greater than 0.75, Table 3.1) represented temperature (°C), moon phase, cloud cover and wind speed ($m.s^{-1}$) based on the weather variables that loaded highest on each component. A GLM on these components, sampling period and absence or presence of predators revealed that only sampling period significantly affected peak emergence times over all three sampling periods [Temperature $F_{1, 211}= 0.30$, $p= 0.59$; Moon phase $F_{1, 211}= 0.01$, $p= 0.92$; Cloud cover $F_{1, 211}= 0.002$, $p= 0.96$; Wind speed $F_{1, 211}= 0.00$, $p= 1$; Presence of a predator $F_{1, 211}= 0.16$, $p= 0.69$; Sampling period $F_{2, 211}= 7.55$, $p< 0.001$; and sampling Period*Predator $F_{2, 211}= 3.01$, $p= 0.05$]. Peak emergence time was later in early summer (when sunset is later) than in mid and late summer (Fig. 3.1, $p< 0.05$ and $p< 0.0005$, respectively). There was little variation in weather variables over the three sampling periods (Table 3.3)

Table 3.1: Eigenanalysis of the correlation matrix and factor loadings for the first four principle components extracted from the weather variables (across all sampling periods).

Principal component	PC1	PC2	PC3	PC4
Eigenanalysis of the correlation matrix				
Eigenvalues	2.033	1.315	1.041	0.760
Percentage variance explained	33.9	21.9	17.4	12.7
Cumulative percentage variance explained	33.9	55.8	73.1	85.8
Factor Loadings:				
Moon Phase	0.082	-0.843	-0.262	-0.201
Temperature	-0.784	0.077	-0.358	0.315
Humidity	-0.631	-0.370	0.237	-0.518
Air Pressure	0.733	-0.176	0.525	0.098
Wind Speed	-0.422	-0.540	0.424	0.556
Cloud Cover	0.547	-0.372	-0.577	0.182

Table 3.2: Mean ± SD for weather variables measured during each sampling period.

	Early Summer		Mid-Summer		Late Summer	
Environmental Factors	Mean	± SD	Mean	± SD	Mean	± SD
Temperature (°C)	17.58	1.7	21.04	1.61	18.92	1.4
Humidity (%)	70.02	10.23	73.34	9.5	72.59	8.27
Air Pressure (inHg)	30.19	0.15	30.06	0.2	30.13	0.12
Wind Speed ($m.s^{-1}$)	0.77	0.36	1.17	0.45	0.78	0.33
Cloud Cover (Octa)	3.5	2.95	2.39	1.71	3.74	3.05

3.3. Timing of emergence within sampling periods

3.3.1. Early summer

Sunset ranged from 19:23 to 19:38 during the early summer sampling period. Peak emergence time ranged from 16 to 169 minutes after sunset. The order of peak emergence time (mins after sunset) during early summer was *R. clivosus* (26.64±5.92), *R. capensis* (35.73±10.51), *My. tricolor* (53.91±14.59), *M. natalensis* (54.82±21.59), *N. thebaica* (75.00±23.70), *N. capensis* (90.69±46.03) and *T. aegyptiaca* (91.46±43.86; Fig. 3.3, ANOVA, $F_{6, 68}$=10.27, p< 0.001). Peak emergence by *Rhinolophus clivosus* was significantly earlier than *M. natalensis*, *My. tricolor, N. thebaica, N. capensis* and *T. aegyptiaca* (Fig. 3.3, Tukey's test, all p's< 0.01). *Rhinolophus capensis* emerged significantly earlier than *N. thebaica, N. capensis* and *T. aegyptiaca* (Fig. 3.3, Tukey's test, all p's< 0.05).

3.3.1.1. Timing of peak emergence: weather variables, sunset and presence of a predator

The first three components extracted by the PCA (with eigenvalues greater than 1.34, Table 3.3) corresponded to cloud cover, air pressure (inHg) and humidity (%) based on the variables that had the highest factor loadings on these three components (Table 3.3). A GLM using these three components, sunset and predation revealed that only the presence or absence of a predator significantly affected peak emergence time [Cloud cover $F_{1, 69}$= 0.06, p= 0.81; Air pressure $F_{1, 69}$= 0.03, p= 0.87; Humidity $F_{1, 69}$= 1.14, p= 0.29; Presence of a predator $F_{1, 69}$= 5.36, $p < 0.05$ and Sunset $F_{1, 69}$ = 0.39, p= 0.53]. Peak emergence occurred later in the presence of a predator during early summer (Fig. 3.4, Tukey's test, $p < 0.01$).

Table 3.3: Eigenanalysis of the correlation matrix and factor loadings for the first four principle components extracted from the weather variables for early summer.

Principal component	PC1	PC2	PC3
Eigenanalysis of the correlation matrix			
Eigenvalues	1.957	1.655	1.344
Percentage variance explained	32.6	27.6	22.4
Cumulative percentage variance explained	32.6	60.2	82.6
Factor Loadings:			
Moon Phase	-0.680	0.442	-0.494
Temperature	0.768	0.348	0.321
Humidity	0.412	-0.148	-0.819
Air Pressure	-0.316	-0.807	0.413
Wind Speed	0.032	-0.798	-0.372
Cloud Cover	-0.797	0.171	0.128

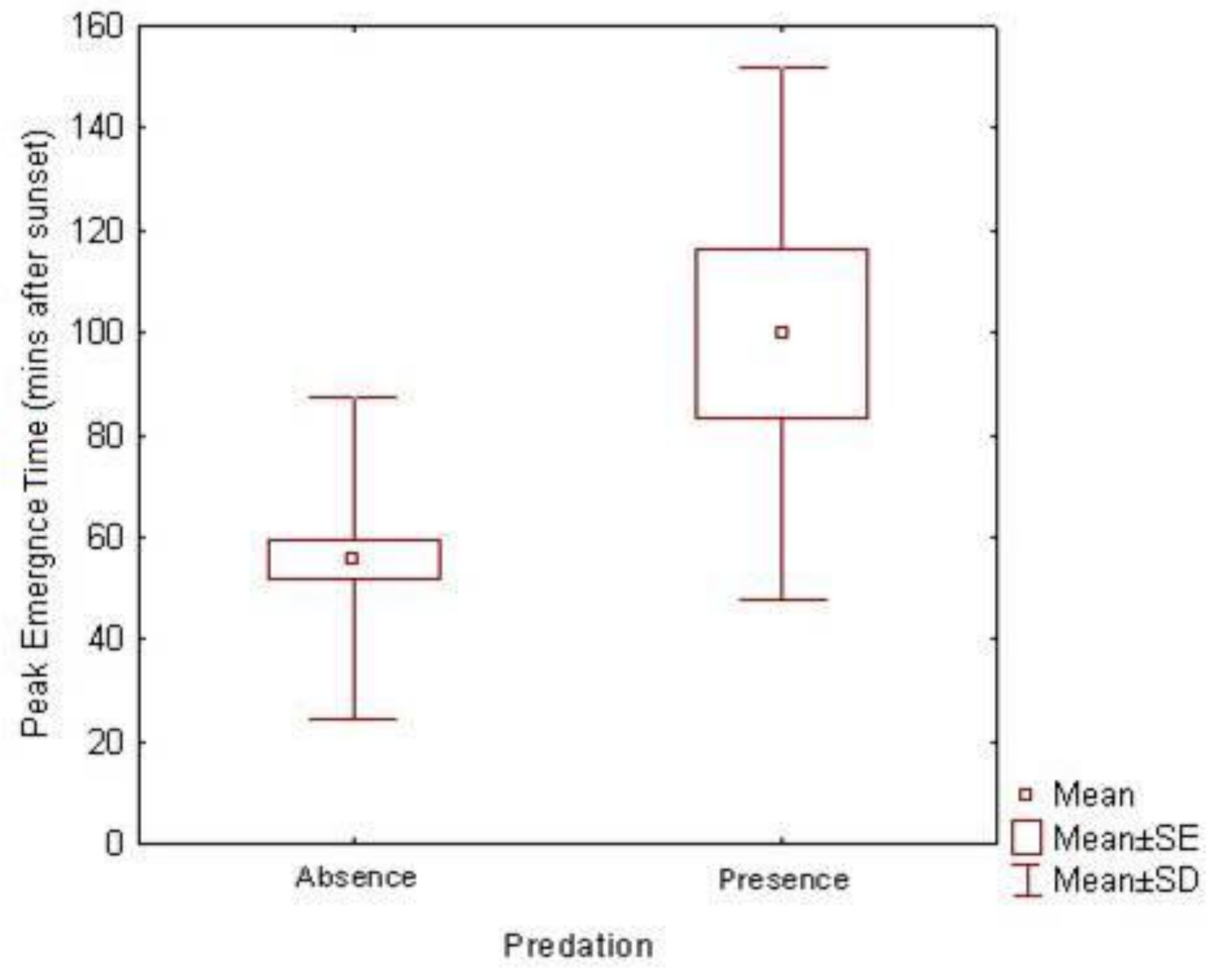


Figure 3.4: Bat peak emergence time in the absence or presence of a predator during early summer.

3.3.1.2. Timing of peak emergence: life history traits, diet and body mass

Peak emergence time was significantly affected by foraging strategy in early summer (Fig. 3.5, ANOVA, $F_{2, 72}$= 14.46, p< 0.001). Clutter foragers emerged earlier during early summer than bats that foraged in the clutter-edge and open (Fig. 3.5, Tukey's test, p's < 0.005). Clutter-edge and open air foragers emerged around the same time (Fig. 3.5, Tukey's test, p= 0.18). Diet was also significantly related to peak emergence time (Fig. 3.6, ANOVA, $F_{3, 71}$= 8.39,

$p < 0.0001$). Bats feeding on Coleoptera emerged earliest in early summer followed by bats feeding on Lepidoptera, Hemiptera and Diptera. However, differences were only statistically significant for species feeding on Coleoptera versus those eating Hemiptera and Diptera, and between bats feeding on Lepidoptera and bats feeding on Diptera. Bats feeding on Coleoptera left roosts significantly earlier than bats feeding on Hemiptera and Diptera (Fig. 3.6, Tukey's test, p's< 0.005). Bats feeding on Lepidoptera came out significantly earlier than bats feeding on Diptera (Fig. 3.6, Tukey's test, p's < 0.05). The timing of peak emergence was not correlated with body mass (g, Linear regression, $F_{1, 5} = 0.98$, $p = 0.37$).

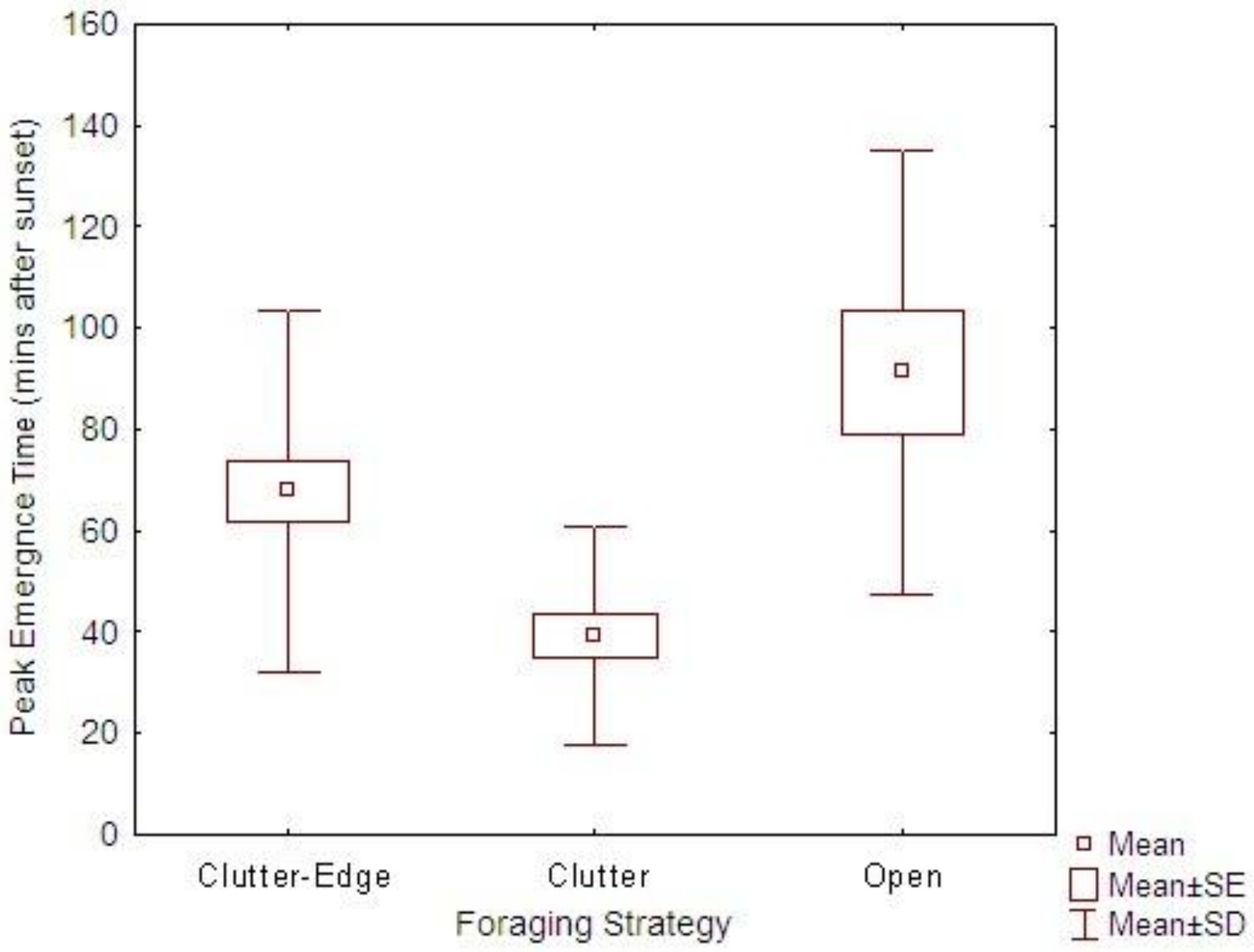


Figure 3.5: Peak emergence times (mins after sunset) during early summer based on bat foraging strategies.

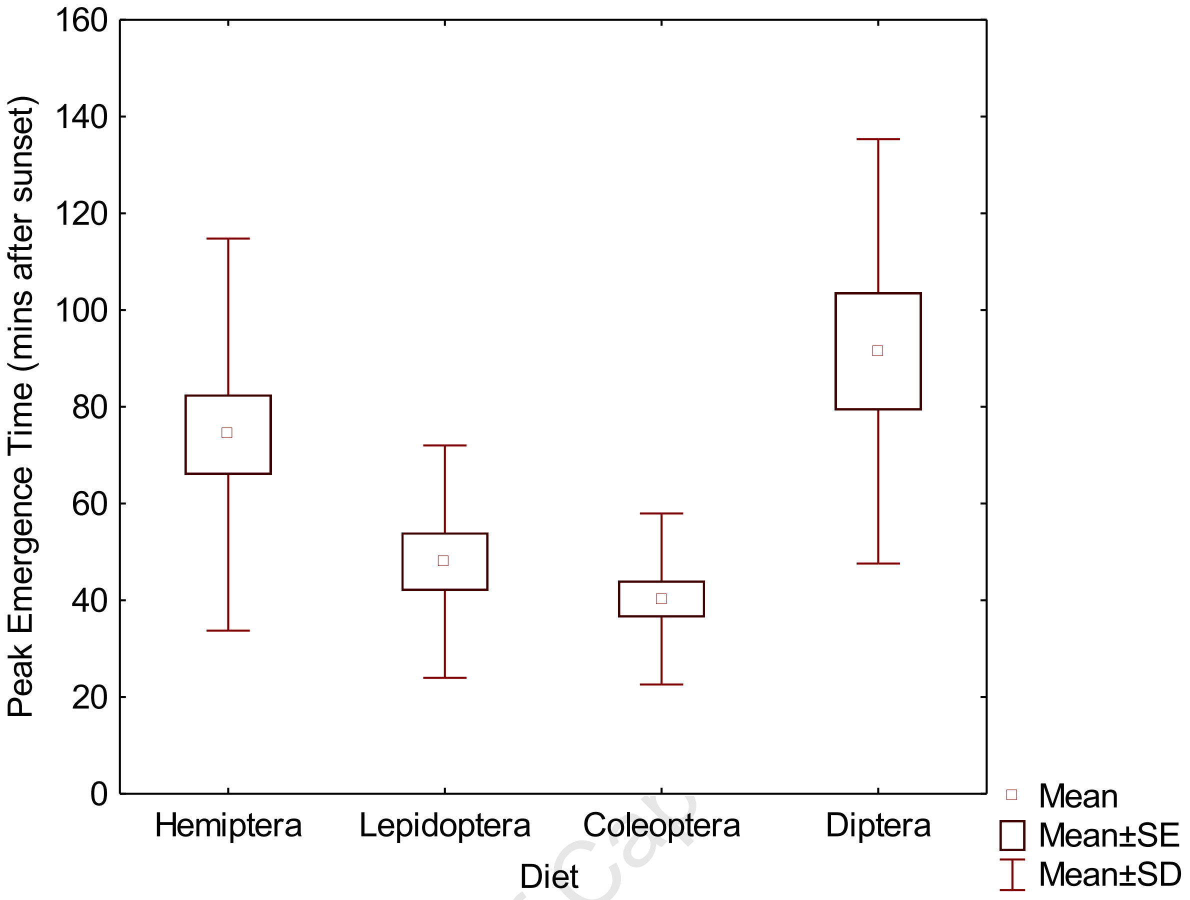


Figure 3.6: Bat peak emergence time (mins after sunset) during early summer based on diet (main insect orders eaten).

3.3.2. Mid-summer

During mid-summer, sunset ranged from 19:35 to 19:18. Peak emergence time ranged from 15 to 132 minutes after sunset. The order of peak emergence was *N. thebaica* (24.60±1.82), *R. clivosus* (27.93±6.26), *M. natalensis* (30.83±5.72), *My. tricolor* (52.50±5.90), *R. capensis* (59.75±82.91), *N. capensis* (60.22±40.01) and *T. aegyptiaca* (75.78±40.57;

Fig. 3.3, ANOVA, $F_{6, 64}= 5.22$, $p< 0.005$). *Rhinolophus clivosus* emerged earlier than *My. tricolor* and *T. aegyptiaca* (Fig. 3.3, Tukey's test, all p's < 0.05). *Tadarida aegyptiaca* emerged significantly later than *M. natalensis* (Fig. 3.3, Tukey's test, $p< 0.01$).

3.3.2.1. Timing of peak emergence: weather variables, sunset and presence of a predator

The first four components extracted by the PCA (with eigenvalues greater than 0.78, Table 3.4) corresponded to temperature (°C), moon phase, cloud cover and wind speed ($m.s^{-1}$) based on variables with the highest factor loadings for each component. A GLM revealed that peak emergence time was related to the time of sunset ($F_{1, 64}= 4.88$, $p< 0.05$) during mid-summer [Temperature $F_{1, 64}= 2.19$, $p= 0.14$; Moon phase $F_{1, 64}= 1.33$, $p= 0.25$; Cloud cover $F_{1, 64}= 0.05$, $p= 0.82$; Wind speed $F_{1, 64}= 1.65$, $p= 0.20$; Presence of a predator $F_{1, 64}= 0.22$, $p= 0.64$; and Sunset $F_{1, 64}= 4.88$, $p< 0.05$].

Table 3.4: Eigenanalysis of the correlation matrix and factor loadings for the first four principle components extracted from the weather variables for mid-summer.

Principal component	PC1	PC2	PC3	PC4
Eigenanalysis of the correlation matrix				
Eigenvalues	1.999	1.802	1.033	0.782
Percentage variance explained	33.3	30.0	17.2	13.0
Cumulative percentage variance explained	33.3	63.3	80.6	93.6
Factor Loadings:				
Moon Phase	0.207	0.864	0.018	-0.295
Temperature	0.880	-0.380	0.065	-0.157
Humidity	0.724	0.545	-0.179	-0.226
Air Pressure	-0.760	0.451	-0.283	-0.227
Wind Speed	0.192	0.635	0.233	0.702
Cloud Cover	0.206	-0.092	-0.929	0.272

3.3.2.2. Timing of peak emergence: life history traits, diet and body mass

During mid-summer both foraging strategy (Fig. 3.7, ANOVA, $F_{2,\,68}$= 7.61, p< 0.005) and diet (Fig. 3.8, ANOVA, $F_{3,\,67}$= 3.26, p< 0.05) were significantly related to peak emergence time. Clutter foragers emerged earlier than open foragers (Fig. 3.7, Tukey's test, and p < 0.005). The peak emergence times of clutter-edge foragers was not significantly different from clutter (Fig. 3.7, Tukey's test, p= 0.07) or open air foragers (Fig. 3.7, Tukey's test, p= 0.06). Bats feeding on Lepidoptera emerged first followed by those eating Hemiptera, Coleoptera and Diptera. Only the bats feeding on Diptera emerged significantly later than the other bats during mid-summer (Fig. 3.8, Tukey's test, $p < 0.05$). The time of peak emergence was not affected by body mass (g, Linear regression, $F_{1,5} = 0.02$, $p = 0.97$).

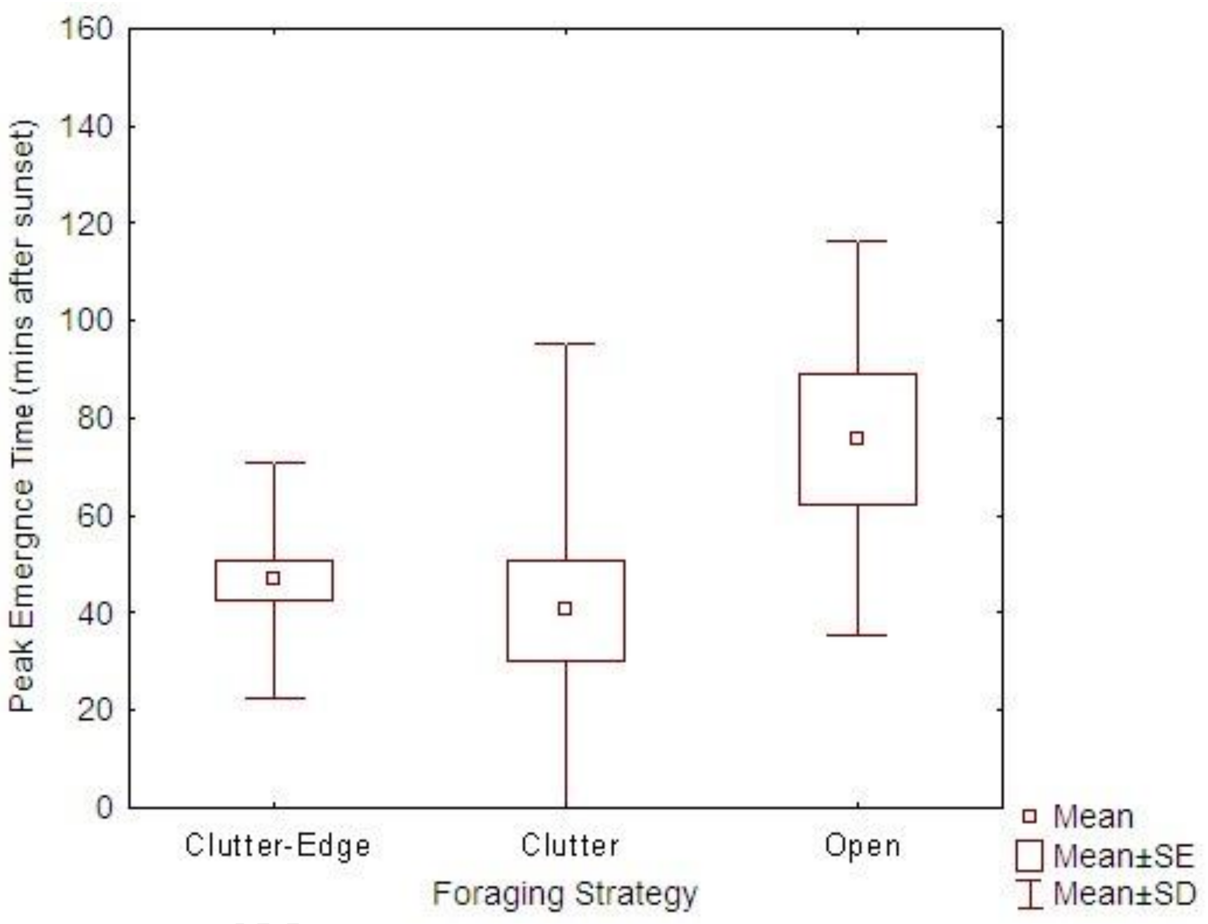


Figure 3.7: Bat peak emergence times (mins after sunset) during mid-summer based on their foraging strategies.

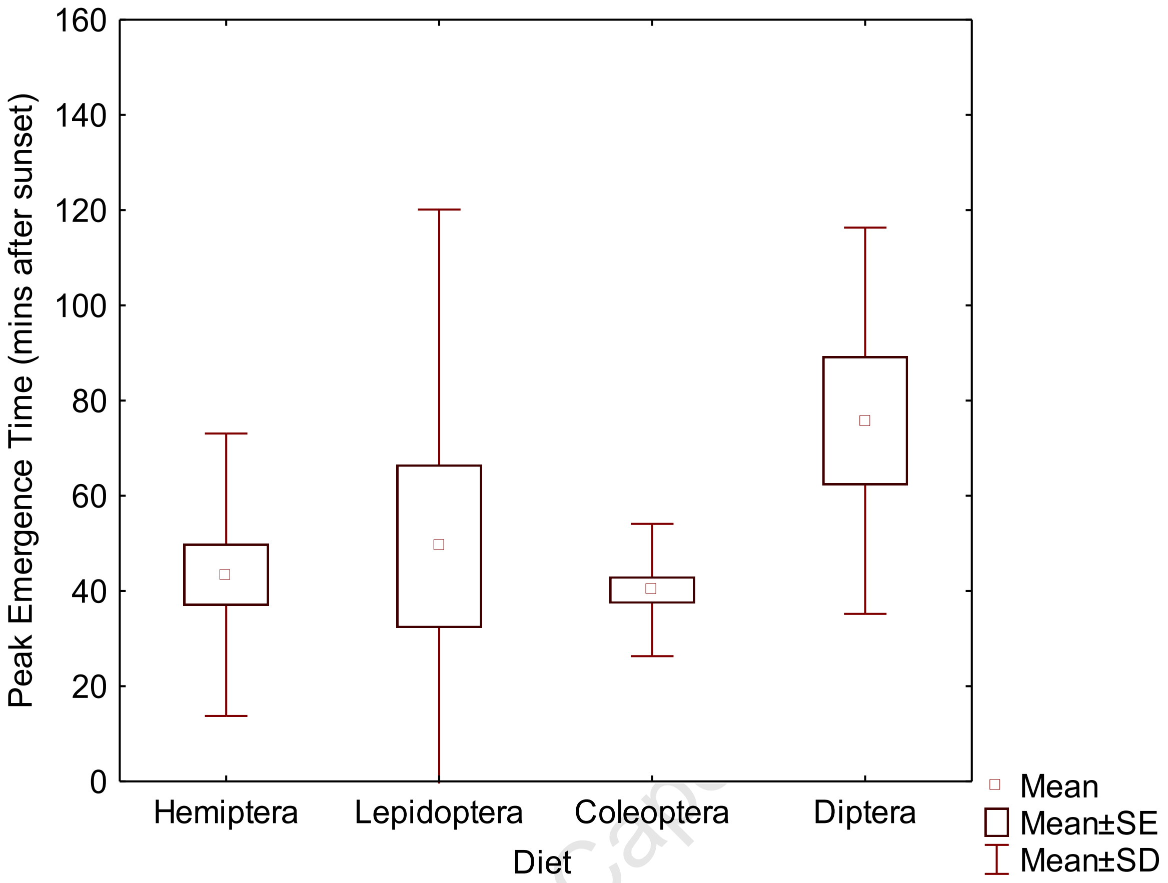


Figure 3.8: Bat peak emergence time (mins after sunset) during mid-summer based on diet (main insect order eaten).

3.3.3. Late Summer

Sunset ranged from 18:38 to 18:18 during the late summer sampling period. Peak emergence time ranged from 8 to 154 minutes after sunset. The order of peak emergence during late summer was *R. clivosus* (15.67±5.28), *M. natalensis* (21.50±6.50), *R. capensis* (29.83±12.25), *My. tricolor* (43.58±7.65), *N. thebaica* (54±0), *N. capensis* (76.07±36.92), and *T. aegyptiaca* (85.50±46.54; Fig. 3.3, ANOVA, $F_{6, 68}$= 16.71, p< 0.001). *Miniopterus natalensis* emerged significantly earlier than *My. tricolor,* *N. capensis* and *T. aegyptiaca* (Fig. 3.3, Tukey's test, all p's< 0.01). *Rhinolophus capensis* emerged significantly later than *R. clivosus* (Fig. 3.3, Tukey's test, p< 0.05) but significantly earlier than *N. capensis* and *T. aegyptiaca* (Fig. 3.3, Tukey's test, all p's< 0.001). *Rhinolophus clivosus* emerged earlier than *My. tricolor*, *N. capensis* and *T. aegyptiaca* (Fig. 3.3, Tukey's test, all p's< 0.001).

3.3.3.1. Timing of peak emergence: weather variables, sunset and presence of a predator

The first four components extracted by the PCA (with eigenvalues greater than 0.65, Table 3.5) corresponded to air pressure (inHg), temperature (˚C), wind speed (m.s^{-1}) and humidity (%) based on variables which loaded highest on each component. During late summer peak emergence time was not affected by any of these variables [Air pressure $F_{1,\ 68}$= 0.59, p= 0.44; Temperature $F_{1,\ 68}$= 0.05, p= 0.83; Wind speed $F_{1,\ 68}$= 0.16, p= 0.7; Humidity $F_{1,\ 68}$= 0.26, p= 0.61; Presence of a predator $F_{1,\ 68}$= 0.04, p= 0.85 and Sunset $F_{1,\ 68}$= 0.26, p= 0.62].

Table 3.5: Eigenanalysis of the correlation matrix and factor loadings for the first four principle components extracted from the weather variables for late summer.

Principal component	PC1	PC2	PC3	PC4
Eigenanalysis of the correlation matrix				
Eigenvalues	2.042	1.548	1.033	0.651
Percentage variance explained	34.0	25.8	17.2	10.9
Cumulative percentage variance explained	34.0	59.8	77.0	87.9
Factor Loadings:				
Moon Phase	0.4938	0.665	-0.153	0.445
Temperature	-0.311	0.749	-0.436	-0.286
Humidity	-0.716	0.244	0.324	0.512
Air Pressure	0.778	-0.041	0.510	-0.001
Wind Speed	0.034	0.685	0.594	-0.317
Cloud Cover	0.763	0.115	-0.320	0.096

3.3.3.2. Timing of peak emergence: life history traits, diet and body mass

Foraging strategy (Fig. 3.9, ANOVA, $F_{2, 72}$= 15.75, p< 0.005) and diet (Fig. 3.10, ANOVA, $F_{3, 71}$= 6.41, p< 0.001) were related to peak emergence time during late summer. Clutter foragers emerged earlier than clutter-edge and open air foragers (Fig. 3.9, Tukey's test, p's< 0.001) and clutter-edge emerged earlier than open (Fig. 3.9, Tukey's test, p< 0.05) during late summer. Bats feeding on Coleoptera emerged first during late summer followed by Lepidoptera, Coleoptera and Diptera. However, only bats feeding on Diptera emerged significantly later than bats feeding on Lepidoptera and

Coleoptera (Fig. 3.10, Tukey's test, p's< 0.05). The timing of peak emergence was not affected by body mass (g, Linear regression, $F_{1,5}$= 0.516, p= 0.505).

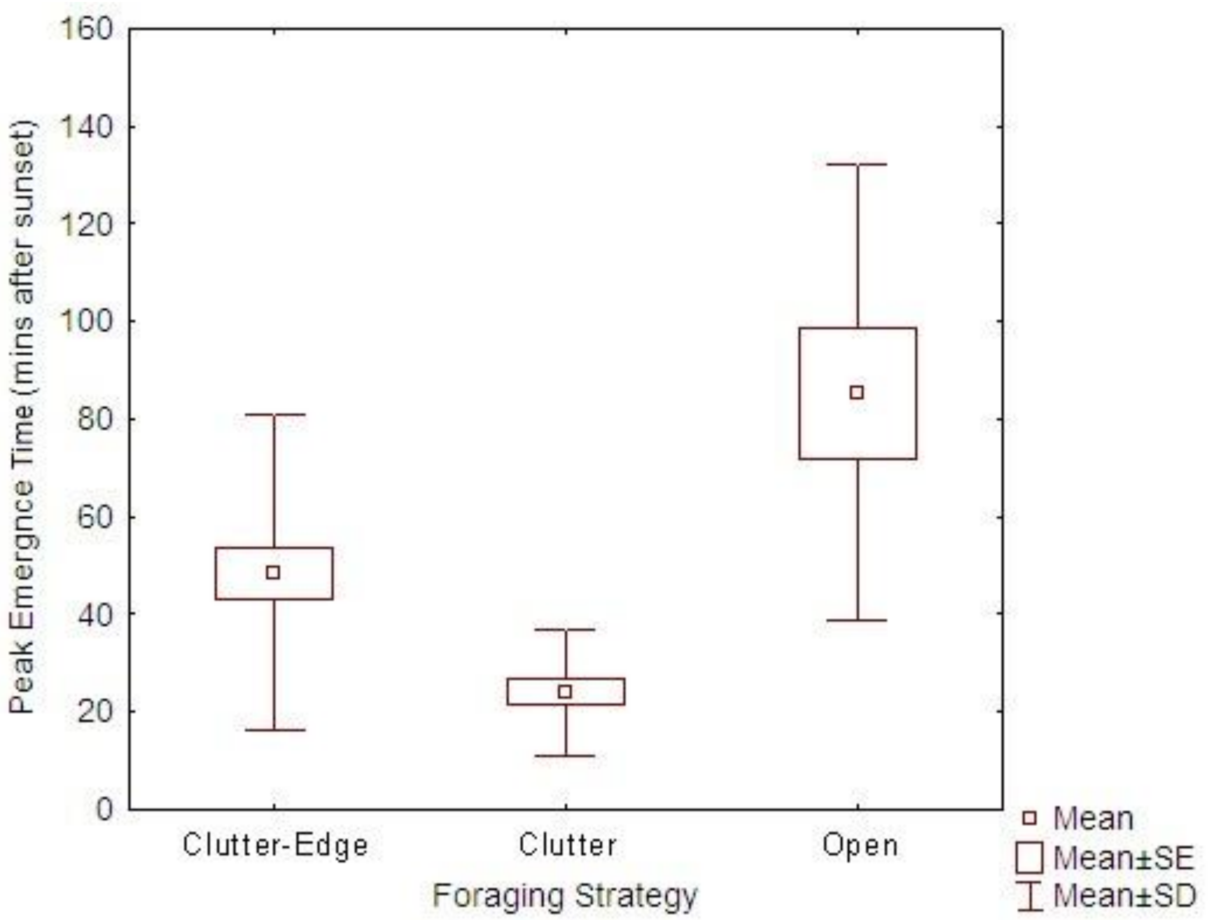


Figure 3.9: Bat peak emergence time (mins after sunset) during late summer based on foraging strategy.

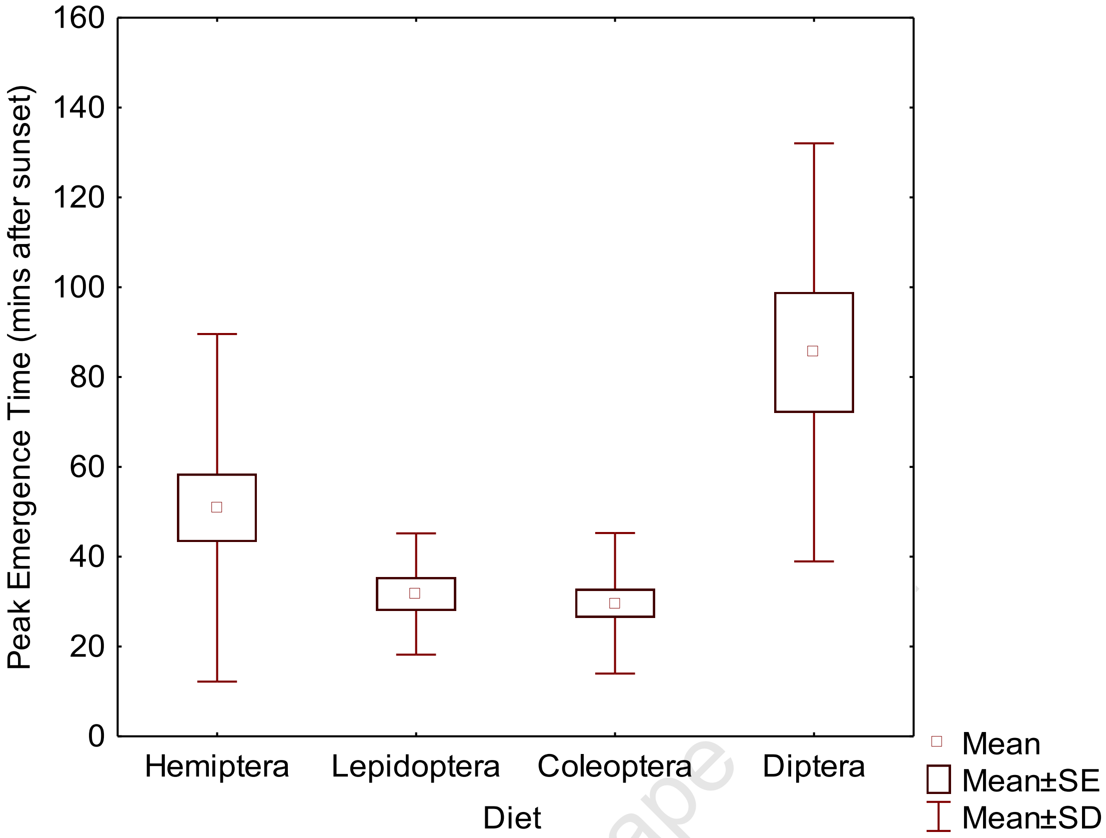


Figure 3.10: Bat peak emergence time (mins after sunset) during late summer based on their diets (main food order eaten).

3.4. Bat and Insect peak emergence times

Insect peak activity based on count data was not significantly different from data on biomass at both cave and house [Fig. 3.11, T-test, cave t= 1.57, df= 86, p= 0.12 and Fig. 3.11, house t= 0.19, df= 101, p= 0.85]. However, insect peak activity was later at the house than at the cave based on biomass data (Fig. 3.12; T-test, t= -2.13, df= 73, p= 0.04). Insect peak activity was highly variable and did not differ statistically between sampling periods or species at the cave (ANOVA, $F_{2,\,81}$= 0.38, p= 0.68 and $F_{3,\,81}$= 0.83, p= 0.48) or house (ANOVA, $F_{2,\,93}$= 3.01, p= 0.05 and $F_{3,\,93}$ = 1.27 p= 0.21). Also, insect peak activity was not influenced by sampling period, species, temperature (°C), moon phase, cloud cover, wind speed ($m.s^{-1}$), air pressure (inHg), humidity (%) or sunset at the cave (GLM's, all F's> 0.01 and p's> 0.075) or house (GLM's, all F's> 0.003 and p> 0.096).

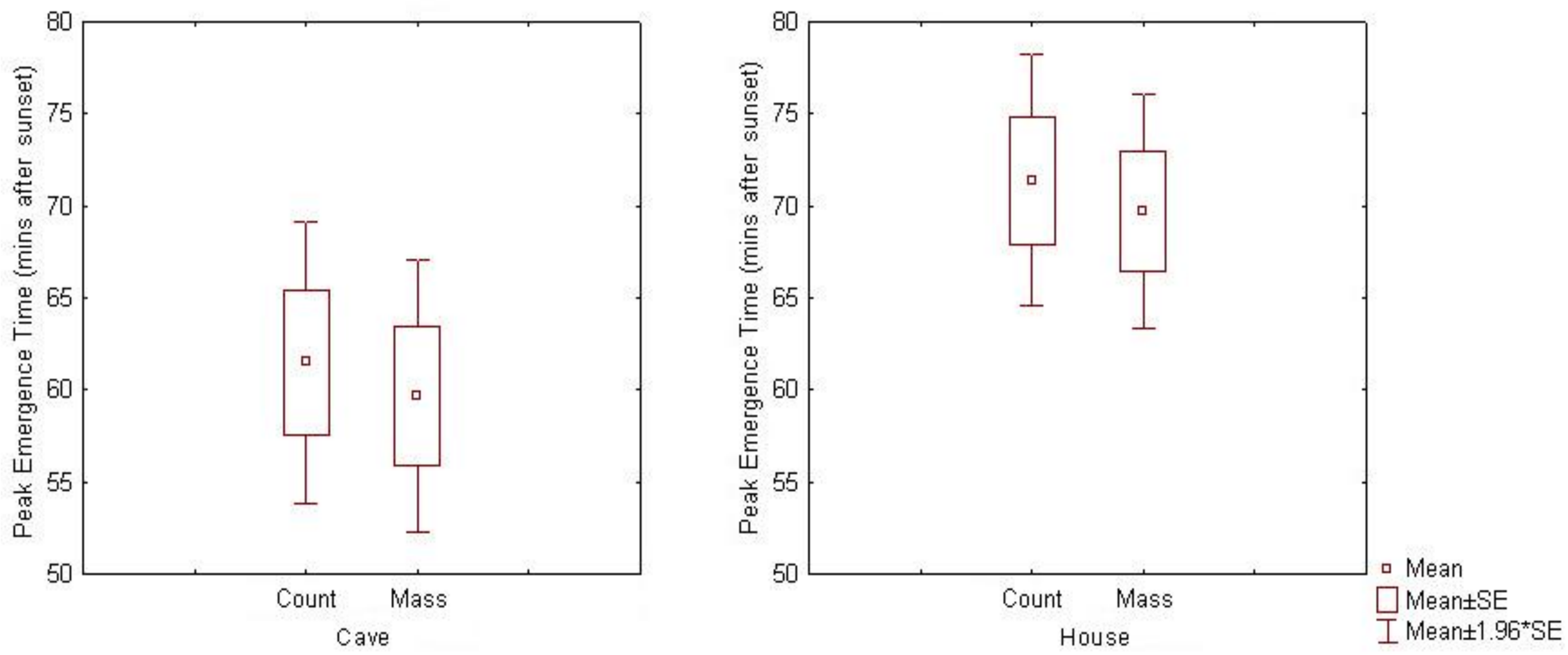


Figure 3.11: Peak activity of insects based on count and biomass data from the De Hoop Guano cave and the house.

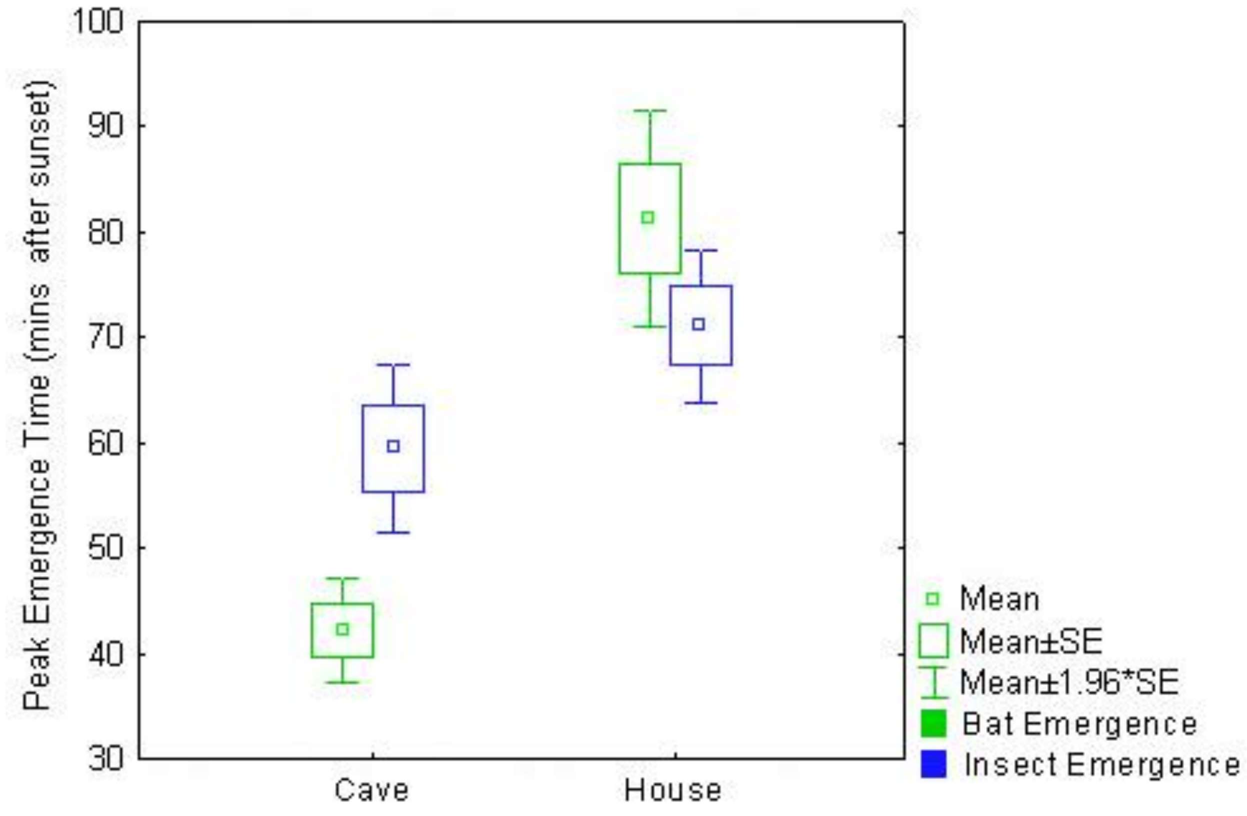


Figure 3.12: Bat and insect (mass data) peak emergence time (mins after sunset) between the cave and house over all three trips.

Bat peak emergence time was not related to insect peak activity (mass data) time at the cave or the house over all three sampling periods (Linear regression, $F_{1, 99}$= 0.27, p= 0.61 and $F_{1, 40}$= 0.87, p= 0.36, respectively). However, both bats and insects emerged later at the house than at the cave (Fig. 3.12, T-test, t= -6.76, df= 65, p< 0.001 and t= -.2.13, df= 73, p< 0.05, respectively).

Chapter 4

DISCUSSION

My results indicate that peak emergence behaviour of the seven species of bats is related to sunset, foraging strategy, diet and predation pressure which taken together are consistent with the predation hypothesis. Peak insect activity was not related to the peak emergence times of bats at the separate roosts but insect emergence was later at the house and so was bat emergence. I found no evidence to support the weather hypothesis as none of the variables measured (temperature (°C), humidity (%), wind speed ($m.s^{-1}$), air pressure (inHg), and cloud cover) affected peak emergence time. Similarly there was no effect of moon phase or cloud cover, which could influence moon phase through its exclusion of moon light.

4.1. Emergence time and sunset

Over all three sampling periods and for the mid-summer period alone, emergence by all bats was correlated with sunset. This was not the case for early and late summer but even during these periods peak emergence was always after sunset at both the cave and house. During early summer, peak emergence time was on average later than during mid and late summer which is expected because sunset was later during early summer. During this period owls (*Tyto alba* and *Bubo capensis*) were seen on several occasions at the house and an unsuccessful attack was recorded which may have delayed emergence. The influence of sunset time on emergence may thus be mediated by predation. This is logical given that it is still light during civil twilight for a little while after the sun sets making the bats more vulnerable to visually orienting predators. Delaying emergence in these situations would afford bats more protection. It is generally accepted, and my results support this, that the timing of emergence is related to sunset (Herreid and Davis 1966; Erkert 1982; Isaac and Marimuthu 1993; Kunz and Anthony 1996; Lee and McCracken 2001; Clark *et al*. 2002; Thies *et al*. 2006; Kaňuch 2007) and that predation may be one reason for this (Erkert 1982; Speakmen 1991; Jones and Rydell 1994; Rydell and Speakmen 1995; Rydell *et al*. 1996; Pavey 2001).

4.2. Emergence time and environmental conditions

Weather conditions (in terms of temperature, humidity, wind, etc) during the study were benign and not severe enough to affect bat activity (Table 3.2). Temperatures over the sampling period ranged from 13 - 23°C which is not likely cold enough to induce changes in emergence behaviour. Ambient temperature does affect emergence behaviour (Anthony *et al*. 1981; Maier 1992 and Hayes 1997; Erickson & West 2002); however the temperatures in summer ranged between 5 and 21 °C for these studies. Avery (1985) estimated a critical minimum temperature (8-10 ˚C) below which foraging would be less beneficial than remaining torpid. I never recorded temperatures below 10˚C in the 3 hours after sunset during recording of bat emergence. Perhaps there was not a large enough variation in temperatures over the study period to reveal any behavioural change that may be associated with temperature. Similarly, it rarely rained during the sampling period and when it did it was never more than a short light drizzle. I was therefore unable to test the effect of rain on peak emergence time. Several studies have reported that only heavy rain decreases bat activity (DeCoursey and DeCoursey 1964; Kunz 1982; Erkert 1982, 1987; Rydell 1989; Shiel and Fairley 1999; Weinbeer *et al*. 2006).

Similarly, there was little variation in air pressure (Table 3.2) over the three sampling periods; in fact, the range for each sampling period was 29.6 - 30.5 inHg. Thus it is not surprising I found no effect of pressure. Pressure is the only physical environmental characteristic that changes in a cave while all others remain constant (Paige 1995). Ambient temperature is known to affect insect activity; lower temperatures lead to decreased activity (Taylor 1963; Erkert 1982; Kunz 1988; Paige 1995). While, temperature and insect activity are negatively correlated with air pressure (Paige 1995); as temperature increases, air pressure declines and insect activity increases. Paige (1995) suggested that small changes in barometric pressure can be used by bats to indirectly track insect activity (which is directly affected by temperature) outside roost entrances, using this as a cue for when to emerge. Considering the small changes in air pressure (29.13 - 29.72 inHg) during Paige’s (1995) study, the variation between air pressure during my study would most certainly be large enough to affect peak emergence time if the bats were using it as a cue to emerge during periods of high insect activity. However, insect peak activity was not correlated with bat peak emergence during this study, suggesting that bats are not timing their emergence to coincide with peaks in insect activity. So, they have no use for changes in air pressure as cues for changes in insect activity.

Wind speed had no effect on peak emergence time. The wind at De Hoop Nature Reserve can reach up to 60 km/h but it usually dies down once the sun sets (De Hoop vlei South Africa, 1988). During the sampling period the wind ranged from 0.16 to 2.29 m.s^{-1} with an average speed of 0.90±0.42 m.s^{-1} during the time of recording. Moderate wind speeds likely have no effect on bat activity (Maier 1992; Erickson and West 2002; Welbergen 2006; Russo *et al*. 2007). However, some studies have found bat activity to be reduced as a result of strong wind (O'Farrell and Bradley 1970; Erkert 1982; Petrželková and Zukal 2001). O'Farrell and Bradley (1970) found that wind only affected activity once it reached above 4.02 m.s^{-1}. I never recorded wind speeds above 3 m.s^{-1} during recording, leaving the possibility that wind only affects bat activity when it is very strong, such that bats may be physically unable to fly.

The amount of lunar illumination which is dependent on moon phase, can suppress bat activity (Erkert 1982; Speakmen 1991; Jones and Rydell 1994; Rydell and Speakmen 1995; Meyer *et al*. 2004). The brighter it is the more vulnerable bats are to predation (Speakmen 1991; Jones and Rydell 1994; Rydell and Speakmen 1995). Similarly, cloud cover likely affords bats more protection from predators on moonlit nights by blocking the light from the moon (Herried and Davis 1966; Kunz and Anthony 1996; Elangovan and Marimuthu 2001). However, my results show no effect of cloud cover or moon phase on peak emergence time. Given the support we found for predation, this suggests that perhaps predation is not affected by the level of light in this community of bats, possibly because 5 of the 7 species were clutter or clutter-edge forages and may receive adequate cover from predators in the low vegetation, even on moonlit, cloudless nights.

Several studies have found no effect of weather on bat activity. Hecker and Brigham (1999) found ambient temperature, wind speed, cloud cover, rain and fog had no affect on bat activity. Similarly Clark *et al*. (2002) found no effect of cloud cover or any other indices of brightness on the activity patterns of *Corynorhinus townsendii ongens*. Contrary to my findings and theirs, a number of authors have proposed that emergence is suppressed by specific weather conditions (temperature, rain, cloud cover, humidity, wind; Lacki 1984; Kunz and Anthony 1996; and Shiel & Fairly 1999; O'Donnell 2000; Erickson and West 2002). However, it seems that in these studies, there was more variation in weather, for example heavy rain, strong wind and cold temperatures.

4.3. Emergence time and life-history strategies

4.3.1. Emergence time and foraging strategy

Bats in a multi-species community exhibit a wide range of morphologies and echolocation strategies allowing them to hunt in particular habitats (Schoeman and Jacobs 2010). At De Hoop, foraging strategy, rather than flight speed, influences emergence time, contrary to bats in Europe where flight speed seems to have a significant effect on emergence (Jones and Rydell 1994). Although, I did not measure flight speed directly, I used foraging strategy (clutter, clutter-edge and open) as a proxy to make inferences. Open-air and clutter-edge foragers are adapted for faster more agile flight than clutter foragers (Norberg and Rayner 1987; Schoeman 2006). I would therefore have expected clutter foragers to emerge later (if flight speed was important) as their flight is slower due to their adaptations to foraging in clutter (Jones and Rydell 1994). However, clutter foragers (*R. clivosus*, *R. capensis* and *N. thebaica*) on average emerged earlier than clutter-edge (*M. natalensis*, *My. tricolor* and *N. capensis*) and open foragers (*T. aegyptiaca*). The gleaning species, *N. thebaica*, which is probably the slowest flier in this community, was one of the species to emerge earlier than edge and open foragers

The Guano Cave is located in a cove, and is surrounded by dense shrubbery providing sufficient cover (i.e. cover from brush and less light penetrating through the leaves) for clutter foragers to emerge and quickly take cover within vegetation. Thus, the roost is an ideal location for clutter foragers to emerge earlier and take advantage of foraging while protected by vegetative cover. This is consistent with my results showing that cave roosting bats generally emerged earlier than the roof-roosting bats as there was little vegetation cover around the roof roost. The two roof-roosting species, *N. capensis* and *T. aegyptiaca*, were clutter-edge and open foragers, respectively. This meant that even if there was cover, they probably would not have been able to take advantage of it to forage while avoiding predation.

This is probably why even at the cave, the clutter–edge and open foragers like *My. tricolor* and *M. natalensis* emerged later than clutter foragers like *R. capensis* and *R. clivosus*. Similarly, Russo *et al*. (2007) also reported that bats emerging into open habitats emerged later than those roosting beneath a closed canopy.

4.3.2. Emergence time and diet

Diet was also one of the life history traits related to peak emergence time within the three sampling periods. As with foraging strategy, no consistent pattern was found across the three sampling periods. However the general trend suggests that bats feeding on Diptera (*T. aegyptiaca*) emerged later than bats feeding on Lepidoptera (*R. capensis* and *N. thebaica*) which is contrary to Jones and Rydell (1994). This difference is probably only partly due to the different patterns of insect activity. At other locations, Diptera emerge earlier than other insects, especially Lepidoptera which are said to emerge the latest (Racey and Swift 1985; Jones and Rydell 1994; Fenton *et al*. 1998).

Bats time activity to coincide with the peak activity of preferred prey items, with moth eaters emerging latest (Jones and Rydell 1994; Meyer *et al*. 2004; Lang *et al*. 2006). My results are only partly consistent with this trend because roof-roosting bats emerged later than cave roosting bats which coincided with the later peak activity of insects at the roof roost (Fig. 3.12). However, the peak activity time of different insect orders was highly variable and there was no statistical difference in the peak activity time of the different orders. Hence there really was no relationship between bat emergence times and that of their preferred prey. Furthermore, the bats at De Hoop do not specialize on any particular prey and displayed very little prey preference (Schoeman and Jacobs 2010). Existing data cannot explain why peak insect activity is later at the roof roost.

4.3.3. Emergence time and body size

Although *R. clivosus,* one of the bigger species, emerged early over all three sampling periods, and *N. capensis*, the smallest species emerged late, there was no overall significant correlation between body size and emergence time as predicted by the predation hypothesis. This is contrary to finding by Jones and Rydell (1994) and may be due to the relatively low variation in body mass (7.9 to 18 g) amongst the seven species I studied. Jones and Rydell's (1994) meta-analysis incorporate data from many more species of bats with a much greater range in body size. The relationship between body mass and emergence time may thus be obscured by the small number of species considered for this study, especially in light of the other evidence supporting predation as a factor in bat emergence times.

4.4. Emergence time and predation

Predation has long been suggested as a factor influencing behavioural patterns; reducing or suppressing activity (Erkert 1982; Speakman 1991 a, b;

Jones and Rydell 1994; Rydell and Speakman 1995; Lang *et al*. 1996; Gannon and Willig 1997). Their nocturnal nature and ability to fly make bats a difficult subject to study the effect of predation, therefore in most instances predation is inferred though the effect of light, cloud cover, habitat change and flight performance (Fenton 1977; Morrison 1978 a; Reith 1982; Jones and Rydell 1994; Duvergé *et al*. 2000; Elangovan and Marimuthu 2001; Meyer 2004). Predation events on bats are likely opportunistic and do not constitute a major part of predators diet but this is not to say that predation did not exert selection on behaviour (Baker 1962; Vernon 1972; Morrison 1978 a; Ruprecht 1979; Speakman 1991 a). Barn owl (*Tyto alba)* pellets from De hoop Nature Reserve contained all seven species of bats but in small proportions when compared to all the other species taken, data suggests that more *N. capensis* are taken (Avery *et al*. 2005). Typically, bats are eaten by a variety of predators but they only make up a small proportion of predator diets (Twente 1954; Baker 1962; Gustavo and Reagan 1984; DeFrees and Wilson 1988; Bautenbach *et al*. 1990; Speakman 1991 a; Swengel and Swengel 1992; Fenton *et al*. 1994; Sparks *et al*. 2003; Lang *et al*. 2006).

Bats have been reported to reduce or suppress activity in bright light with increased activity on cloudy and moonless nights, leading to the inference of predation as the cause of the behavioural changes (Morrison 1978 a; Reith 1982; Isaac and Marimuthu 1993; Kunz and Anthony 1996; Shiel and Fairley 1999; Elangovan and Marimuthu 2001; Meyer *et al*. 2004; Welbergen 2006; Russo 2007). Other authors have experimentally shown that in the presence of stuffed predators and their acoustic cues, activity decreases consistent with an avoidance response (Petrželková and Zukal 2001; Baxter *et al*. 2006). The problem with these types of studies is that it is unclear if the response is not simply a reaction to the noise itself. There is also the risk of the bats becoming habituated. On the other hand, a number of studies have found no affect of light or cloud cover on bat activity (Anthony *et al*. 1981; Negraeff and Brigham 1995; Hecker and Brigham 1999; Clark *et al*. 2002; Karlsson *et al*. 2001; Thies *et al*. 2006).

My direct observations of predation were limited with no successful events witnessed. I found no effect of light level, cloud cover or flight speed. However, the emergence of bats after sunset, the emergence of clutter-foragers and gleaners before edge and open foragers and the emergence of cave-roosting bats before the house-roosting bats suggest that predation may have a significant influence on the emergence times of bats. During the study period both owls (*Tyto alba* and *Bubo capensis*; house and cave) and genets (*Genetta genetta*; cave) were frequently seen around the entrance to the roosts both of which prey on bats (DeFrees and Wilson 1988; Speakman 1991 a; Taylor 1994; Avery *et al*. 2005). The presence of a predator only seemed to significantly affect peak emergence in early summer, during which predators (owls, *Tyto alba* and *Bubo capensis*) were only observed at the house. This may explain why the bats from the house emerged later from the roof roosts than from the cave roost (Fig. 3.12). I also noted that roof roosting bats would occasional change their departure between a number of exits, most likely to avoid predators.

Clustering (*i.e.* large number of bats emerge from a roost entrance at the same time) has been described as either an anti-predator behaviour or a bottle neck effect (where emergence is clustered due to the small entrance to the cave, Kalcounis and Brigham 1994; Speakman *et al*. 1999; Petrželková and Zukal 2001). I did not test this hypothesis but it may explain why predators were more inclined to attack bats emerging from buildings where only a few individuals emergence each night avoiding the clustered emergence at the cave and why roof-roosting bats emerged later than cave roosters.

4.5. Measuring peak emergence

Using echolocation calls as means of assessing peak emergence time enabled me to record data for a number of species simultaneously, allowing easy species identification. It removed the uncertainty associated with using the first and or the median bats emergence as a proxy for the whole species, as this ignores within species variation. The use of bat detectors is also a passive non-invasive method which decreases the risk that behavioural changes were due to presence of observers. The major caveats associated with this method of identifying peak emergence are that nothing can be said about number of individuals, sex, age, reproductive status, lactation and body condition. Some or all of these factors could influence emergence (Kunz 1974; Anthony *et al*. 1981; Taake 1985; Rydell 1989; Jones and Rydell 1994; Rydell *et al*. 1996; Duvergé *et al*. 2000; Lee and McCracken 2001; Clark *et al*. 2002; Thies *et al.* 2006).

4.6. Conclusions

In conclusion, life history traits (foraging strategy and diet) were the factors most consistently related to emergence times of the seven species of bats. Clutter foragers emerged earlier than clutter-edge and open air forager, suggesting foraging in vegetation may afford more protection than flying fast. The effect of the presence of a predator (during early summer) together with the effect of foraging strategy suggests that emergence is affected by predation. Although variable, the general pattern suggests that bats feeding on Lepidoptera emerged earlier than bats feeding on Diptera. Weather had no effect on emergence but it was consistent throughout the sampling period giving little cause for behavioural changes. Emergence is affected by a number of factors which are not mutually exclusive. Long term studies across seasons may improve our understanding of how all these factors including life history traits not considered here, such as sex, age, body condition and reproduction status, interact to determine inter- and intra specific variation in bat emergence times.

Chapter 5

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