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# **Factors affecting the activity patterns of *Myotis tricolor* (Chiroptera: Vespertilionidae).**

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**Stacey Jordaan**

SUPERVISOR: Assoc. Prof. David Jacobs

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**Declaration:**

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I, Stacey Jordaan, know the meaning of plagiarism and declare that all of the work in this document, save for that which is properly acknowledged, is my own.

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University of Cape Town

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## **Abstract:**

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**Foraging behaviour is an important component of an animal's ecology. Increases in energetic costs associated with reproduction, should have marked effects on foraging behaviour, but may be compounded by the effects of environmental factors. I investigated the activity patterns of female *M. tricolor* over the reproductive period using radio telemetry. Six female bats were radio-tagged during each reproductive period: early pregnancy, late pregnancy and lactation. Times at which bats entered and exited the cave were recorded, as was the temperature, moon-phase, cloud cover, wind speed, rainfall and insect abundance. These data were used to calculate emergence time, number of foraging bouts and foraging duration for each reproductive period, which were then correlated with the environmental variables. During September (early pregnancy/ non-reproductive) females emerged later and had more, shorter foraging bouts per night. The costs of reproduction increased foraging time during late pregnancy but had no impact on the number of foraging bouts or emergence time. Foraging duration during lactation did not exceed that during pregnancy, despite higher costs, thus females may use compensation, such as torpor, during this time. Lactating bats may also use fat storage to cope with energetic requirements of lactation. Weather conditions accounted for further patterns of activity. Rain delayed nightly emergence and wind decreased foraging duration and increased the number of foraging bouts per night. Low minimum temperatures also resulted in more foraging bouts. Insect abundance had no effect on**

activity patterns. Thus both environmental factors and the energetic costs of reproduction influenced the activity patterns of female *M. tricolor*.

## CHAPTER 1:

### **Introduction:**

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Foraging behaviour is an important component of the ecology of animals and includes where, when and how an animal feeds as well as what it feeds upon. Through its foraging behaviour, an animal interacts with its environment and with the species with which it shares a habitat, either by acting as a predator of or prey for other species, **competing with them, or by altering the environment in some way. An animal's foraging** behaviour is the product of an evolutionary trade-off between maximising energy intake, while minimising the energetic costs of foraging, as well as the risk of predation (MacArthur & Pianka, 1966; Iwasa *et al.*, 1981; Kotler *et al.*, 1991).

**An animal's foraging behaviour will** vary in terms of where and when it forages. Travel rates, activity times and habitat selection will vary between and within species with morphological and perceptual differences, diet (Robinson & Holmes, 1982) and various environmental factors (Kotler *et al.*, 1991). The structure (and particularly the vegetation structure) of a habitat will influence foraging behaviour (Robinson & Holmes, 1982) as it will influence the ease of locomotion, cover from predators and the accessibility to food. In addition to the accessibility of resources within a habitat, the characteristics of the resources will have great impacts on the foraging behaviour of an animal (Iwasa *et al.*, 1981; Robinson & Holmes, 1982; Kotler *et al.*, 1991; Eide *et al.*, 2004). In particular, the

abundance, size, distribution, predictability and diversity of prey will affect foraging decisions (Robinson & Holmes, 1982; Eide *et al.*, 2004). With regard to the cover from predation provided by the habitat, an individuals' **foraging behaviour** should be selected to minimise exposure to predators, while maximising accessibility to prey. Nevertheless, when this is not possible, the individuals of some species are more likely to rank cover from predators higher (Brown, 1988; Hughes & Ward, 1993), while others will favour accessibility to prey, irrespective of cover (Brown, 1988; Hopcraft *et al.*, 2005). The risk of predation will also influence both when and where an animal forages (Kotler *et al.*, 1991; Hughes & Ward, 1993; Aubret *et al.*, 2007). Besides the habitat structure, this predation risk also involves the innate vulnerability to predation of a specific species (Brown, 1988) and individual and the immediate predation risk based on the environmental conditions (Kotler *et al.*, 1991). For example, when exposed to higher light levels or the obvious presence of a predator, gerbils reduce activity and are more likely to leave a foraging patch (Kotler *et al.*, 1991).

Environmental factors will affect the foraging behaviour of individuals seeking to optimize energy budgets and will interact with the costs of foraging, which include commuting to foraging site(s). This may be particularly important for volant animals that fly large distances to foraging sites given that flight is energetically expensive (Thomas, 1975; Racey & Speakman, 1987; Thomas, 1987), not only in terms of cost per unit distance, but it also results in a greatly increased metabolic rate (Thomas, 1975; Norberg, 1990). The costs of foraging also include the costs of searching for prey and the time spent handling and consuming prey (MacArthur & Pianka, 1966; Iwasa *et al.*, 1981), which

may vary with both the nature and size of a particular item. In addition, **an animal's** foraging behaviour is expected to vary with changes in energy demand, such as those associated with reproduction (Barclay *et al.*, 2000).

One can measure foraging behaviour by investigating temporal activity patterns. The activity patterns of an animal can be quantified in terms of the times during which an animal is active, and the duration of and number of foraging bouts. In addition, how these patterns change in response to weather conditions, light levels, prey abundance and distribution, and the energetic costs of foraging, as well as reproduction can be quantified (Robinson & Holmes, 1982; Iwasa *et al.*, 1981; Kotler *et al.*, 1991).

Despite being nocturnal it is possible to quantify the foraging behaviour of bats directly through observation at emergence from roosts and methods such as radio telemetry. However, bats are highly diverse in terms of their number of species, morphology, feeding and roosting behaviour (Altringham, 1996). This ecological diversity means that extrapolation of general patterns from individual studies is difficult and necessitates species specific investigations of foraging behaviour (Racey & Entwistle, 2003; Ciechanowski *et al.*, 2007). In addition, the high mobility afforded by flight allows bats access to a wide range of habitats and may release them from dependence on a particular location for foraging (Walsh & Harris, 1996; Fenton, 1997; Ciechanowski *et al.*, 2007), increasing the potential for variation in foraging behaviour. Furthermore, many insectivorous bats appear to be opportunistic (Kunz, 1974a; Heithaus *et al.*, 1975; Belwood & Fenton, 1976; Fenton *et al.*, 1977; de Jong & Ahlen, 1991; Brigham *et al.*,

1992; Blake *et al.*, 1994; Rydell *et al.*, 1996; Racey & Entwistle, 2003) and flexible (Heithaus *et al.*, 1975; Fenton & Thomas, 1980; Aldridge & Rautenbach, 1987; Meyer *et al.*, 2005; Ciechanowski *et al.*, 2007) in their foraging behaviour. Therefore, it is expected that individuals of a bat species will alter temporal foraging patterns in response to various environmental factors and specific energy and nutrient demands.

Wing morphology and echolocation call structure give researchers an indication of a bat's flight and foraging capabilities and can be used to predict the most likely general foraging behaviour of a species (Norberg & Rayner, 1987; Jacobs, 1999; Fenton & Bogdanowicz, 2002). However, while these characteristics may set limits on flight capabilities and the structure of the habitat in which an individual can forage, they are not informative about temporal activity patterns (Audet, 1990) and environmental conditions will further affect foraging behaviour within these constraints. In addition, many bat species use habitats in ways that do not conform to predictions from morphology and echolocation call structure. For example, Audet (1990) found that *Myotis Myotis* (Vespertilionidae) spent much more time in flight than con-specifics, despite having a lower aspect ratio and consequent higher cost of flight. *Macrophyllum macrophyllum* (Phyllostomidae) has an average wing loading and aspect ratio (and therefore relatively manoeuvrable and agile, albeit costly, flight) but flies long distances (Meyer *et al.*, 2005) and *Chalinolobus tuberculatus* (Vespertilionidae) has large home ranges, despite its small size and average wing-loading and aspect ratio (O'Donnell, 2001). Therefore, an understanding of species-specific variation in activity patterns is needed to formulate general models of foraging behaviour (Audet, 1990).

Temporal activity patterns and emergence times vary between insectivorous bat species depending on the foraging strategy (Jones & Rydell, 1994; Brown, 1968; Rydell *et al.*, 1996; Entwistle *et al.*, 1996), diet (Jones & Rydell, 1994; Brown, 1968; Rydell *et al.*, 1996; Entwistle *et al.*, 1996) and flight speed (determined by wing loading, Rydell *et al.*, 1996). Within a species, activity patterns of individuals also vary greatly (Hayes, 1997; Shiel & Fairley, 1998), between individuals and over time (Fenton, 1970; Barclay, 1985; Fenton *et al.*, 1993; Milne *et al.*, 2005). Many studies have evaluated the correlation between these differences and environmental conditions (Clark *et al.*, 2002; Thies *et al.*, 2006; Rydell *et al.*, 1996; Audet, 1990; Russ *et al.*, 2003; Shiel *et al.*, 1999) but it is necessary to consider variation in energetic requirements as well.

An environmental parameter that is regularly investigated is temperature. Low temperatures are hypothesised to reduce activity levels in bats (Brown, 1968; O'Farrell & Bradley, 1970; O'Farrell & Bradley, 1970; Lacki, 1984; Erickson & West, 2002). This is because of the energetic costs of maintaining a high metabolism to regulate high body temperature of such small endotherms (Brown, 1968; O'Farrell & Bradley, 1970; Erickson & West, 2002; McNab, 1982) and because of low prey (insect) activity levels at low ambient temperatures (Williams, 1961; Taylor, 1963). Reduced activity levels have been positively correlated with low temperatures (Rydell, 1991; Maier, 1992; Shiel & Fairley, 1998; Clark *et al.*, 2002; Erickson and West, 2002); although Kunz (1974a) and Entwistle *et al.* (1996) found no evidence of this in *Myotis velifer* (Vespertilionidae) and *Plecotus*

*auritus* (Vespertilionidae), respectively. Therefore, I expected that bats should remain in the roost and possibly employ torpor during periods of low temperatures.

Increased light levels have also been reported to be associated with decreased activity (Rydell *et al.*, 1996; Russ *et al.*, 2003; Lang *et al.*, 2006). It is hypothesised that increased light exposes bats to a higher risk of detection by visually orienting predators (Rydell *et al.*, 1996; Russ *et al.*, 2003), but, moonlight has also been shown to negatively affect insect activity (Anthony *et al.*, 1981; Hecker & Brigham, 1999; Lang *et al.*, 2006) and thus may result in decreased activity of insectivorous bats through both of these mechanisms. However, the effects of moonlight on activity are not consistent as other studies have found no evidence of this effect (Clark *et al.*, 2002; Thies *et al.*, 2006) and so the response of bat species to light intensity needs to be explored further.

Rain may increase the energetic costs of thermoregulation as a wet bat may lose heat to the environment more quickly (McNab, 1982). In addition rain drops in the air attenuate echolocation calls and may make target detection more difficult (Schnitzler & Kalko, 2001). For these reasons I expect rain to result in decreased activity, as the costs of foraging in rain may be too great. This has been found in some species (Entwistle *et al.*, 1996; Erickson & West, 2002; Ciechanowski *et al.*, 2007) but, rain had no effect on the activity of *Eptesicus serotinus* (Vespertilionidae; Catto *et al.*, 1995), *Corynorhinus townsendii ingens* (Vespertilionidae; Clark *et al.*, 2002) and *Carollia castanea* (Phyllostomidae; Thies *et al.*, 2006). The last two species do not rely on echolocation for active prey searching and thus this may indicate that rain has its greatest effect on bats

by interfering with echolocation. However, these species-specific effects indicate that it is necessary to investigate the response to rainfall when investigating foraging behaviour, particularly for aerial-hunting insectivorous bats whose echolocation may be impaired under these conditions.

Strong winds make flight more difficult, particularly for animals as small as bats, and have been shown to negatively affect bat activity (O'Farrell *et al.*, 1967; O'Farrell & Bradley, 1970). Insect distributions (and so availability to predators) are also affected by strong winds (Lewis & Stephenson, 1966; Lewis & Dibley, 1970), and thus may increase the costs of foraging or decrease the profitability of foraging by decreasing the rate at which bats encounter prey, compounding the effect on bat activity. Thus I expected decreased bat activity under these conditions.

All of the weather conditions expected to directly affect bat activity are also hypothesised to affect insect abundance. It is difficult to separate the effects on prey from the direct effects on the bats. Despite patterns of insect abundance being highly variable (McDonald *et al.*, 1990), most evidence suggests that temporal patterns of insect abundance have the strongest correlation with bat activity patterns (Barclay, 1991; Rydell *et al.*, 1996; Hayes, 1997; Vaughan *et al.*, 1997; O'Donnell, 2000; Thies *et al.*, 2006; Lang *et al.*, 2006).

Changes in energetic requirements are likely to have profound effects on foraging behaviour. Reproduction in female mammals, in particular, is energetically expensive (Hanwell & Peaker, 1977; Gittleman & Thompson, 1988; Kurta *et al.*, 1990). The costs of reproduction vary within and between species, populations and individuals (Gittleman & Thompson, 1988; Barclay *et al.*, 2000). In addition, the energetic costs of reproduction vary over the reproductive cycle (Hanwell & Peaker, 1977; Gittleman & Thompson, 1988) and lactation is more energetically expensive than pregnancy (Kunz, 1974a; Hanwell & Peaker, 1977; Racey & Speakman, 1987; Gittleman & Thompson, 1988; Kurta *et al.*, 1989; Kurta *et al.*, 1990). This is because milk has high levels of fats, proteins and carbohydrates (Hanwell & Peaker, 1977; Oftedal, 1984). In cows, goats and pigs, milk production requires 50-80% of the dietary glucose, 15-40% of the acetate and most of the amino acids (Hanwell & Peaker, 1977). In addition the energetic costs of lactation increase from parturition to weaning, as the offspring grow and have increasing demands (Kunz, 1974a; Racey & Speakman, 1987; Kurta *et al.*, 1989; Gittleman & Thompson, 1988). In *Eptesicus nilssonii* (Vespertilionidae), for example, the energetic costs of lactation are 100% greater at weaning than at parturition (Rydell, 1993).

Bats have a slow life history strategy, which is unusual for such a small bodied mammal. They have long life-spans and produce few, large offspring, once or twice per year (Barclay & Harder, 2003). They typically invest more energy per offspring than other small mammals, such as shrews, but extend their reproductive investment over a long lifetime (Barclay & Harder, 2003). Smaller animals also generally have higher milk yields, higher energy outputs and more mammary tissue per gram of body mass (Hanwell &

Peaker, 1977). In *Eptesicus fuscus* (Vespertilionidae), for example, the daily assimilated energy requirements during lactation may be more than double that during pregnancy (Kurta *et al.*, 1990). Due to the costs of flight (Thomas, 1975; Norberg, 1990), bats may use a greater proportion of their energy intake on maintenance and so have relatively less energy to allocate to reproduction compared to other mammals (Barclay & Harder, 2003). Therefore, increases in energetic costs associated with reproduction, should have marked effects on foraging behaviour.

Bats are unique in that many species mate in autumn and then employ various mechanisms to delay pregnancy including: sperm storage, delayed implantation and delayed foetal development, over winter and during hibernation, before re-commencing development again in spring (Oxberry, 1979; Neuweiler, 2000). Cold temperatures and low prey abundance during winter necessitate hibernation by many species (and migration in several species). The reproductive cycle needs to begin in autumn and resume again at the start of the next season, because if mating occurred in spring, parturition, lactation and weaning of the young would occur later and, in some instances, would not overlap with the summer peaks in insect abundance, particularly at higher latitudes with shorter summers (Bernard, 1989; Neuweiler, 2000). Delayed pregnancy therefore enables bats to meet the energetic costs of reproduction earlier in the summer season and also allows enough time post weaning on to deposit fat (for approximately a month) before hibernation and migration in some species (Oxberry, 1979; Bernard, 1989; Neuweiler, 2000). In general, for tropical bats food sources are not (or at least are less) seasonal. These species tend to be polyoestrous, while temperate populations are generally monoestrous, with reproduction occurring during peak food abundance

(Oxberry, 1979; Bernard, 1982; Neuweiler, 2000; Barclay & Harder, 2003). These trends in the reproductive cycles of bats indicate that resource availability may limit reproductive output in some bats (Bernard, 1989; Barclay & Harder, 2003) and that reproduction should have an effect on foraging behaviour.

An animal can use three different strategies to counteract the increased energetic costs of reproduction: storage, compensation and consumption (Racey & Speakman, 1987). Storage is the accumulation of body fat or the deposition of food stores external to the body and compensation is a decrease in energy expenditure on a portion of the energy budget that is not associated with reproduction (Racey & Speakman, 1987). Consumption is an increase in food intake, which is generally accompanied by an increase in the mass of the liver and gut and elongation of the gut, to keep assimilation efficiency constant (Racey & Speakman, 1987).

In general, small animals cannot rely heavily on internal storage as their small size means that only a small amount of fat can be stored (Racey & Speakman, 1987). Flying animals, in particular, cannot increase mass substantially as it will decrease manoeuvrability and thus increase flight and foraging costs (Aldridge & Brigham, 1988; Kalcounis & Brigham, 1995). Furthermore, the roosting behaviour and food type (insectivorous species) of bats do not allow for the external storage of food. Although bats cannot use storage extensively, they should build up the maximum possible fat stores, without substantially affecting manoeuvrability, before or during reproduction and before migration and/or hibernation.

Bats are unique in that they can use daily torpor to reduce energetic costs (McNab, 1982; Speakman & Thomas, 2003) and so can use compensation to balance reproductive costs. However, since torpor involves a decrease in metabolic rate, it slows all metabolic processes and thus may delay parturition when used in late pregnancy (Racey, 1973; Racey & Speakman, 1987; Audet & Fenton, 1988; Bernard, 1989; Kelm & Helversen, 2007). Similarly, torpor will also slow milk production (Wilde *et al.*, 1999) and thus, although pregnant and lactating bats do enter torpor, they do so far less than males and non-reproductive females (Audet & Fenton, 1988; Russ *et al.*, 2003; Dietz & Kalko, 2006). Therefore while bats can use torpor to offset energetic costs, other mechanisms, such as increased consumption, are needed because the extensive use of deep torpor during reproduction may decrease the survival probability of young.

To compensate for increases in energy requirements, I predict that food intake should increase from pregnancy to lactation, and over the course of lactation (Racey & Speakman, 1987; Gittleman & Thompson, 1988). Peak food intake should occur at mid-pregnancy and just before weaning, when energetic requirements are the greatest. Shortly before parturition the increase in wing-loading and cost of flight should result in decreased foraging time (Catto *et al.*, 1995). In accordance, *Eptesicus nilsonii* (Vespertilionidae) showed a decrease in foraging time in late pregnancy (Rydell, 1993). Food consumption was higher during lactation than pregnancy in *Myotis velifer* (Vespertilionidae) and peaked in late lactation in *M. velifer* (Kunz, 1974a). McDonald *et al.* (1990) found increased activity by *Miniopterus schreibersii* (Vespertilionidae) during the reproductive period and attributed this to increased energy demands. However, this is assuming that increased foraging time results in increased consumption, which would

depend on the rate of capture, and ultimately, the abundance and distribution of insects. To increase food consumption, the variation in energy demands over the reproductive period may be associated with a switch in foraging strategy or food type or changes in temporal activity, particularly increased foraging time.

On the basis of these patterns of energetic costs over the reproductive period pregnant females should forage for longer than non-reproductive females, and lactating females should forage for longer than pregnant females. Some lactating female bats emerge earlier (Shiel *et al.*, 1999) and forage longer (Rydell, 1991; Shiel *et al.*, 1999; Rydell, 1993) than pregnant and non-reproductive females. In addition, Clark *et al.* (1993) found that the time spent foraging increased from mid- to late-lactation in *Plecotus townsendii* (Vespertilionidae). Conversely, Clark *et al.* (2002) found lactating females emerged later, and attributed this to time taken to groom young. Other lactating females do not increase foraging time (Fuhrmann & Seitz, 1992; Entwistle *et al.*, 1996) but instead, increase the number of foraging bouts during the night (without an increase in overall activity; Clark *et al.*, 2002; Shiel *et al.*, 1999; Mackie & Racey, 2007; Kunz, 1974). This has been attributed to the need to return to the roost to suckle young. Thus there is a need for the examination of species-specific patterns of activity over the female reproductive cycle.

The genus *Myotis* (**Vespertilionidae**) is one of the world's most diverse mammalian genera, with over 100 species distributed worldwide (Findley, 1972; Ruedi & Mayer, 2001; Simmons, 2004) and is the most widely distributed group of bats (Walker, 1964;

Stadelmann *et al.*, 2004). *Myotis* encapsulates a wide morphological and ecological diversity with a number of species that display similar morphological and echolocation adaptations in conjunction with similar foraging strategies (Ruedi & Mayer, 2001; Findley, 1972). However, these groupings reflect ecological convergences rather than phylogenetic relationships (Ruedi & Mayer, 2001; Stadelmann *et al.*, 2004) making generalisation about foraging behaviour within a genus difficult (Racey & Entwistle, 2003).

*Myotis tricolor* (Temmick, 1832) is a medium sized (16 g, Norberg & Rayner, 1987; Stoffberg & Jacobs, 2004) insectivorous bat (Skinner & Smithers, 1990; Taylor, 2000) with low wing-loading and aspect ratio (Norberg & Rayner, 1987; Stoffberg & Jacobs, 2004). This species uses broadband echolocation calls of short duration (Taylor, 2000; Stoffberg & Jacobs, 2004). Fenton and Bogdanowicz (2002) and Findley (1972) predicted that it would be capable of both aerial hawking flying insects and gleaning prey from substrates. This is because its **morphology is intermediate between that of a 'typical' aerial forager and a 'typical' gleaner** (Fenton & Bogdanowicz, 2002; Stoffberg & Jacobs, 2004). Its wing-tips are more pointed than those of known gleaners (Stoffberg & Jacobs, 2004). The echolocation call structure is intermediate between those of aerial foragers and gleaners (Stoffberg & Jacobs, 2004). Despite this, Stoffberg and Jacobs (2004) could not induce *M. tricolor* to glean in a flight room, under a variety of circumstances. The authors attributed this to the lack of harmonics in its echolocation call, preventing precise resolution of insect targets against background clutter (vegetation). They hypothesised that this species is an aerial forager that is mostly active on the edge of

vegetation (a 'clutter-edge forager'; Fenton, 1989; Schnitzler *et al.*, 2003; Stoffberg & Jacobs, 2004; Schoeman & Jacobs, 2010).

Given its intermediate wing morphology and echolocation call structure, it is reasonable to expect that *Myotis tricolor* is flexible in its foraging habits, as intermediate morphology is typical of *Myotis* species that use multiple foraging strategies (Fenton & Bogdanowicz, 2002; Stoffberg & Jacobs, 2004). Many bats use multiple foraging strategies (Fenton *et al.*, 1990) and this plasticity occurs in many *Myotis* species (Norberg & Rayner, 1987; Todd & Waters, 2007; Jones & Rayner, 1988; Fenton & Bogdanowicz, 2002; Ratcliffe & Dawson, 2003). For example, *Myotis nattereri* (Siemers *et al.*, 2001) *M. lucifugus*, *M. septentrionalis* (Ratcliffe & Dawson, 2003), *M. evotis* (Faure & Barclay, 1994) and *M. emarginatus* (Krull *et al.*, 1991) all hawk aerial prey and glean, while *M. daubentonii* (Kalko & Schnitzler, 1989; Boonman *et al.*, 1998), *M. capaccinii* (Almenar *et al.*, 2006), *M. adversus* (Dwyer, 1970; Jones & Rayner, 1991) and *M. yumanensis* (Brigham *et al.*, 1992) can switch between aerial foraging and trawling for insects from the water surface. Natural selection should favour individuals that are behaviourally flexible and therefore able to exploit unpredictable situations and cope with change (Aldridge & Rautenbach, 1987). This potential flexibility of foraging habits in *M. tricolor* makes investigation of its foraging behaviour important since it should alter its foraging behaviour in response to changes in environmental conditions and particularly to changes in energy demand, such as those over the reproductive period. These changes should be reflected in changes in its temporal activity patterns and should reflect strategies used to cope with the energetic requirements of breeding in females.

The purpose of my study was to investigate the temporal aspects of the foraging behaviour of *Myotis tricolor*, specifically how the factors of reproduction, prey abundance and weather change it. I expected foraging behaviour to be influenced by the energetic costs of reproduction, and thus predicted that late pregnancy females will forage for longer than early pregnancy/non-reproductive females; that the number of foraging bouts will not differ between early and late pregnancy females and that lactating females will have more foraging bouts per night than pregnant females, because they need to return to their roost to suckle their young. I assume that the energetic costs of lactation exceed those of pregnancy (Hanwell & Peaker, 1977; Racey & Speakman, 1987; Gittleman & Thompson, 1988; Kurta *et al.*, 1989; Kurta *et al.*, 1990), and that the costs of foraging in late pregnancy are higher and thus I expect the foraging time of lactating females to exceed that of late pregnancy bats. The foraging behaviour of *M. tricolor* should also be affected by environmental conditions. If this is true, peaks in activity should be associated with temporal peaks in insect abundance. In addition, shorter and an increased number of foraging bouts throughout the night should be associated with low temperatures, strong winds and rain because bats should avoid these conditions but resume foraging again later in the night, when environmental conditions improve, or energy requirements demand foraging despite poor weather. Later emergence times and shorter foraging bouts should also be associated with high light levels due to the proposed increased predation risk under these conditions. However, reproductive state has marked effects on the energy budget of an animal (Hanwell & Peaker, 1977; Racey & Speakman, 1987; Gittleman & Thompson, 1988), thus the foraging behaviour of *M. tricolor* should change more dramatically with reproductive state than environmental factors. These results should enable a better understanding of how energetic costs and

environmental conditions interact to affect the patterns of foraging behaviour of an animal.

## CHAPTER 2:

### **Materials and Methods:**

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#### **Study Site:**

The study was undertaken at De Hoop Nature Reserve approximately 50 km south-east of Bredasdorp in the Western Cape Province, South Africa. Data were collected from September 2008 to March 2009 and during October 2009. The group I studied roosted in a sinkhole called Hothole Cave (34°27.448'S 20°26.675'E; Jacobs *et al.*, 2007). *Miniopterus natalensis*, *Rhinolophus capensis* and *Rhinolophus clivosus* roost together in this cave with *M. tricolor* (Jacobs *et al.*, 2007). The dominant vegetation in the area is coastal fynbos (evergreen, sclerophyllous shrubs) dominated by restios (*Chondropetalum* spp.) with a maximum height of approximately 2 m. In addition to coastal fynbos, other potential foraging habitats for *M. tricolor* in the reserve include coastal dunes, dune vegetation (dune fynbos and dune thicket), the De Hoop vlei (a lake that is periodically dry) and riparian vegetation around the vlei. The reserve is surrounded by agricultural land, mostly for sheep farming. The riparian vegetation consisted of *Phragmites australis* reed beds as well as White Milkwood trees (*Sideroxylon inerme*) interspersed within the coastal fynbos. The vlei is closed off from the ocean and is approximately 18 km long and 0.5 km wide (Butcher, 1988). The water depth varies from almost nothing to a maximum depth of 7.7 m (Butcher, 1988). During my study, the vlei was approximately full, providing a large water surface over which bats could forage.

## **Bat capture:**

Bats were captured as they emerged at dusk using mist nets placed about 3 m from the entrance to Hothole Cave. When I did not capture sufficient bats (six bats per sampling period) using this method, they were captured by hand from the cave roof during the day. Juveniles were identified by the presence of cartilaginous epiphyseal plates in the finger bones (Anthony, 1988) which I assessed by trans-illuminating the extended wings with a head torch. They were excluded from all further measurement and experimentation due to the ontogeny of flight and echolocation (Buchler, 1980; Jones & Kokurewicz, 1994). For each adult bat, I measured body mass (to the nearest 0.1 g) **using a portable electronic balance (Scout Pro Balance, O’Haus Corp., NJ, USA)** and forearm length (to the nearest 0.1 mm) using dial-callipers. The sex of each bat was recorded. The extended right wing was photographed following the protocol of Saunders and Barclay (1992) using a digital camera (Nikon Coolpix S1, Nikon Corp., Japan) positioned directly above the wing, which was extended over graph paper, to provide calibration of a computer software program (SigmaScan<sup>®</sup> Pro version 5.0; Systat Software Inc. 1999), used to calculate wing and body lengths and areas. The wing area ( $S$ ) of all adult *M. tricolor* captured was measured and used to calculate wing loading ( $Mg/S$ , where  $M$  is body mass and  $g$  is gravitational acceleration,  $9.8 \text{ m/s}^2$ ) (Norberg & Rayner, 1987). Bats captured in January were not included as wing-photos were not taken. Pregnant females were identified by palpation of the abdomen (Racey, 1988) and the stage of pregnancy was evaluated and scored from 0-8 according to an relative belly

palpation guide (Mason *et al.*, 2010, see Table 1). Lactating females were identified by the enlarged, bare nipples and the expression of milk (Racey, 1988).

**Table 1:** Features used to assess the stage of pregnancy in *Miniopterus natalensis* (Chiroptera: Vespertilionidae) taken from Mason *et al.* (2010).

<b>Code:</b>	<b>Abdominal Palpitation description:</b>	<b>Stage of Pregnancy:</b>
0	Abdomen not distinct, flaccid stomach that dips inwards	Not Pregnant
1	Small Abdomen, sides are concave below ribs	Early/ not pregnant (fed)
2	Small abdomen, turgid stomach, sides are concave below ribs	Early
3	Medium abdomen, turgid stomach, no roundness, sides are flush with ribs	Early
4	Medium abdomen, turgid rounded stomach, sides are flush with ribs	Early
5	Large abdomen, turgid rounded stomach, sides protrude from beneath ribs	Mid
6	Large abdomen, turgid stomach bulges out in front and sides protrude from beneath ribs	Mid
7	Large abdomen, turgid rounded stomach, can see distinct protrusion on right hand side	Mid
8	Very large abdomen, turgid and rounded, sides of abdomen protrude greatly from all regions below ribs (ball shaped)	Mid

In the midlands of Kwa-Zulu Natal Province, copulation in *Myotis tricolor* occurs in mid-April, before hibernation, with ovulation and fertilization occurring in mid-September, following a period of sperm storage (Bernard, 1982). Gestation lasts 63 days, with parturition occurring between mid-November and mid-December, followed by approximately six weeks of lactation (Bernard, 1982), allowing a maximum of two months post-weaning before migration (Bernard, 1989). I used this information as a rough guide to select the months during which bats would be captured and fitted with radio tags to study temporal aspects of their foraging behaviour: early pregnancy (or not pregnant) during September 2008 (soon after the bats had returned from hibernation and migration), late pregnancy during November 2008 and lactation during January 2009 (Bernard, 1982). These bats were radio-tagged as described below. Additional bats were captured and measured but not radio-tagged during March 2009 (just prior to migration and hibernation; Bernard, 1989) and October 2009.

### **Radio telemetry:**

I used radio telemetry to determine the activity patterns of female bats during different stages of their reproductive cycle. Six adult bats were captured during each of three reproductive periods described above (early pregnancy/non-reproductive bats during September 2008, pregnant bats during November 2008 and lactating bats during 2009). The fur between the scapula was clipped and 0.42 g radio transmitters (LB-2N with 10.5 mm aerial length, Holohol Systems Ltd., Carp, ON, Canada) were attached to the area of clipped fur using skin bond surgical adhesive (Smith & Nephew, Inc., Largo, FL). The transmitters constituted 2.5-3.65% of the bats' body mass, well below the 5% maximum

proposed by Aldridge & Brigham (1988). Tagged bats were subsequently released back into the cave on the same night of capture or the following evening, just before sunset.

I recorded activity patterns of radio-tagged bats using an automatic receiver and data-logger (ATS R4500S Receiver/Data-logger, Advanced Telemetry Systems, Inc., Isanti, MN, USA) fitted with a horizontal 3-element antennae which was positioned approximately 5 m from the entrance to the cave in such a way that it detected bats in the entrance of the cave and within a 100 m radius. The receiver scanned for the presence or absence of each radio-tagged bat for seven seconds, in succession and continuously, over the entire night. If two pulses were detected, the receiver scanned for another 20 seconds and recorded a data point when it detected five or more pulses. One data point was recorded per minute. A bat thus had to be detectable for approximately between 8 and 48 seconds to be defined as present (pulse rate of radio tags was: 0.58-0.63 pulses/second). Thus I was able to record any bats who entered or left the roost within this window. The radio-tags remained functional for approximately 21 days and bats that continued to roost at Hothole during the course of the study and used the same entrance/exit were monitored for the entire battery life. I used these data to calculate the 'emergence time' (in minutes after sunset, sunset time calculated as described below), number of foraging bouts per night and duration of foraging bouts (time spent away from the cave per foraging bout, in minutes). For the purpose of this study, emergence times refer to any time at which bats were detected exiting the cave, **throughout the night, and not just the first time the bats 'emerged' to forage in a night.** In addition 'foraging time' is assuming that the time spent away from the roost is proportional to the time spent foraging (Fenton *et al.*, 1993).

## **Environmental Conditions:**

### *Insect Abundance:*

*Myotis tricolor* feeds predominantly on Coleoptera but also takes some Hemiptera, Hymenoptera, Neuroptera and Diptera (Schoeman & Jacobs, 2003; Stoffberg & Jacobs, 2004). I measured insect abundance using 22W black light-traps (BioQuip Products Inc., Rancho Dominguez, CA USA) each night I monitored activity patterns of radio tagged bats. Light traps may introduce some bias in that they only represent insects that are attracted to light (Kunz, 2009), but this was the most feasible option available and since Hosking, (1979) and Kato *et al.*, (2000) found that coleopterans are attracted to light traps I felt that the use of this method was valid in this instance. Light traps were erected in both the fynbos and near the edge of the water in the vlei to get a better representation of insect abundance across habitat types at De Hoop. Traps were emptied 2.5-3.5 hours after sunset (22h00 in September and 22h30 in November and January) and again after sunrise, resulting in **insect abundance data from the 'early evening' and the rest of the night.**

Insect samples were separated by order, counted, dried to a constant mass at 55°C and weighed by taxon **to the nearest 1 mg (O'haus Corp., NJ, USA)** (Barclay, 1991; Rydell *et al.*, 1996; Boonman *et al.*, 1998). To account for variation in size within and between orders, as well as mass differences between orders due to body composition (for example, a beetle will weigh more than a similar sized moth) both mass and numbers were investigated. Insects with wingspans less than 5 mm or body length < 2 mm were not included as they are generally not consumed by bats because they are too small to

be detected by echolocation (Anthony & Kunz, 1977; Jones, 1990; Rydell *et al.*, 1996; Houston *et al.*, 2004; Jacobs & Barclay, 2009). Insects with body lengths greater than 20 mm were also excluded as they are too large for bats of this size to eat (Jacobs, 2000; Jacobs *et al.*, 2007; Jacobs & Barclay, 2009). Bat jaw morphology places an upper limit on prey size. None the less, the insects excluded from my analysis made up a minute proportion of the total sample. The insect abundance (in numbers and biomass of each order) was standardised to numbers/hour and mg/hour, respectively, to account for variation in the time over which insects were captured and the length of night, which varied from approximately 9.7 hours in early December (mid-summer) to approximately 12.5 hours in early September (spring). Exact sunrise and sunset times were calculated for the location of the study site using an online algorithm (Meeus, 1998) to determine the length of night in minutes.

*Weather conditions:*

During each night when I monitored activity patterns of radio tagged bats, the average and minimum nightly temperatures were measured using a max-min thermometer (Russell Scientific Instruments Ltd, Norfolk, England). The moon-phase was recorded and converted to percentage illuminated (full moon 100%, new moon 0% and first quarter is 25%). The time of moon-rise and -set were recorded and with the sunrise and -set times were used to calculate the duration of night (in hours, to the nearest quarter hour) that the moon was visible. The percentage moon illumination was divided by this to produce a moonlight index. For example, if the moon was at first quarter (25% illuminated) and above the horizon for five hours and 10 minutes of the night, the

moonlight index would be  $25\% / 5.25 = 4.76$ . To quantify cloud cover, the sky was visually divided into eight parts and the number of sectors covered by clouds was recorded, resulting in a value from zero (no cloud at all) to eight (overcast, whole sky covered in cloud) (World-Meteorological-Organisation, 1972, 1974; UK-Meteorological-Office, 2006 as used by Madsen *et al.*, 1985; Minnis *et al.*, 2001; Wibig, 2008) and converted to a percentage. These observations were done by the same observer, the author, outside the entrance to the roost, at sunset. Wind strength was rated as light, light-moderate, moderate, moderate-strong, strong or very strong (rated 0-6). All measures were made by the same observer. Rainfall was not measured at the study site so I used total rainfall per hour (in mm) at a weather station in Struisbaai, approximately 50 km from the study site, (South African Weather Service) for the months during which radio-telemetry was conducted. From these data, I calculated total rainfall per night.

### **Statistical Analyses:**

All statistical tests were done using Statistica version 9.0 and 10.0 (Statsoft Inc., 2009 and 2010) unless otherwise stated.

#### *Morphology.*

The mass of bats was standardized for the size of the bat by dividing mass by the forearm length, providing a body condition index (BCI, Siemers *et al.*, 2005a). I compared mass/forearm length (body condition) of female bats between September (early pregnancy or not pregnant, just post hibernation and migration), early pregnancy or not pregnant bats with a palpation score less than three (not captured in September),

mid-late pregnancy bats with a palpitation score of four and above (captured in October and November), lactating bats captured in January (as well as some in November) and non-reproductive bats captured in March (just prior to migration and hibernation) using a Kruskal-Wallis ANOVA and post-hoc multiple comparison test. Wing-loadings were statistically compared in the same manner as body condition. Wing-loading, body condition index and wing area (in m<sup>2</sup>) of males was compared to pregnant females in October, lactating females in November and pre-migration (and hibernation) females captured in March using Mann-Whitney U-tests.

#### *Activity Patterns:*

Before analysis the activity pattern data were averaged per bat and transformed. The log mean emergence time (in minutes after sunset) was compared for all three reproductive periods using a one-way ANOVA (Levene  $p=0.78$ ), followed by a Newman-Keuls post-hoc test. Variation between months in the average foraging bout duration and mean number of foraging bouts per night were investigated using a nonparametric Kruskal-Wallis ANOVA and post-hoc multiple comparisons tests (Levene  $p<0.05$ ).

#### *Insect Abundance:*

The insect abundance data for the fynbos and vlei/ riparian habitats were combined as differences between habitats were not being investigated and there were no significant differences in the total insect numbers and biomass between the two habitats each month. Differences between the three sampling periods (September, November and

January), for each order, were investigated using **Kruskal-Wallis ANOVA's, followed by** multiple comparison tests. Nonparametric tests were used as most of the data were not normally distributed (Lilliefors  $p < 0.05$ , Shapiro-Wilks  $p < 0.05$ ), had unequal variances (Levene  $p < 0.05$ ), and the sample sizes were small ( $n < 20$  in all cases). Following this, the effects of month and time of night (**'early evening' vs. 'rest of the night'**) together on the total insect abundance (mass and numbers) were investigated using factorial **ANOVA's. The data were natural log transformed to achieve** normality of residuals (Lilliefors  $p > 0.05$ ).

Mean insect abundance (numbers and biomass) per night was calculated for those nights when insects were trapped in more than one location. These data were used in the generalized linear/non-linear models (**GLZ's**) to assess which environmental variables were correlated with bat activity patterns.

#### *Weather conditions:*

The minimum nightly temperature and moonlight index were compared between months using **one-way ANOVA's, followed by Newman-Keuls** tests. The temperature approximately one hour after sunset, percentage cloud cover, wind strength and the total nightly rainfall (in mm) were compared using nonparametric **Kruskal-Wallis ANOVA's. Nonparametric tests were used** because the data for these variables were not normally distributed (Lilliefors  $p < 0.05$ ) and the variances were not equal (Levene  $p < 0.05$ ).

*Variables influencing activity patterns:*

I used generalized linear/nonlinear models to investigate which variables influenced the number of foraging bouts, the foraging duration and emergence times using R statistical computing (R version 2.11.1, 2010). The activity pattern parameters were averaged per night, across bats and investigated in relation to: month (as a factor), the length of night (foraging duration only), temperature shortly after sunset, minimum temperature, wind strength, percentage cloud cover, moonlight index and total nightly rainfall. In addition, the mass and number of Coleoptera, Diptera, Hymenoptera, Hemiptera and Lepidoptera were included in the **GLZ's** for emergence times and number of foraging bouts per night. These orders were included because these are the orders eaten by *M. tricolor* (Schoeman & Jacobs, 2003; Stoffberg & Jacobs, 2004), and although it does not feed on moths, lepidopterans (together with coleopterans and dipterans) made up the majority of the available insect biomass. However, only the number of Diptera and mass and numbers of Coleoptera could be included with the weather variables in the GLZ investigating the foraging duration as all other variables resulted in an error. Thus another GLZ was run on foraging duration using the same weather variables and total insect number and biomass.

For each run, the results for each variable were compared using an ANOVA and non-significant variables (with the largest p-value) were removed in a step-wise manner to find which variables were interacting and directly affecting activity pattern parameters (had a significant effect when investigated alone). Following this, each GLZ was run again, multiple times, excluding co-varying (interacting) variables in various

combinations to confirm that the same variables consistently had significant effects, and significant outcomes were not just the result of interaction effects.

## CHAPTER 3:

### **Results:**

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#### **Morphology:**

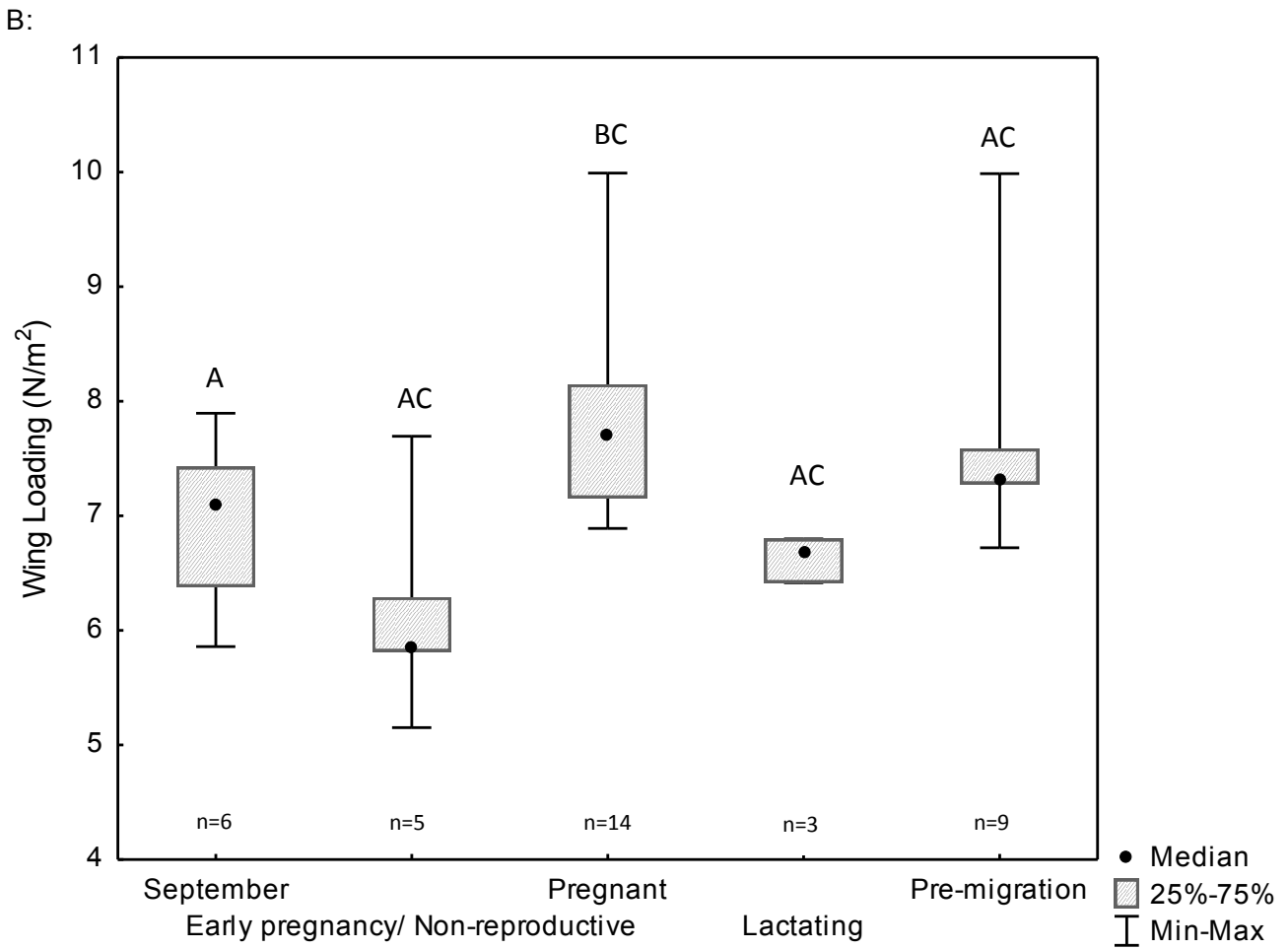
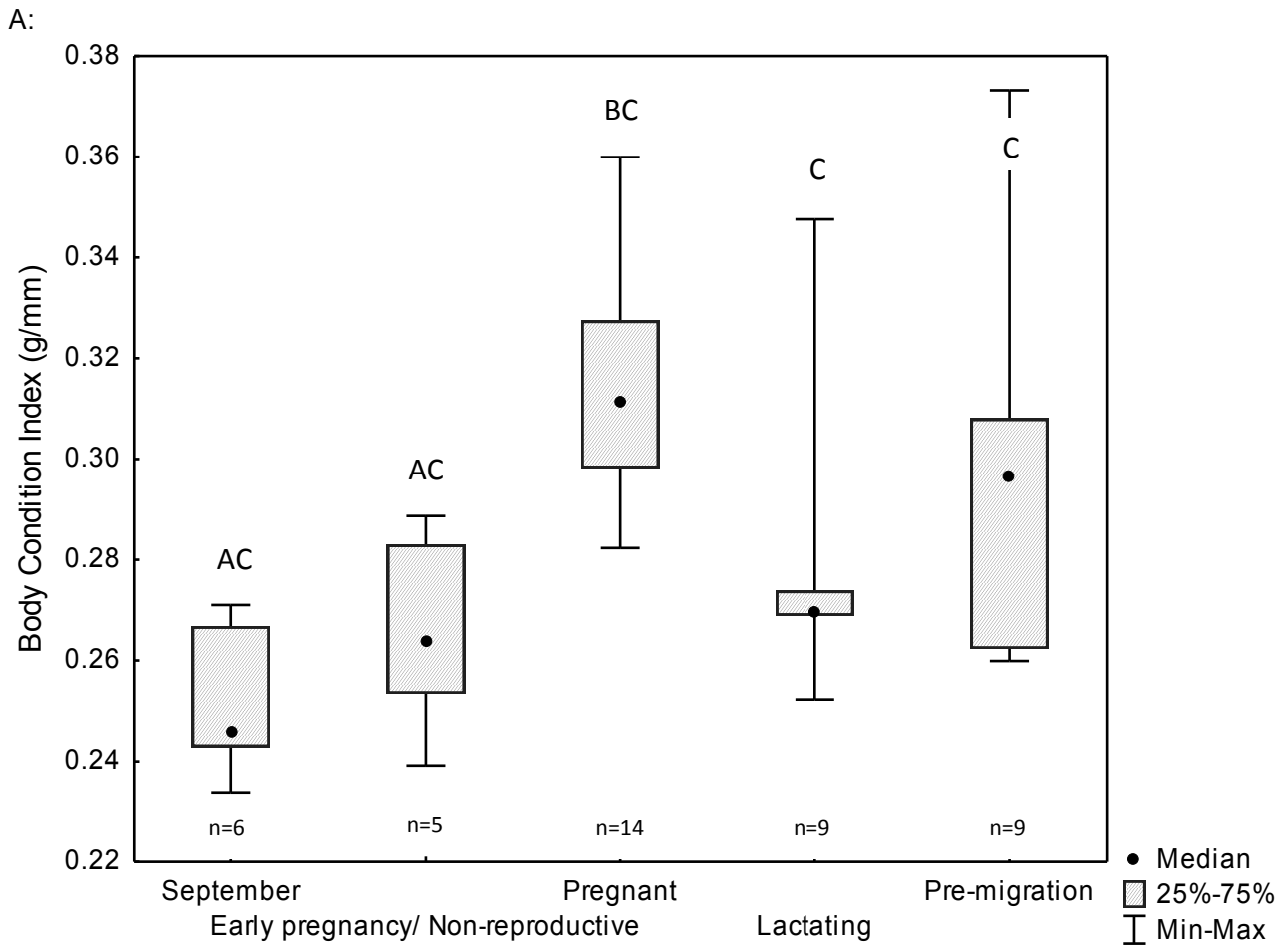
Table 2 indicates the sample sizes of bats captured over the course of the study, as well as mean body mass and wing-loading.

Bats captured and radio-tagged in November 2008 had an abdominal palpation score between 4 and 6, indicating that they were all in early-mid pregnancy at the start of the November sampling period. Some females that were clearly not pregnant (palpation score less than two) were also captured in this sampling period. These were assumed to be non-reproductive females. Females captured and radio-tagged during September 2008 had small, concave abdomens and were either not pregnant or in early pregnancy while those captured during January 2009 were clearly lactating (Racey, 1988). In addition, some lactating bats were captured in October 2009.

**Table 2:** Sample sizes of *M. tricolor* captured at De Hoop Nature Reserve over the study period. The sex, mean ( $\pm$  standard deviation) body mass and mean ( $\pm$  standard deviation) wing-loading as well as the reproductive state of each group is indicated. Bats captured during months marked with ^ were used in radio-tracking.

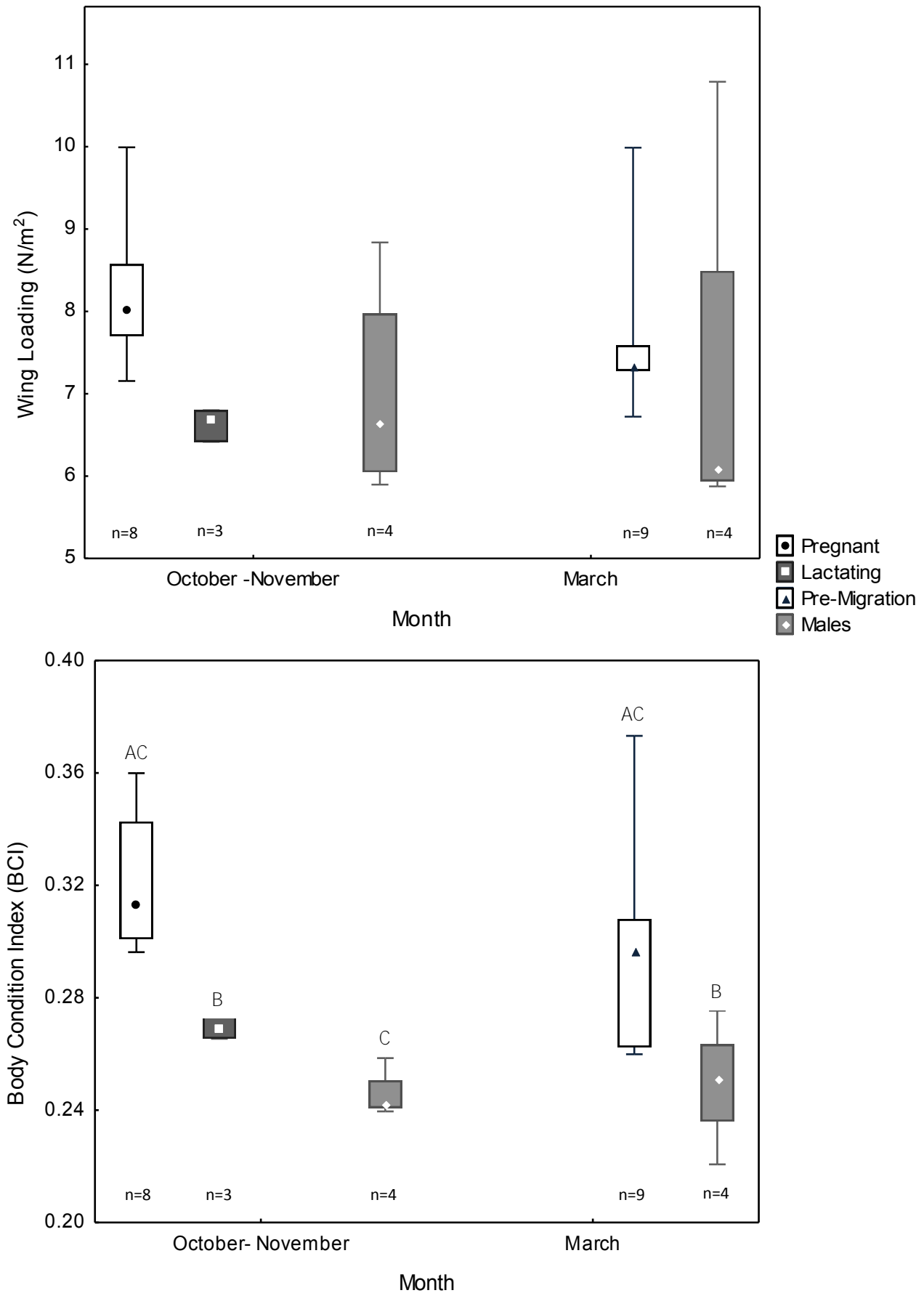
<b>Year</b>	<b>Month</b>	<b>Sex</b>	<b>Reproductive state</b>	<b>Sample Size (n)</b>	<b>Mean Mass (g)</b>	<b>Mean Wing Loading (N/m<sup>2</sup>)</b>
2008	September <sup>^</sup>	F	Early pregnancy/ non-reproductive	6	12.36 $\pm 0.62$	6.96 $\pm 0.74$
	November	F	Early pregnancy/ non-reproductive	3	12.97 $\pm 0.77$	5.99 $\pm 0.26$
	November <sup>^</sup>	F	Pregnant	6	15.50 $\pm 1.16$	7.36 $\pm 0.59$
2009	January <sup>^</sup>	F	Lactating	6	14.36 $\pm 1.63$	*No wing - loading data for these bats
	March	F	(Pre-migration)	9	14.96 $\pm 2.17$	7.73 $\pm 1.07$
	March	M	(Pre-migration)	4	12.16 $\pm 1.03$	7.21 $\pm 2.39$
	October	F	Non-reproductive	2	14.04 $\pm 0.39$	6.42 $\pm 1.80$
	October	F	Pregnant	8	16.05 $\pm 1.32$	8.22 $\pm 0.89$
	October	F	Lactating	3	13.62 $\pm 0.15$	6.63 $\pm 0.20$
	October	M		4	11.96 $\pm 0.61$	7.01 $\pm 1.32$

Body condition index (BCI, mass/forearm length; Figure 1) was significantly higher in pregnant bats compared to bats captured in September 2008 (early pregnancy/ not pregnant; Kruskal-Wallis ANOVA ( $H = 20.41$ ,  $N = 43$ ,  $p < 0.001$ ; multiple comparison  $p < 0.001$ ) and early pregnancy/ not pregnant bats captured in November (i.e. bats with a palpation score less than three; multiple comparison  $p = 0.03$ ), but not different from lactating bats or those captured in March 2009 (just before migration and hibernation; Bernard, 1989) (**multiple comparisons  $p$ 's  $> 0.16$** ; Figure 1). The wing-loading of pregnant bats was significantly greater than early pregnancy/ non-reproductive bats captured in November 2008 (Kruskal-Wallis ANOVA  $H = 13.85$ ,  $N = 37$ ,  $p = 0.007$ , multiple comparison  $p = 0.02$ , Figure 1), but there were no significant differences **between all other reproductive groups (multiple comparisons  $p$ 's  $> 0.16$ )**. There were no significant differences in the wing-loading between males and females captured in March 2009 (Mann-Whitney  $U = 9.0$ ,  $Z = 1.31$ ,  $N = 9, 4$ ,  $p = 0.19$ , Figure 2) and between males and pregnant as well as lactating females in October- November 2009 (pregnant: Mann-Whitney  $U = 6.0$ ,  $Z = 1.61$ ,  $N = 8, 4$ ,  $p = 0.11$ ; lactating:  $U = 6.0$ ,  $Z = 0$ ,  $N = 3, 4$ ,  $p = 1.0$ ). However, both pregnant females in October 2009 (Mann-Whitney  $Z=2.63$ ,  $N=8, 4$ ,  $p=0.008$ ) and females preparing for migration and hibernation in March 2009 (Mann-Whitney  $U = 4.0$ ,  $Z = 2.08$ ,  $N = 9, 4$ ,  $p < 0.04$ ) had greater **BCI's** than males, while there was no significant difference to lactating females in October - November 2009 (Mann-Whitney  $Z = 1.94$ ,  $N = 3, 4$ ,  $p = 0.052$ ; Figure 2). The same was true of wing area (pregnant: Mann-Whitney  $U = 11.0$ ,  $Z= 0.76$ ,  $N = 8, 4$ ,  $p = 0.44$ ; lactating:  $U = 3.0$ ,  $Z = 0.88$ ,  $N = 3, 4$ ,  $p = 0.38$ ; Pre-migration:  $U = 17.0$ ,  $Z = 0.08$ ,  $N = 9, 4$ ,  $p = 0.94$ ).



**Figure 1:** Body condition index (A, mass/forearm length) and wing-loading (B) of female *M. tricolor* captured at De Hoop Nature Reserve in various reproductive states. Bats captured during September 2008 were either non-reproductive or in very early stages of pregnancy. Letters indicate significant differences and the sample size (n = number of bats) for each group is indicated.

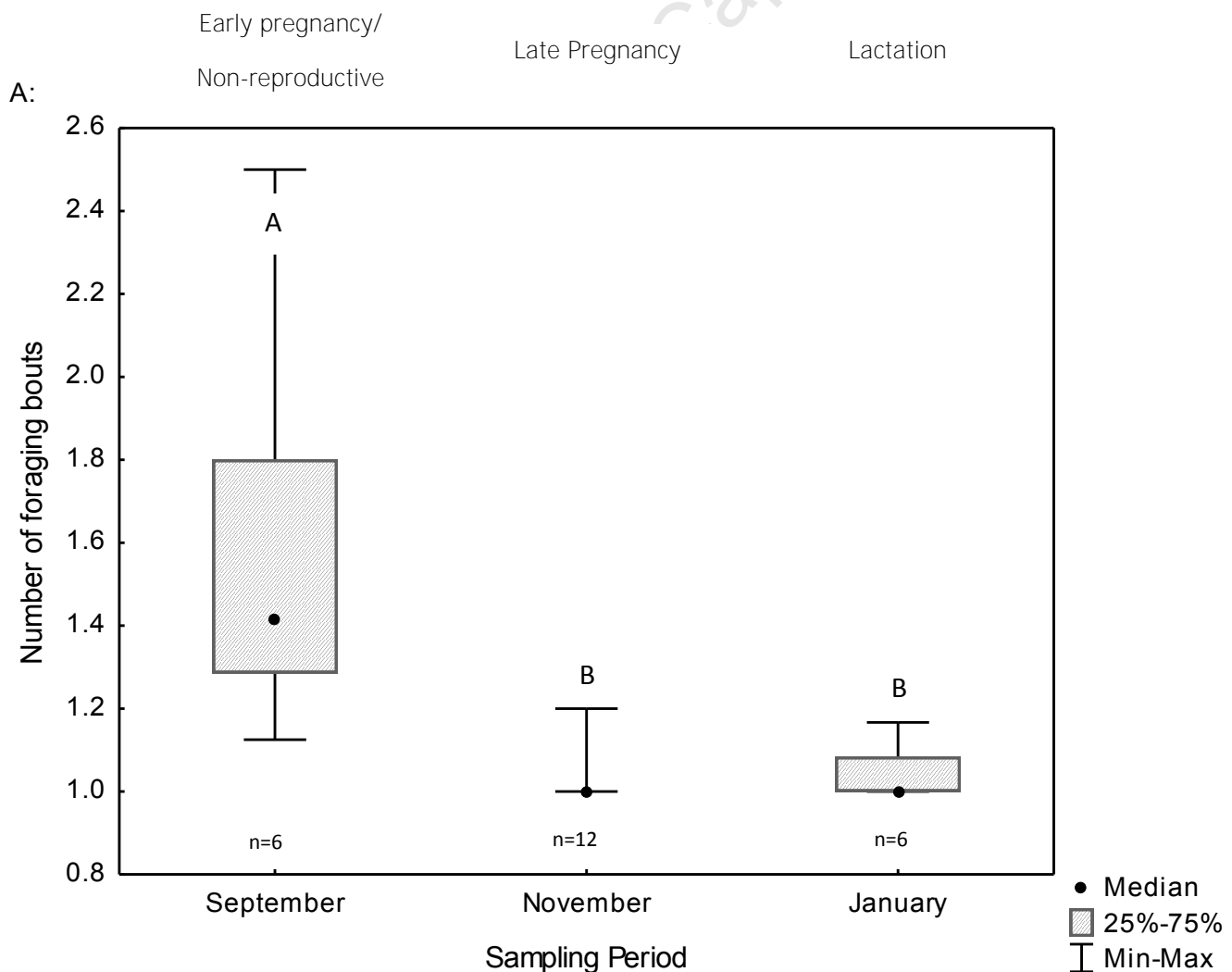
A:



**Figure 2:** The wing-loading (A) and body condition index (B, mass/forearm length) of bats captured at De Hoop Nature Reserve. Males are compared to females during pregnancy in October, lactation in November and just before migration and hibernation in March. The median (points, ●/□), 25 – 75 percentiles (boxes) and ranges (whiskers) are shown. Letters indicate significant differences and the sample size (n= number of bats) is indicated.

## Activity Patterns:

There were significantly more foraging bouts in September 2008 (early pregnancy/non-reproductive) than November 2008 (late pregnancy) or January 2009 (lactation; Kruskal-Wallis test:  $H(2) = 9.64$ ,  $N = 15$ ,  $p = 0.008$ , Multiple comparisons  $p$ 's  $< 0.049$ , Figure 3A). The duration of foraging bouts in September were significantly shorter than those in November (Kruskal-Wallis test:  $H(2) = 7.87$ ,  $N = 13$ ,  $p < 0.02$ , Multiple comparisons  $p < 0.02$ , Figure 3B), but no different to those in January (Multiple comparisons  $p = 0.31$ ). The bats also emerged significantly earlier (in relation to sunset) in November and January than in September (ANOVA  $F = 17.10$ ,  $n = 6, 5, 4$ ,  $p < 0.001$ , Newman-Keuls  $p < 0.001$ , Figure 3C).

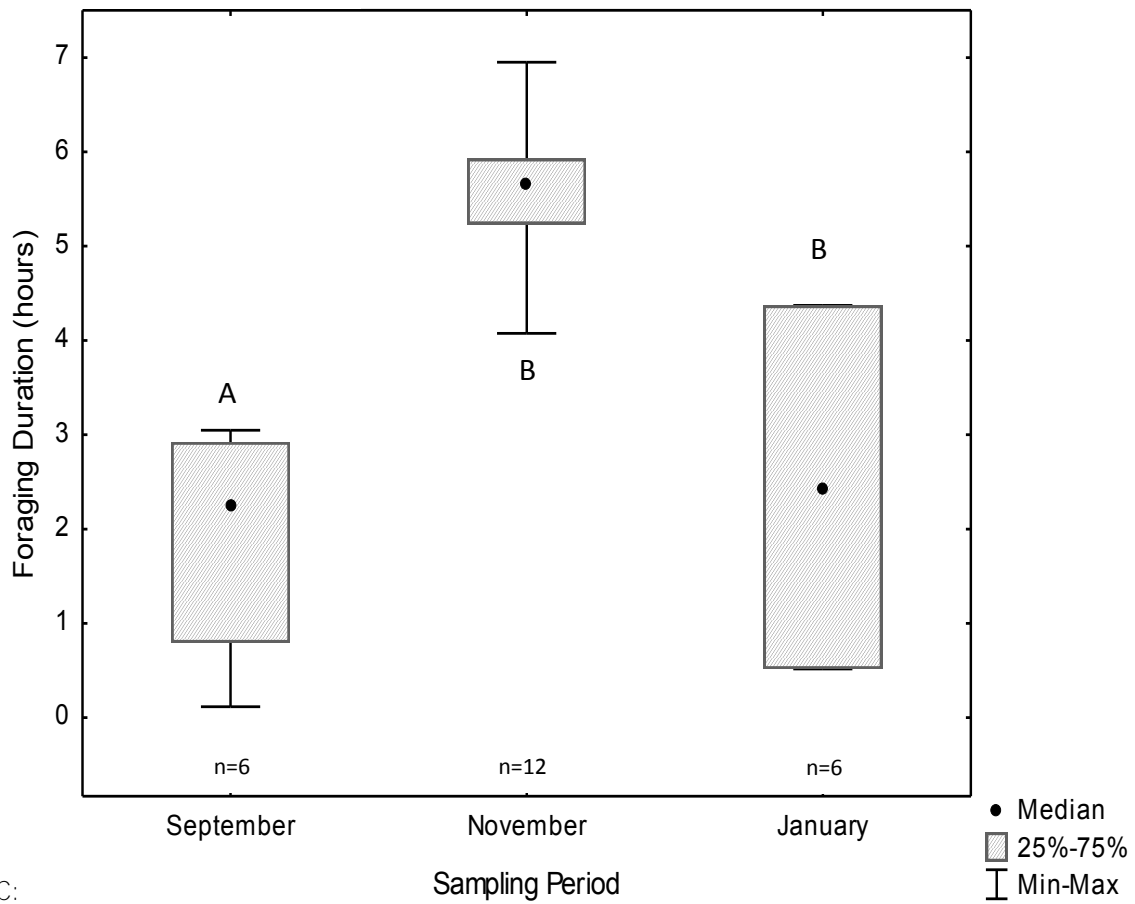


Early pregnancy/  
Non-reproductive

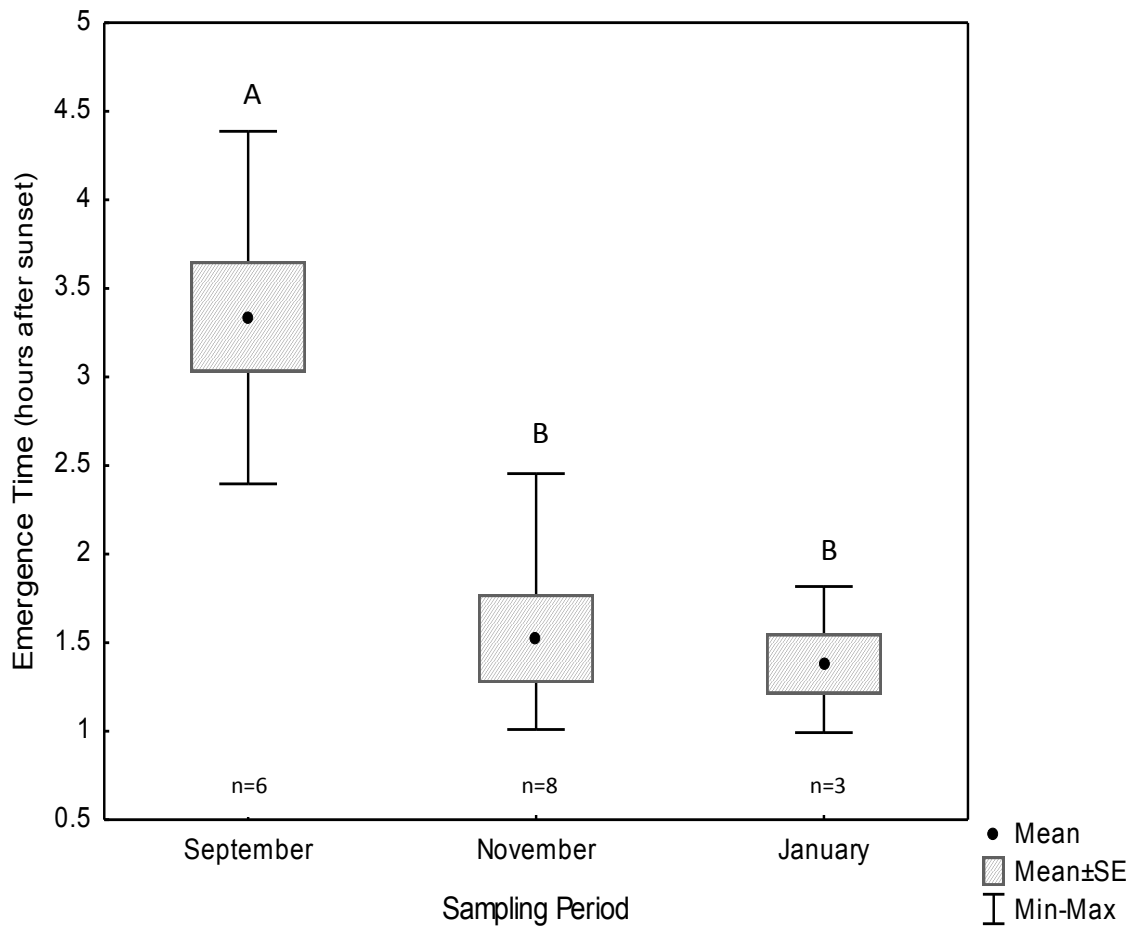
Late Pregnancy

Lactation

B:



C:



### Figure 3

(including the previous page): The number of foraging bouts per night (A, page 34), foraging duration (B) and emergence times (hours after sunset) (C) in September 2008 (early pregnancy), November 2008 (late pregnancy) and January 2009 (lactation) of radio-tagged female *M. tricolor* at De Hoop Nature Reserve. Letters indicate significant differences and the sample size (n=number of bats) for each group is indicated.

## **Environmental Conditions:**

### *Insect Abundance:*

Coleoptera, Diptera and Lepidoptera together made up more than 98.4% of the total insect numbers in September 2008; more than 87.2% in November 2008 and 78.7% in January 2009. In September these three orders made up a minimum of 94.8% of the total insect biomass, while this was 72.5% in November and 57.4% in January (Figure 5).

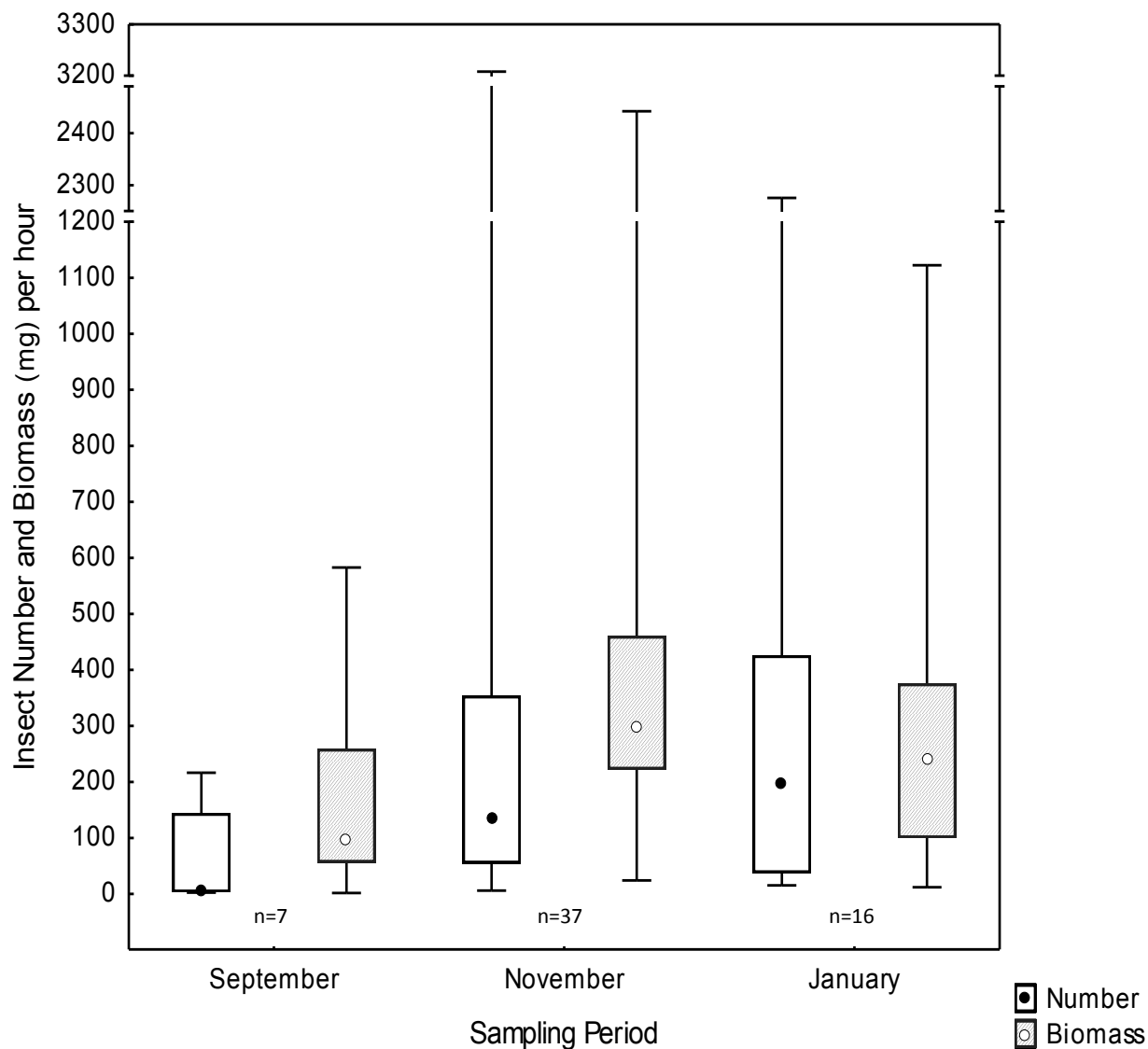
### *Insect Abundance: Variation between Months:*

I caught significantly lower numbers of insects in September 2008 than in November 2008 and January 2009 (Kruskal-Wallis ANOVA  $H = 7.87$ ,  $N = 60$ ,  $p = 0.02$ , multiple comparisons  $p < 0.03$ , Figure 4), but there were no significant differences in biomass between months (Kruskal-Wallis ANOVA  $H = 4.58$ ,  $N = 60$ ,  $p = 0.10$ , Figure 4). Significantly lower numbers of Coleoptera (Kruskal-Wallis ANOVA  $H = 16.99$ ,  $N = 60$ ,  $p < 0.001$ ; mult. comp.  $p < 0.01$ ), Lepidoptera (Kruskal-Wallis ANOVA  $H = 7.60$ ,  $N = 60$ ,  $p = 0.02$ ; mult. comp.  $p < 0.03$ ), Hymenoptera (Kruskal-Wallis ANOVA  $H = 11.98$ ,  $N = 60$ ,  $p = 0.003$ ; mult. comp.  $p < 0.004$ ) and Hemiptera (Kruskal-Wallis ANOVA  $H = 8.32$ ,  $N = 60$ ,  $p < 0.02$ ; mult. comp.  $p < 0.02$ ) were captured in September than in November and January while the number of dipterans captured was only less than January (Kruskal-Wallis ANOVA  $H = 6.87$ ,  $N = 60$ ,  $p < 0.03$ ; mult. comp.  $p = 0.03$ ), but not November (Figure 5A). Significantly less biomass of Coleoptera (Kruskal-Wallis ANOVA  $H = 18.35$ ,  $N = 60$ ,  $p < 0.001$ ; mult. comp.  $p < 0.001$ ) and Hemiptera (Kruskal-Wallis ANOVA  $H =$

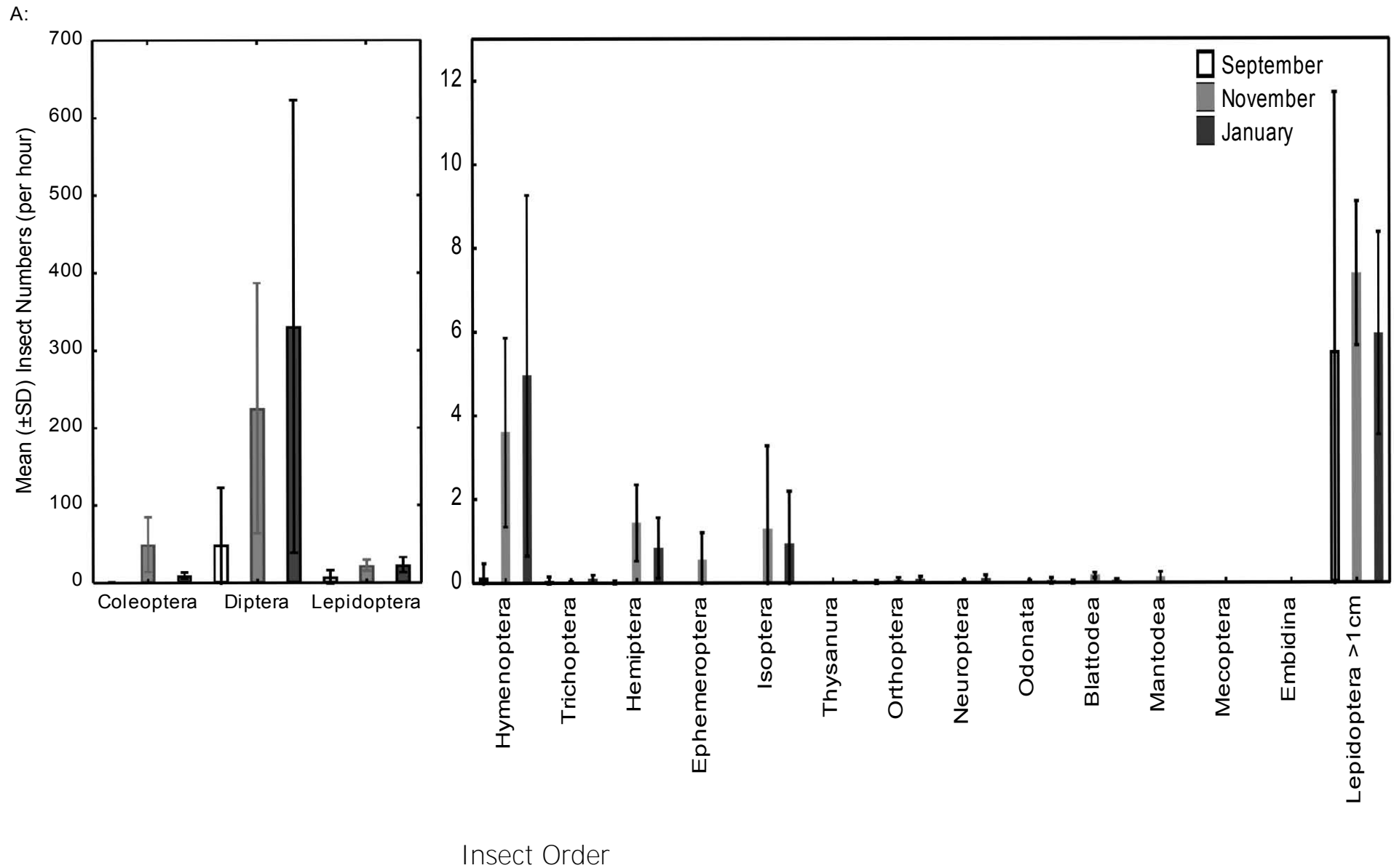
8.42,  $N = 60$ ,  $p < 0.02$ ; mult. comp.  $p < 0.02$ ) was captured in September than in November, but there was no difference to January, while Hymenoptera captured during this time was less than both November and January (Kruskal-Wallis ANOVA  $H = 13.53$ ,  $N = 60$ ,  $p < 0.002$ ; mult. comp.  $p < 0.003$ , Figure 5B).

*Insect Abundance: 'early evening' and the rest of the night:*

Using a factorial ANOVA, I found month had a significant effect on both insect numbers ( $F = 4.18$ ,  $df = 2$ ,  $p = 0.02$ , Figure 4) and biomass ( $F = 4.10$ ,  $df = 2$ ,  $p = 0.02$ ), while there was no significant effect of time of night ('early evening' - 2.5 - 3.5 hours after sunset - compared to the rest of the night; number:  $F = 0.013$ ,  $df = 1$ ,  $p = 0.9$ ; biomass:  $F = 0.94$ ,  $df = 1$ ,  $p = 0.34$ , Figure 6), nor a significant interaction (number:  $F = 0.19$ ,  $df = 2$ ,  $p = 0.82$ ; biomass:  $F = 1.02$ ,  $df = 2$ ,  $p = 0.37$ ).

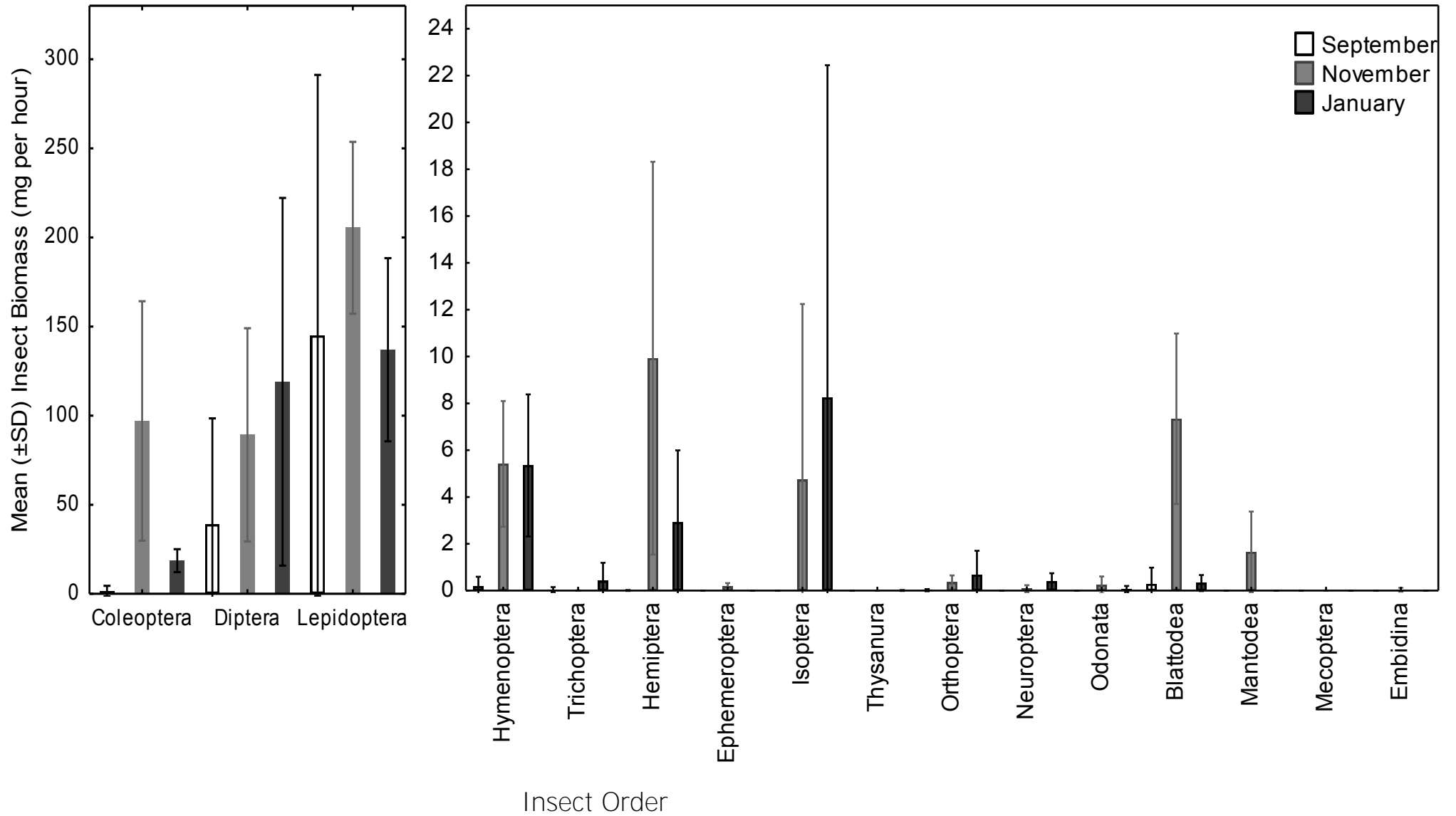


**Figure 4:** Total insect number and biomass (mg) per hour in September (early pregnancy/non-reproductive), November (pregnant) and January (lactation) captured at De Hoop Nature Reserve using light traps. **The median (●/○), 25 – 75 percentiles (boxes) and ranges (whiskers) are shown and the sample size (n=number of nights) for each group is indicated.**

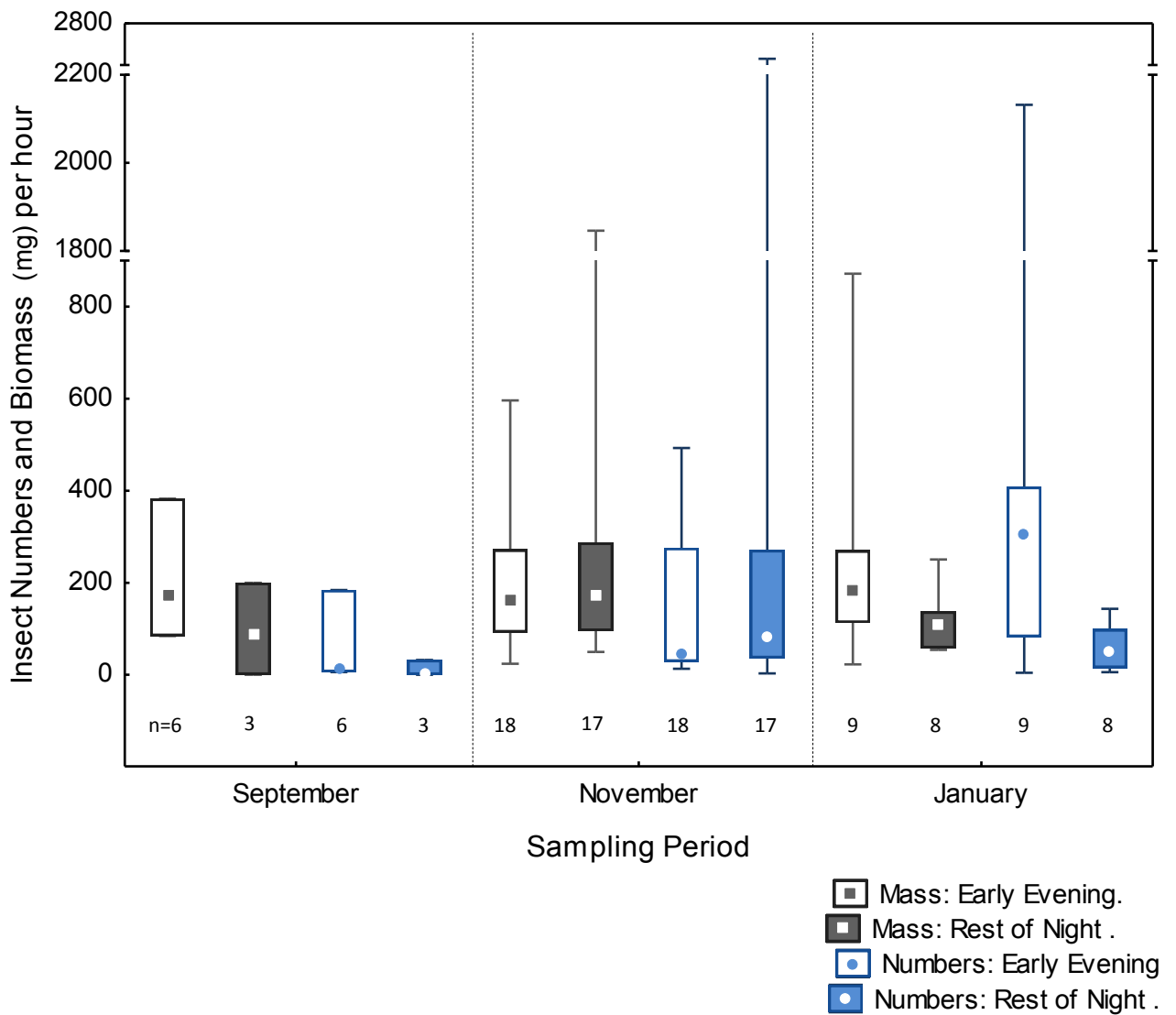


**Figure 5A:** Insect Numbers by order captured per hour (using light-traps) in September 2008 (early pregnancy/ non-reproductive), November 2008 (pregnancy) and January 2009 (lactation) at De Hoop Nature Reserve.

B:



**Figure 5B:** Insect Biomass by order captured per hour (using light-traps) in September 2008 (early pregnancy/ non-reproductive), November 2008 (pregnancy) and January 2009 (lactation) at De Hoop Nature Reserve.

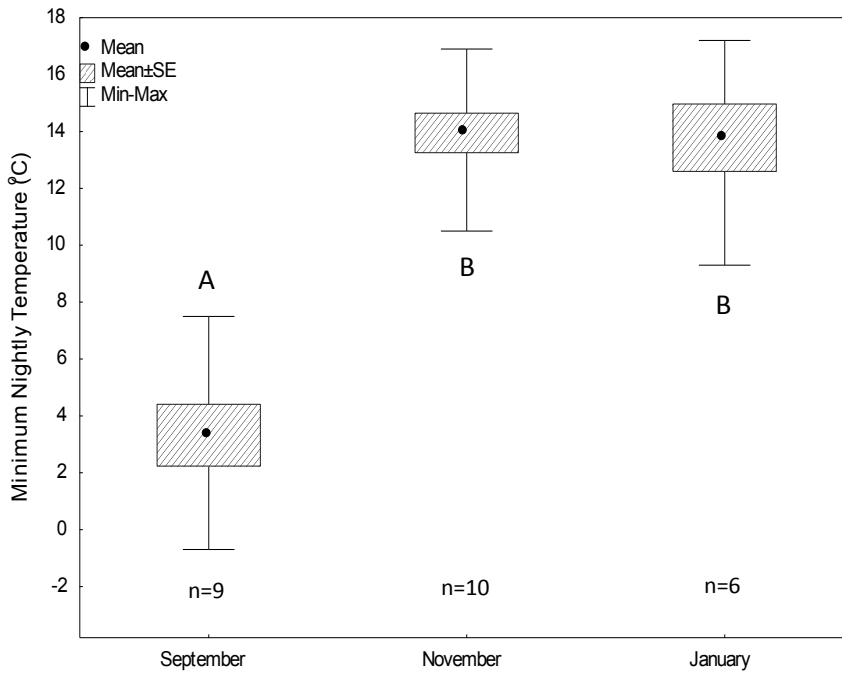


**Figure 6:** Total insect biomass (grey) and numbers (blue) per hour captured in the 'early evening' (two to three hours after sunset) and during the rest of the night, for September 2008, November 2008 and January 2009. The **medians (points, ●/□)**, percentiles (boxes) and ranges (whiskers) are shown and the sample size (n=number of nights) for each group is indicated.

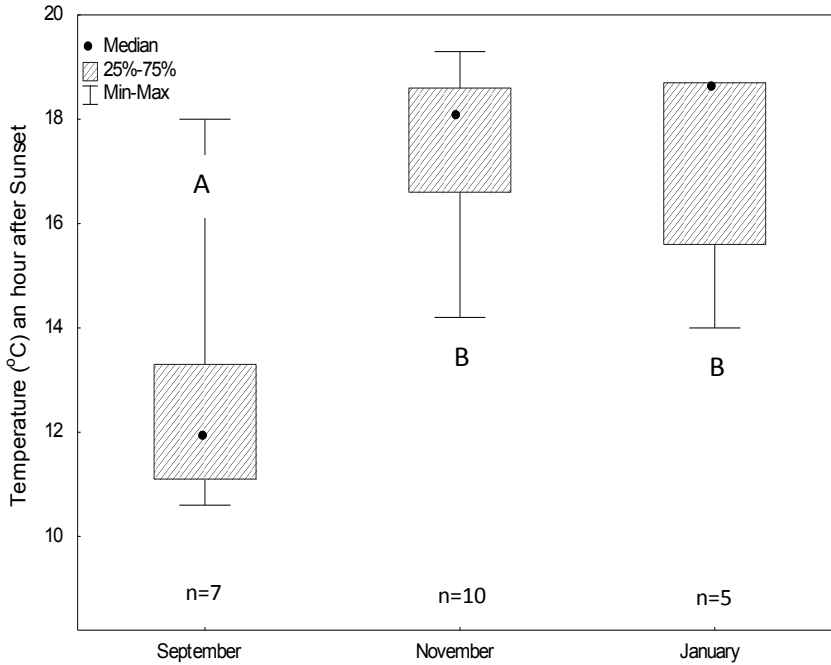
### *Weather Conditions:*

The minimum temperature (1-way ANOVA  $F = 41.51$ ,  $df = 2$ ,  $p < 0.0001$ , Newman-Keuls  $p$ 's  $< 0.0002$ , Figure 7A) and temperature approximately an hour after sunset (Kruskal-Wallis ANOVA  $H = 10.33$ ,  $N = 22$ ,  $p = 0.006$ , multiple comparison  $p$ 's  $< 0.04$ , Figure 7B) were significantly lower in September 2008 than in November 2008 or January 2009. Conversely, there were no significant differences between months in the percentage cloud cover (Kruskal-Wallis ANOVA  $H = 2.65$ ,  $N = 33$ ,  $p = 0.26$ , Figure 7C), the moonlight index (percentage face illuminated per hour moon was up, 1-way ANOVA  $F = 0.30$ ,  $df = 2$ ,  $p = 0.74$ , Figure 7D) and the wind speed (Kruskal-Wallis ANOVA  $H = 0.803$ ,  $N = 31$ ,  $p = 0.67$ , Figure 7E). The total rain per night did vary significantly between months (Kruskal-Wallis ANOVA  $H = 7.41$ ,  $N = 34$ ,  $p = 0.02$ ) but post-hoc tests found no pair-wise differences (multiple comparisons  $p$ 's  $< 0.12$ ). This is because the median for all three months is zero, but the mean, range and percentiles for September are larger (Figure 7F).

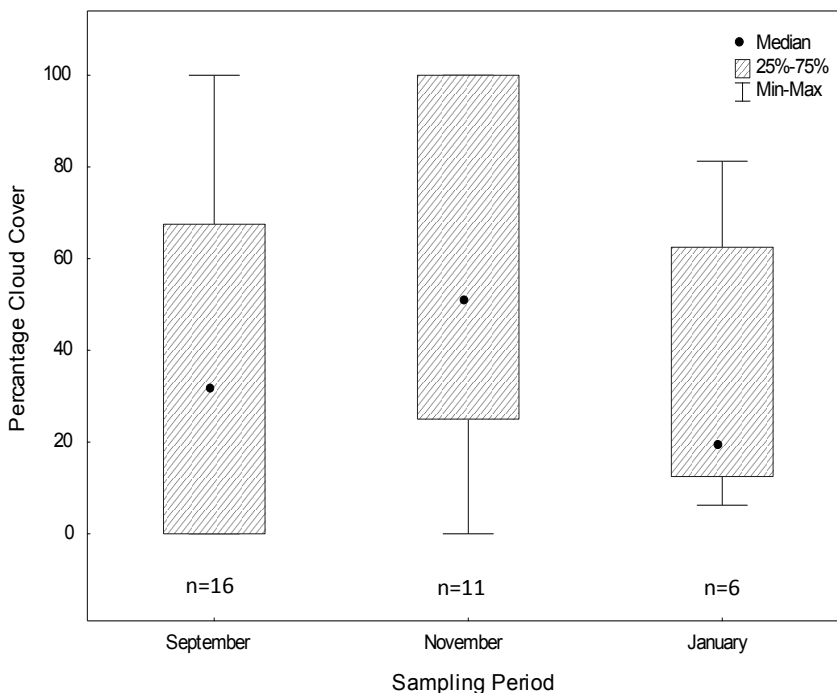
A:



B:

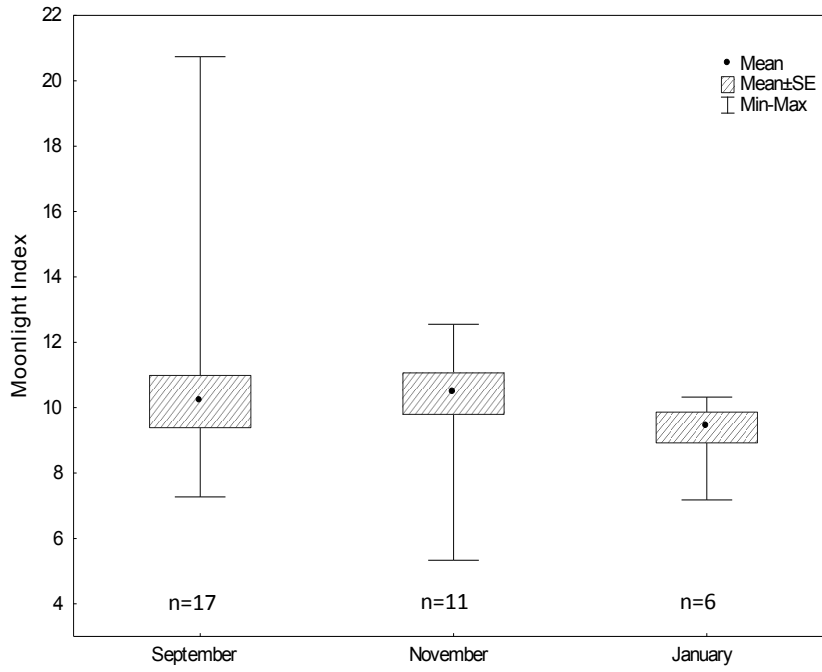


C:

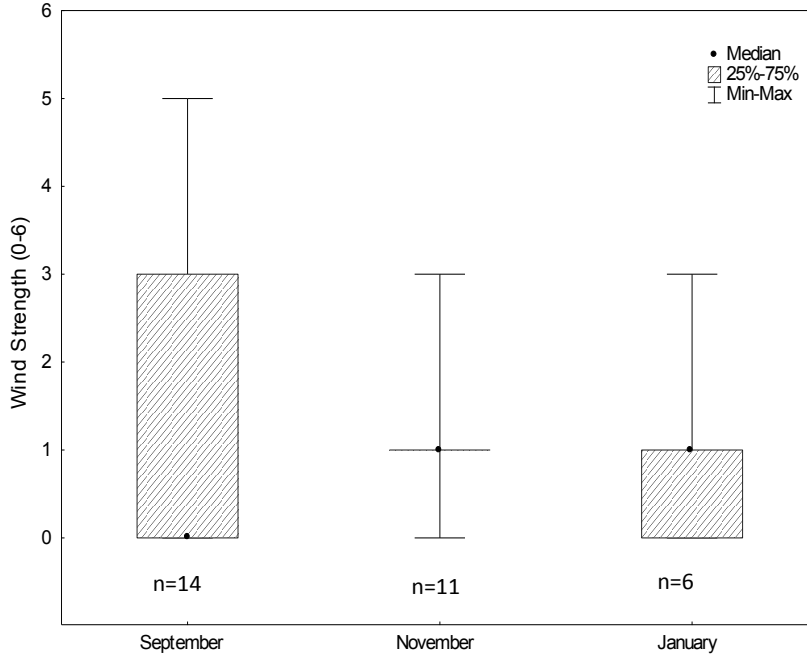


**Figure 7** (left and following page): Weather conditions over September 2008, November 2008 and January 2009 at De Hoop Nature Reserve, Western Cape: minimum temperature (A), temperature approximately an hour after sunset (B), percentage cloud cover (C), moonlight index (D; percentage moon illumination per hour the moon was up), wind strength (E; rated 0 - 6) and total nightly rainfall as recorded by a weather station 50km from the study site (F). Letters indicate significant differences and the sample size (n= number of nights) for each group is indicated.

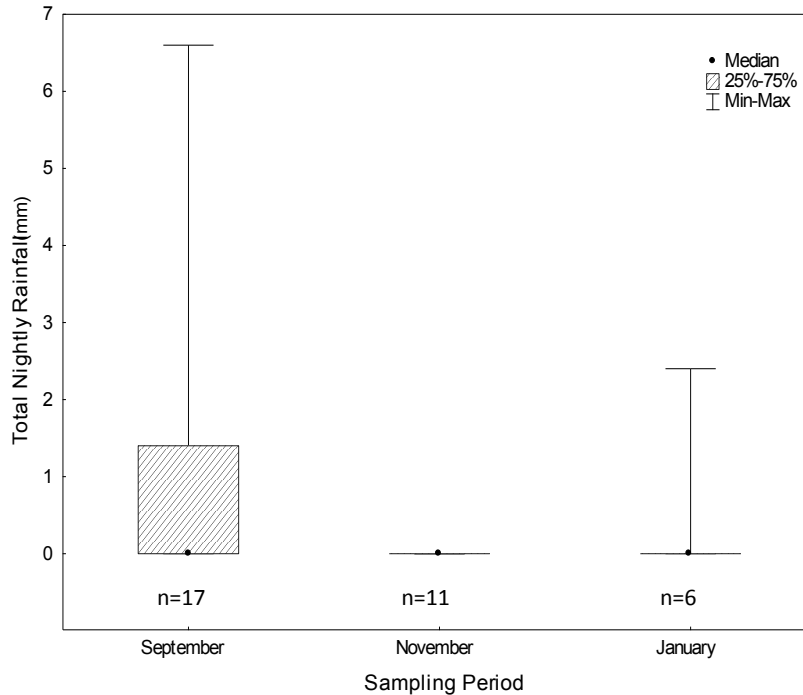
D:



E:



F:



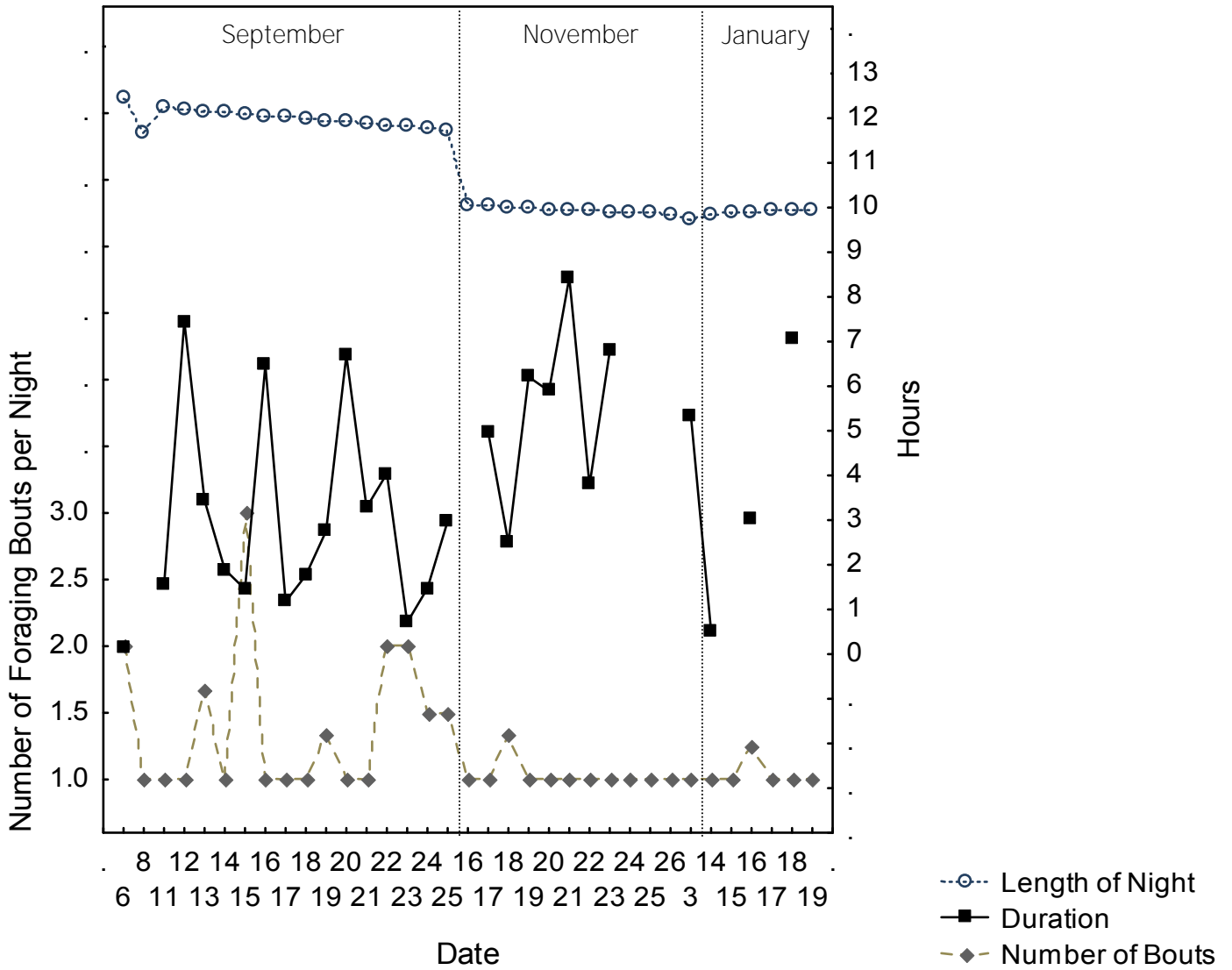
### **Factors affecting bat activity:**

The mean number of foraging bouts per night was significantly positively correlated with wind strength and the duration of night (Table 3, Figures 8 and 9). Number of bouts was negatively correlated with the minimum temperature and significantly varied with month in all GLZ model runs, with and without co-varying variables (Table 3, Figures 8 and 9).

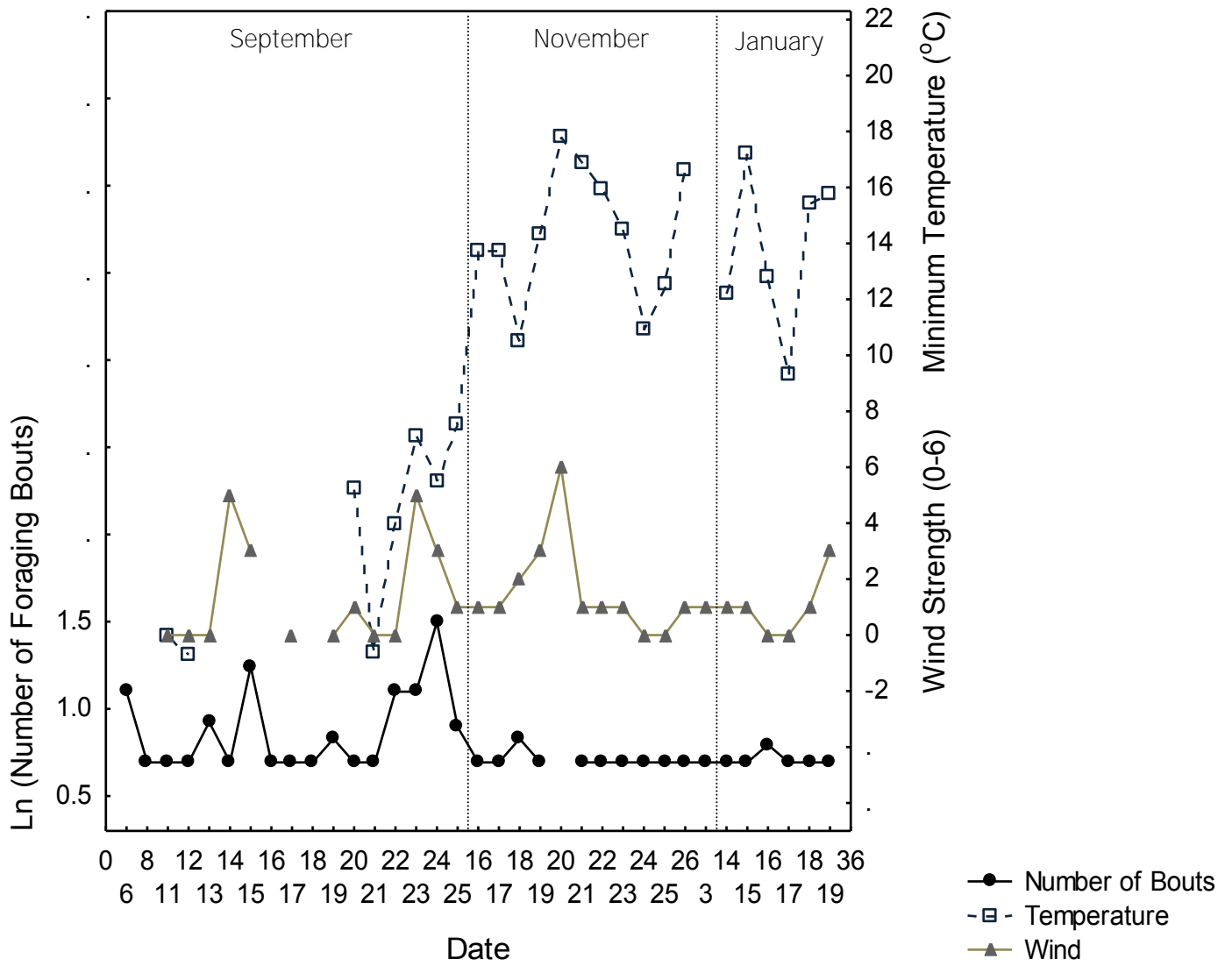
The mean duration of foraging bouts per night and mean emergence time per night **did not vary significantly with month in all GLZ's run with all combinations of** environmental variables (Table 3). However the foraging duration was significantly negatively correlated with wind speed (Figure 10) and emergence time was significantly positively correlated with total rain per night (Table 3, Figure 11). Foraging duration was not correlated with the total insect numbers or biomass.

**Table 3:** Results of generalized linear/nonlinear models (GLZ's) run to investigate which environmental factors are significantly affecting the activity patterns of radio-tagged female *M. tricolor* during September 2008 (early pregnancy/ non-reproductive), November 2008 (pregnancy) and January 2009 (lactation) at De Hoop Nature Reserve.

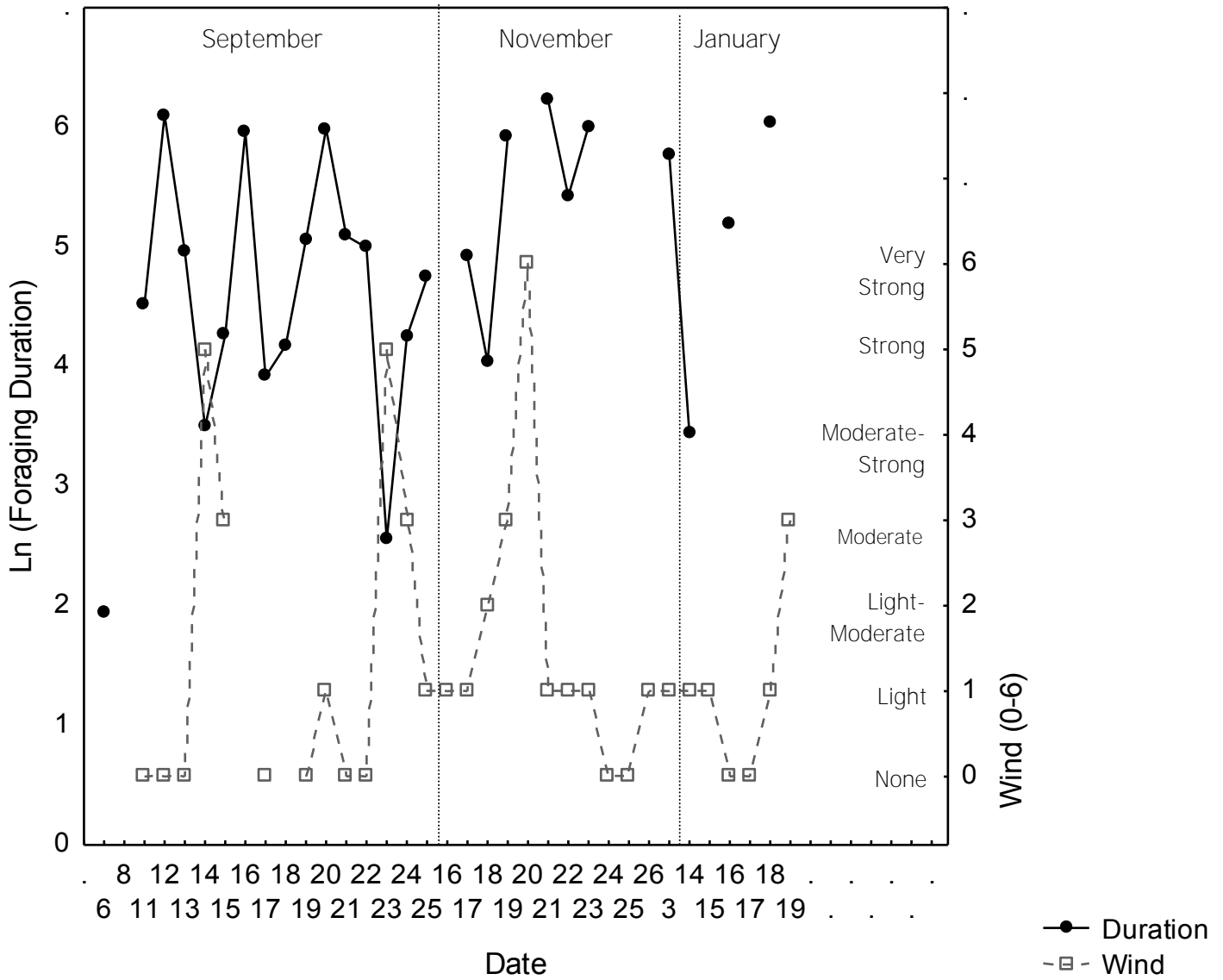
ACTIVITY PARAMETER	FACTOR	ANOVA		ESTIMATE	t- VALUE
		F	P		
NUMBER OF FORAGING BOUNTS	Month	7.65	0.004	SEP: 0.33	2.99
				NOV: -0.01	-0.09
	Wind Strength	4.76	0.04	0.08	2.23
	Minimum Temperature	7.48	0.013	-0.025	-2.78
	Length of Night	14.61	0.001	0.003	3.89
FORAGING DURATION	Month	0.87	0.44	SEP: -0.06	-0.39
				NOV: 0.102	0.68
	Wind Strength	4.92	0.04	-0.09	-2.16
EMERGENCE TIME	Month	1.90	0.18	SEP: 0.09	1.20
				NOV: -0.32	-0.49
	Rainfall	9.30	0.007	0.039	3.13



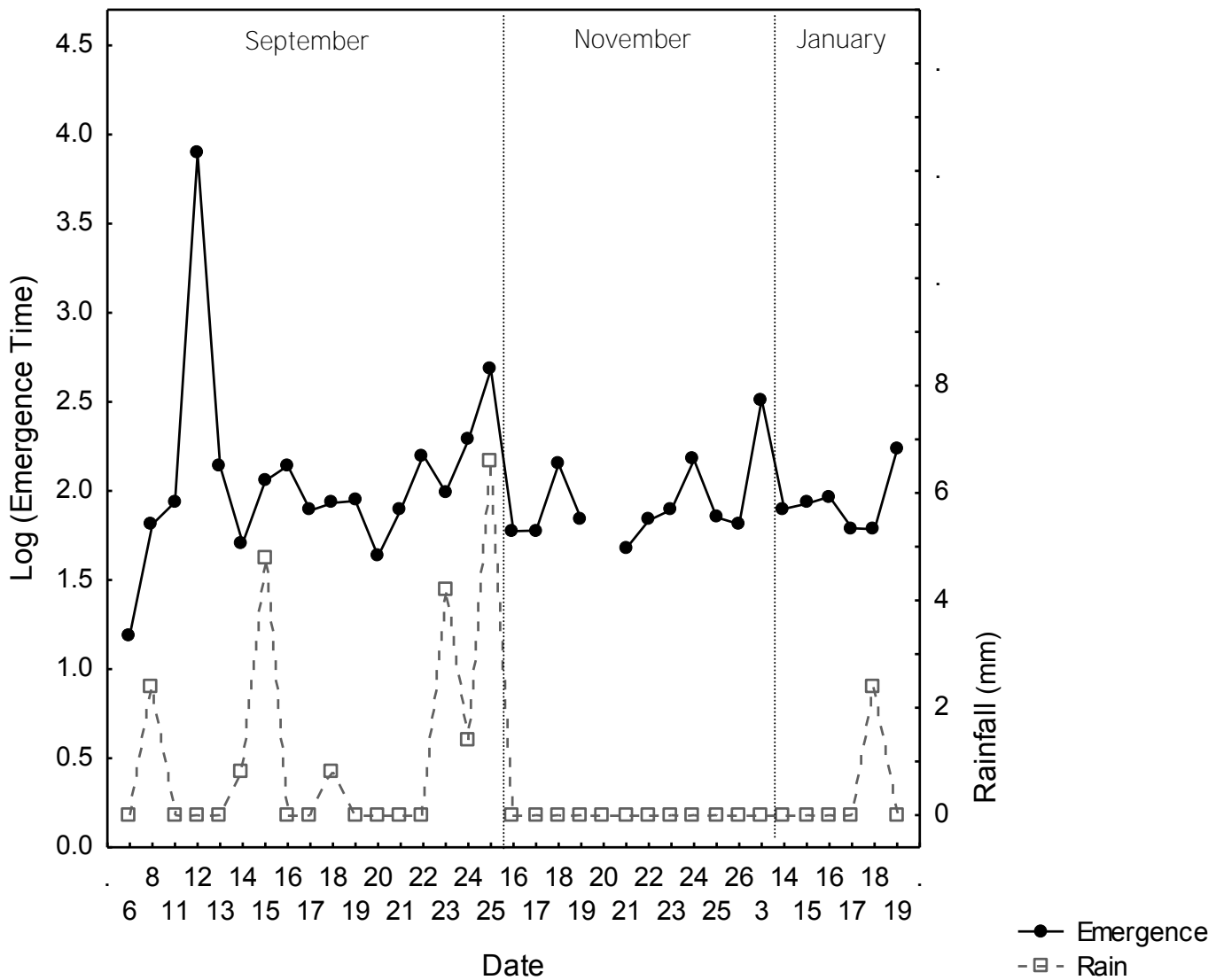
**Figure 8:** The length of night (hours; ○) compared with the mean number of foraging bouts per night (◆) and the mean foraging duration per bout (hours; ■) of all female *M. tricolor* radio-tagged at De Hoop Nature Reserve over the sampling periods (September 2008- January 2009). Numbers on the x-axis indicate the date on which measurements were made.



**Figure 9:** Log of the mean number of foraging bouts per night (across bats; ●) of all female *M. tricolor* radio-tagged over the sampling periods (September 2008- January 2009) compared to the observer-rated wind strength (▲; 0: none, 1: light, 2: light-moderate, 3: moderate, 4: moderate-strong, 5: strong, 6: very strong) and minimum nightly temperature (°C; □) at De Hoop Nature Reserve. Numbers on the x-axis indicate the date on which measurements were made.



**Figure 10:** Log of the mean foraging duration per night (hours; ●) of all female *M. tricolor* radio-tagged over the sampling periods (September 2008- January 2009) relative to observer-rated wind strength (□; 0: none, 1: light, 2: light-moderate, 3: moderate, 4: moderate-strong, 5: strong, 6: very strong) at De Hoop Nature Reserve. Numbers on the x-axis indicate the date on which measurements were made.



**Figure 11:** Log of the mean nightly emergence time (hours after sunset; ●) of all female *M. tricolor* radio-tagged over the sampling periods (September 2008- January 2009) and total nightly Rainfall (mm; □) at De Hoop Nature Reserve. Numbers on the x-axis indicate the date on which measurements were made.

## CHAPTER 4:

### **Discussion:**

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I found that *M. tricolor* were in mid-pregnancy when first captured (thus advancing from mid- to late-pregnancy over the three weeks of study) in early November 2008 (early summer) and lactating in January 2009 (mid-late summer). In September 2008 (early spring), soon after the bats had returned from migration and hibernation (Bernard, 1989), females were either not pregnant or in early pregnancy (sperm storage over hibernation and ovulation and fertilization occurring in September; Bernard, 1982). The timing of reproduction in the temperate fynbos was similar to that reported for this species in the tropical, Savanna-grassland biome of the Kwa-Zulu Natal province (Bernard, 1982). In both the Savanna and the fynbos pregnancy (October-December) and lactation (December – January) proceeded while insect abundances were high, with enough time for post-weaning females and young to forage in summer (March, when insect abundances should still be high, Taylor, 1963; Black, 1979) and store sufficient fat for migration and hibernation. The timing of the reproductive cycle was, therefore, in agreement with the general pattern for bats, where the weaning of young coincides with the peak in insect abundance (Cumming & Bernard, 1997).

Female *M. tricolor* had a greater number of foraging bouts and emerged later (with respect to sunset time) in September 2008 (early pregnancy/not pregnant) than in November 2008 (late pregnancy) and January 2009 (lactation) and foraged for longer in November than in September (Figure 3). Lower reproductive costs may have resulted in the bats starting to forage later in September, but during this month later emergences are generally associated with the bats returning to the roost after an initial emergence soon after sunset and emerging again, later (i.e. a greater number of foraging bouts) (Figure 8). Some lactating bats emerge earlier than pregnant bats (Shiel & Fairley, 1999) purportedly to increase foraging time and meet the high energetic demands of lactation (Racey & Speakman, 1987; Kurta *et al.*, 1990), while others emerge later, possibly because of time spent grooming the young (Clark *et al.*, 2002). Lactating *M. tricolor* did not alter their emergence schedule, compared to pregnant females and bats in both reproductive states generally emerged once within the first hour after sunset (Figure 3). This could be because there was no difference **in the total insect abundance (numbers and mass) between the 'early evening' and the rest of the night** and/or because the length of night did not affect foraging duration (Figure 8). Differential costs between reproductive states should only influence emergence times if earlier emergence times are necessary for an increase in foraging duration (and associated increase in feeding) or for foraging to coincide with a peak in insect abundance.

Pregnant *M. tricolor* foraged for longer than early pregnancy/non-pregnant females (Figure 3). This is consistent with increased energetic demands of pregnancy.

Similarly, pregnant female *Myotis daubentonii* and *Myotis moluccarum* forage for longer than non-reproductive females and males (Barclay *et al.*, 2000; Encarnação & Dietz, 2006). Some lactating female bats forage for longer than pregnant females (Rydell, 1993; Bartoniáka & Zúkal, 2003). However, the length of foraging bouts of lactating *M. tricolor* were not significantly different to those of pregnant females, as was found in *Plecotus auritus* (Fuhrmann & Seitz, 1992; Entwistle *et al.*, 1996). Foraging duration during lactation was less, although not significantly, than during pregnancy (Figure 3). Since lactation is more energetically expensive than pregnancy (Hanwell & Peaker, 1977; Racey & Speakman, 1987; Gittleman & Thompson, 1988; Kurta *et al.*, 1989; Kurta *et al.*, 1990 Hood *et al.*, 2006) it is possible that lactating *M. tricolor* are using torpor to offset some of the costs of milk production, and decrease the energy (and hence foraging time) needed to meet overall energetic requirements. Thus lactating females may be using compensation to cope with the costs of reproduction more than expected.

In addition to compensation, lactating *M. tricolor* appear to use storage to offset the costs of milk production. Bats captured during late pregnancy in November had a significantly greater BCI (mass/ size) than early pregnancy and non-reproductive bats and a similar BCI to lactating bats and those captured just prior to migration and hibernation (Figure 1). This indicates that lactating bats had an increased mass as compared to early pregnancy and non-reproductive bats although these bats (captured in September 2008) were likely in a depleted state after hibernation and migration, and thus were most likely recovering from this. Female *M. lucifugus* gain

approximately 30% of their body mass in preparation for hibernation and this mass increase is the result of fat deposition (Kunz *et al.*, 1998). Similarly, pregnant *M. yumanensis* can increase in mass by up to 30% (Aldridge & Brigham, 1988), indicating that this may be the maximum possible mass gain for these species. During lactation and prior to migration and hibernation female *M. tricolor* store fat to the extent that their BCI is not significantly different from advanced pregnancy and their maximum possible mass gain. **This suggests that despite the bats' small size** (Racey & Speakman, 1987) and the potential effects of mass gain on flight efficiency (Aldridge & Brigham, 1988), storage plays an important role in offsetting the energetic costs of lactation, migration and hibernation in *M. tricolor*. However, these results would be more robust if the same females were measured at different stages of their reproductive cycle, to control for individual variation. Fat stores of *Eptesicus fuscus* significantly decrease by mid-lactation due to the great energetic requirements (Hood *et al.*, 2006). Thus fat stores may be important in offsetting the costs of lactation in other species (Gittleman & Thompson, 1988). These stores in *M. tricolor* would have had to be accumulated after parturition (before the bats were captured and radio-tagged) because the mass and size of the offspring towards the end of gestation would preclude major mass gain (Aldridge & Brigham, 1988; Bernard, 1989). This period would likely have been characterized by an increase in foraging duration compared to pregnancy. Unfortunately, bats were not monitored during this time.

Females captured during pregnancy and just before migration and hibernation had a greater BCI than males, but there were no significant wing-loading differences (Figure 2), indicating that females have a greater capacity for mass gain in preparation for energetic stress than males. This suggests that although the difference was not significant, the larger wing area of females allows an increase in mass with pregnancy, lactation and prior to migration, without a significant increase in wing-loading and the associated decrease in manoeuvrability. Female *M. daubentonii* also have larger wings than males (Jones & Kokurewicz, 1994). This may be an adaptation to carry the increased load imposed by the developing foetus during pregnancy, and milk mass and/or pups after parturition in both *M. daubentonii* (Jones & Kokurewicz, 1994) and *M. tricolor*. But, females of these species also therefore have a greater capacity to deal with energetic requirements by the storage of fat.

Lactating bats often have an increased number of foraging bouts compared to pregnant or non-reproductive bats (Kunz, 1974b; Swift, 1980; Maier, 1992; Rydell, 1993; Catto *et al.*, 1995; Wilkinson & Boughman, 1998; Clark *et al.*, 2002; Milne *et al.*, 2005). The proposed rationale for this is that they need to return to the roost to suckle their young. However, female *M. tricolor* had the greatest number of foraging bouts in September, and there was no difference in the number of foraging bouts between advanced pregnancy and lactation (Figure 3), when the bats generally had one long foraging bout per night. *M. moluccarum* also did not increase the number of foraging bouts during lactation which Barclay *et al.* (2000) attributed to the bats having to travel large distances (10 km) to the foraging grounds. It is possible that lactating *M. tricolor* are travelling large distances to feed on swarming insects. This

may decrease foraging duration (during lactation) if prey is abundant at these sites and thus the foraging efficiency increased dramatically and could result in multiple foraging bouts (during September) if the food source was only available for certain parts of the night. However, this would also imply a patchy prey distribution during November and January, which is possible but unlikely as insect abundances during these months were the same or greater than during September (Figures 4 and 5) in both the vlei and fynbos habitats. Since the higher number of foraging bouts in September cannot be explained by energetic costs of reproduction, the impact of environmental conditions may explain these trends.

When environmental conditions are poor (heavy rain, strong winds, low insect abundances) bats have a choice of either continuing to forage and attempting to feed enough to meet their energetic costs or to return to the roost (Racey & Speakman, 1987; Rydell, 1989; Maier, 1992) and possibly emerge again later to continue to forage if and when conditions have improved. The first scenario may necessitate increasing foraging time to find sufficient prey in the poor conditions and/or to meet the increased energetic costs caused by flying in the cold, rain (thermoregulatory stress) and/or wind. However, returning to the roost enables the bat to save energy, particularly if it enters torpor (Anthony *et al.*, 1981; Racey & Speakman, 1987). Audet and Fenton (1988) showed that bats can actively control their use of torpor. The choice likely depends on the severity of the weather conditions, the scarcity of the prey as well as the energy balance of the individual. *Eptesicus serotinus* foraged on the fourth successive day of inclement weather, after remaining in the roost for the

first three days and Catto *et al.* (1995) attributed this to the energetic requirements exceeding the cost of foraging in poor conditions after three nights without food. In my study, during September, the insect numbers (but not the biomass) was lower (Figure 4) and the minimum and early evening temperatures were lower than November and January (Figure 7). In addition, torpor would not have associated costs during September, as it would during late pregnancy and lactation. It appears that during this time the low temperatures and insect numbers resulted in the bats returning to the roost (and likely entering torpor) after a shorter foraging duration and on some nights subsequently emerging again later, possibly when environmental conditions have improved, or the energetic costs necessitate foraging rather than entering torpor. This would explain the increased number of foraging bouts and associated later emergence times as well as the decreased foraging duration in September.

Many studies have shown bats to decrease activity with low temperatures (O'Farrell & Bradley, 1970; Anthony *et al.*, 1981; Barclay, 1985; Rydell, 1991; Maler, 1992; Catto *et al.*, 1995; Negraeff & Brigham, 1995; Hayes, 1997; Shiel & Fairley, 1998; Wilkinson & Boughman, 1998; O'Donnell, 2000; Ciechanowski *et al.*, 2007) while others have found no effect of temperature on activity (Fenton, 1970; Kunz, 1974a; Entwistle *et al.*, 1996; Seidman & Zabel, 2001; Clark *et al.*, 2002). Temperature determines if *Chalinolobus tuberculatus* fly, but not for how long (O'Donnell, 2000) and the temperature at emergence, not the minimum temperature, impacted on the activity of several species of vespertilionid in South-East England (Parsons *et al.*,

2003), indicating that temperature may influence emergence time. However, I found, that low temperatures resulted in an increased number of foraging bouts (Figure 9), but this variable had no effect on the foraging duration or the emergence time. This indicates that low temperatures do result in the bats returning to the roost (and possibly entering torpor) but the duration of foraging bouts remain unaffected. The fact that on longer nights bats had more foraging bouts (Figure 8) is likely an artefact of the effect of month, as the length of night in September was much greater than November and January and the temperature and insect numbers were lowest during this month.

At low temperatures insect activity typically declines (Taylor, 1963; Kunz, 1973) and so temperature could have indirectly impacted activity patterns through its effect on insect activity. However, neither the number, nor the biomass of the insect orders which *M. tricolor* eat, had any influence on bat activity patterns. This contrasts with many previous studies that found a close association between activity and the temporal activity patterns of insects (Brown, 1968; Swift, 1980; Anthony *et al.*, 1981; Rydell *et al.*, 1996; Hayes, 1997; Vaughan *et al.*, 1997; Shiel & Fairley, 1998; O'Donnell, 2000; Lang *et al.*, 2006; Ciechanowski *et al.*, 2007). I argue that the insect abundances at De Hoop appear high enough that they are not limiting and thus do not affect activity patterns. This is supported by the absence of evidence for the influence of interspecific competition in structuring the trophic niches of bats at De Hoop (Schoeman & Jacobs, 2010). Although the total insect numbers were lower in September, the total biomass was not (Figure 4). This was due to greater numbers

of insects that have large masses (such as Lepidoptera), and reduced numbers of small insects with low mass (such as Diptera) during September (Figure 5). But, total insect abundance may not be indicative of the actual prey available to bats (Barclay, 1985; Todd & Waters, 2007) because diet depends on the detectability of an insect taxon (Barclay, 1985), the echolocation call structure (both due to size and behaviour of the insect; Barclay, 1985; Todd & Waters, 2007), the habitat in which the bat is foraging (insect assemblages likely vary across habitats; Taylor, 1963) and any avoidance behaviour that insects may have evolved (Jacobs *et al.*, 2008). For example, *M. tricolor* has not been shown to eat Lepidopterans (Schoeman & Jacobs, 2003; Stoffberg & Jacobs, 2004) in spite of this order making up a large proportion of the available prey biomass (Figure 5). This is likely to be because tympanate moths make up a large proportion of the Lepidopteran population in this region (Schoeman & Jacobs, 2003). When hunting at the edge **of the vegetation ('clutter-edge forager';** Stoffberg & Jacobs, 2004) the low frequency calls of *M. tricolor*, which attenuate less through the vegetation (than would **a higher frequency call or the calls of a 'clutter-forager'**), allow eared moths to hear them with enough time to manoeuvre and avoid capture (Jacobs *et al.*, 2008). Therefore, since insect abundance may not reflect prey availability, the biomass of insects available to *M. tricolor* may be less during September. Reduced numbers and biomass of Coleoptera, Hemiptera and Hymenoptera were captured in September indicating that this could be the case (Figure 5). However, as the abundance was not related to any change in activity patterns, the insect abundance could simply have no effect on bat activity, as for *M. daubentonii* (Ciechanowski *et al.*, 2007) and *Pipistrellus pipistrellus* (no effect on duration; Maier, 1992).

I found that wind strength was negatively associated with the foraging duration and positively associated with the number of foraging bouts in *M. tricolor* (Figures 9 and 10), indicating that these conditions also result in the bats returning to the roost after a shorter foraging duration and sometimes emerging again, later. Strong winds can interfere with the mechanics of flight, especially for an animal weighing only 14 g. Strong winds decrease activity in other species (O'Farrell *et al.*, 1967; O'Farrell & Bradley, 1970) but in *Pipistrellus hesperus* and *Myotis californicus* there appears to be a threshold, where winds above 4 m/s decrease activity and those in excess of 5.4 m/s push activity to zero. During September, night time wind speed was frequently above 4 m/s at Struisbaai, 50km from the study site (data obtained from the South African Weather Service), indicating that a similar wind speeds may inhibit activity in *M. tricolor*.

Moonlight results in decreased activity (Fenton *et al.*, 1977; Lang *et al.*, 2006; Ciechanowski *et al.*, 2007) and later emergence (Rydell *et al.*, 1996) in some bat species. In addition to reducing insect activity (Anthony *et al.*, 1981; Hecker & Brigham, 1999; Lang *et al.*, 2006), it is proposed that increased light levels may increase their vulnerability to visually oriented predators, particularly on emergence (Rydell *et al.*, 1996). However, this should only be evident in populations that are exposed to visually oriented predators regularly (Fenton *et al.*, 1977; Karlson *et al.*, 2002). Spotted Eagle Owls (*Bubo africanus*), which were frequently present in the vicinity of the roost (personal observation), feed on bats (Demeter, 1982) and Barn Owls (*Tyto alba* (Scopoli)) are known to feed on *M. tricolor* at De Hoop Nature

Reserve (Avery *et al.*, 2005), but it is not evident if these bats were captured in flight or while at rest. However, I found no effect of moonlight on the activity patterns of *M. tricolor*. This is in agreement with many studies which have found moonlight to have no effect on bat activity (Anthony *et al.*, 1981; Wai-Ping & Fenton, 1989; Catto *et al.*, 1995; Negraeff & Brigham, 1995; Hayes, 1997; Hecker & Brigham, 1999; Clark *et al.*, 2002; Karlson *et al.*, 2002; Thies *et al.*, 2006) and may indicate a lack of predation pressure on *M. tricolor* at De Hoop, at least after dark. Alternatively, it could indicate that the insect activity was not affected by moonlight.

Later emergence times were associated with higher total nightly rainfall but did not vary significantly with month (Figure 11). This indicates that heavy rain had a greater impact on the emergence times of bats than reproductive state. This makes intuitive sense because, as discussed earlier, energetic costs should not affect emergence times, since the foraging duration is not limited within a night (Figure 8). Since total nightly rainfall had no effect on the number of foraging bouts, the later emergence times discussed here do not indicate the bats returning to the roost to forage again later, but rather an initial emergence time significantly later in the night. Thus, in heavy rain female *M. tricolor* tend not to forage and I hypothesise that this is because rain will interfere with the acoustic imaging system of echolocation, as well as cause thermoregulatory stress. However, they often emerge (for the first time) later in the night, presumably when either the conditions have improved or the energy balance of the animal necessitates foraging, even in heavy rain. Rain has been shown to have a negative impact on bat activity (Fenton, 1970; Fenton *et al.*, 1977; Wilkinson & Boughman, 1998; Erickson & West, 2002; Parsons *et al.*, 2003;

Ciechanowski *et al.*, 2007) but often the timing (Fenton *et al.*, 1977; Parsons *et al.*, 2003) and intensity (mm per hour) of rain is important (Parsons *et al.*, 2003). Since rain results in the bats remaining within roost, rather than emerging and returning to the roost, *M. tricolor* may be able to ascertain some information about the environmental conditions on any particular night, without exiting the roost. One potential mechanism could be through 'pioneer' conspecifics who 'explore' the conditions first and then return to the roost. Alternatively the bats may be able to detect the weather conditions outside of the cave without leaving the roost. *Pipistrellus subflavus* can detect the barometric pressure and use this as an indicator of environmental air temperature (Paige, 1995). It is possible that *M. tricolor* could detect rainfall without leaving the roost by detecting some other property of the air, such as humidity, although this has not been tested. Alternatively, it is more likely that the bats can simply hear the rain.

Given its intermediate wing morphology (wing loading  $7.31 \text{ Nm}^{-2}$  ( $\pm 1.19$ ) and aspect ratio  $5.48$  ( $\pm 0.53$ )) and echolocation call structure (Norberg & Rayner, 1987; Stoffberg & Jacobs, 2004), it is possible that *Myotis tricolor* is flexible in its foraging habits, as intermediate morphology is typical of *Myotis* species that use multiple foraging strategies (Fenton & Bogdanowicz, 2002; Stoffberg & Jacobs, 2004). Therefore it is possible that increased energetic costs (such as those associated with reproduction) result in bats switching to a different foraging mode, and/or foraging in a different habitat, that allows them to meet increased costs without altering the temporal patterns of activity. In particular, it is possible that *M. tricolor* is capable of

trawling insects from the water surface, and it may switch to this foraging behaviour when the conditions are favourable (smooth water surface, low wind speeds; Boonman *et al.*, 1998; Warren *et al.*, 2000; Almenar *et al.*, 2006) and costs necessitate it. The echolocation and maneuverability tasks associated with foraging over water and trawling are similar to those faced by aerial foraging near the edge of the vegetation (Kalko & Schnitzler, 1989; Schnitzler & Kalko, 2001; Schnitzler *et al.*, 2003; Siemers *et al.*, 2005b) and many *Myotis* species switch between aerial foraging over water and trawling insects from the water surface (*M. daubentonii*, Boonman *et al.*, 1998, Kalko & Schnitzler, 1989; *M. capaccinii*, Almenar *et al.*, 2006; *M. adversus*, Dwyer, 1970, Jones & Rayner, 1991; *M. yumanensis*, Brigham *et al.*, 1992; *M. bocagei*, Fenton & Bogdanowicz, 2002). In addition, insect abundance both on the water surface and in the air above the water are high (Barclay, 1991; Todd & Waters, 2007), the ground effect (a reduction in aerodynamic drag due to the proximity of the wing aerofoil to the plane water surface) decreases the costs of flight for bats that fly close to the water surface (Norberg & Rayner, 1987; Rayner, 1991) and the acoustic mirror effect may increase prey detection distance by up to 1.4 times (Siemers *et al.*, 2001; Siemers *et al.*, 2005b). All of these factors may make trawling more energetically beneficial than terrestrial aerial foraging, when the water surface is smooth and free of vegetation. The ability of *M. tricolor* to trawl was investigated using flight room experiments, and although results suggest that they can, overall they were inconclusive. Further investigation into whether *M. tricolor* is capable of trawling is needed to adequately understand the foraging behaviour of this species.

It is also possible that with increased reproductive costs, female *M. tricolor* shift from aerial foraging at the edge of the vegetation to aerial foraging over the water of the De Hoop Vlei, to exploit high insect abundances there (Barclay, 1991). To adequately answer the question of what factors affect the foraging behaviour of *M. tricolor* during reproduction it is necessary to investigate the spatial patterns of habitat use as well as temporal activity patterns. I attempted to do this using radio-telemetry but was unable to follow the bats to their feeding grounds. This may be because the bats were foraging low over the large De Hoop Vlei. This water body has many inlets with steep limestone cliffs that would have obstructed the signal if the bats were foraging over the water.

To further improve this study, monitoring the activity patterns of the bats over parturition and through the beginning of lactation would shed light on the exact timing of parturition and any activity patterns associated with it. This would also shed light on whether the bats change their activity and increase their foraging duration to build up the fat reserves for late lactation soon after parturition. It would also be advantageous to have data on how the environmental variables changed over the course of the night. Such data would allow for a more accurate investigation of what factors are affecting activity patterns and perhaps illuminate effects not found in this investigation.

In conclusion, the energetic costs of reproduction increase foraging time during late pregnancy, as compared to early pregnancy but appear to have no impact on the

number of foraging bouts or emergence time. Foraging duration during lactation was not greater than that during pregnancy, despite higher costs (Hanwell & Peaker, 1977; Racey & Speakman, 1987; Gittleman & Thompson, 1988; Kurta *et al.*, 1990), indicating that females may use torpor during this time to some extent to compensate for these energetic requirements. In addition, lactating bats have a similar BCI to those just prior to migration, indicating that females may also use fat storage to cope with energetic requirements of lactation. Further investigation into the activity patterns over the first few days of lactation is needed. Not surprisingly, weather conditions also influenced activity patterns. In particular, rain delayed nightly emergence and wind resulted in decreased foraging duration and increased number of foraging bouts per night. Female *M. tricolor* also had more foraging bouts on nights with low minimum temperatures. Unexpectedly, insect abundance had no effect on activity patterns, indicating that prey abundances may not be limiting at this site. Therefore both these environmental parameters and the energetic costs of reproduction interacted, and influenced the activity pattern of female *M. tricolor*, but an investigation of the spatial patterns of habitat use is needed to fully understand the foraging behaviour these bats.

## CHAPTER 5:

### Literature Cited:

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- ALDRIDGE, H. D. J. N. and R. M. BRIGHAM (1988). "Load carrying and maneuverability in an insectivorous bat: a test of the 5% "rule" of Radio-Telemetry." Journal of Mammalogy **69**(2): 379-382
- ALDRIDGE, H. D. J. N. and I. L. RAUTENBACH (1987). "Morphology, Echolocation and Resource Partitioning in Insectivorous Bats." The Journal of Animal Ecology **56**(3): 763-778
- ALMENAR, D., J. AIHARTZA, U. GOITI, E. SALSAMENDI and I. GARIN (2006). "Habitat selection and spatial use by the trawling bat *Myotis capaccinii* (Bonaparte, 1897)." Acta Chiropterologica **8**(1): 157-167
- ALTRINGHAM, J. D. (1996). Bats: Biology and Behaviour. London, UK, Oxford University Press.
- ANTHONY, E. L. (1988). Age determination in bats. Ecological and behavioural methods for the study of bats. T. H. Kunz. Washington DC, USA, Smithsonian Institution: 47-58.
- ANTHONY, E. L. P. and T. H. KUNZ (1977). "Feeding Strategies of the Little Brown Bat, *Myotis Lucifugus*, in Southern New Hampshire." Ecology **58**(4): 775-786
- ANTHONY, E. L. P., M. H. STACK and T. H. KUNZ (1981). "Night roosting and the nocturnal time budget of the little brown bat, *Myotis lucifugus*: Effects of reproductive status, prey density, and Environmental conditions." Oecologia **51**(2): 151-156
- AUBRET, F., X. BONNET and D. BRADSHAW (2007). "Food versus risk: foraging decision in young Tiger snakes, *Notechis scutatus*." Amphibia-Reptilia **28**(2): 304-308
- AUDET, D. (1990). "Foraging Behavior and Habitat Use by a Gleaning Bat, *Myotis myotis* (Chiroptera: Vespertilionidae)." Journal of Mammalogy **71**(3): 420-427
- AUDET, D. and M. B. FENTON (1988). "Heterothermy and the use of torpor by the bat *Eptesicus fuscus* (Chiroptera: Vespertilionidae): A Field Study." Physiological Zoology **61**(3): 197-204
- AVERY, D. M., G. AVERY and N. G. PALMER (2005). "Micromammalian distribution and abundance in the Western Cape Province, South Africa, as evidenced by barn Owls *Tyto alba* (Scopoli)." Journal of Natural History **39**(22): 2047-2071
- 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**(11): 2507-2515
- BARCLAY, R. M. R. (1991). "Population Structure of Temperate Zone Insectivorous Bats in Relation to Foraging Behaviour and Energy Demand." The Journal of Animal Ecology **60**(1): 165-178
- BARCLAY, R. M. R., B. J. CHRUSZCZ and M. RHODES (2000). "Foraging behaviour of the large-footed myotis, *Myotis moluccarum* (Chiroptera : Vespertilionidae) in south-eastern Queensland." Australian Journal of Zoology **48**: 385-392
- BARCLAY, R. M. R. and L. D. HARDER (2003). Life Histories of Bats: Life in the Slow lane. Bat Ecology. T. H. Kunz and M. B. Fenton. Chicago, USA, University of Chicago Press. **2**: 209-253.
- BARTONIÁKA, T. and J. ZUKAL (2003). "Flight activity and habitat use of four bat species in a small town revealed by bat detectors." Folia Zoology **52**(2): 155-166
- BELWOOD, J. J. and M. B. FENTON (1976). "Variation in the diet of *Myotis lucifugus* (Chiroptera: Vespertilionidae)." Canadian Journal of Zoology **54**(10): 1674-1678

- BERNARD, R. T. F. (1982). "Monthly changes in the females reproductive organs and the reproductive cycle of *Myotis tricolor* (Vespertilionidae: Chiroptera)." South African Journal of Zoology **17**: 17-84
- BERNARD, R. T. F. (1989). "The adaptive significance of reproductive delay phenomena in some South African Microchiroptera." Mammal Review **19**(1): 27-34
- BLACK, H. L. (1979). "Precision in prey selection by the trident-nosed bat (*Cloeotis percivali*)." Mammalia **43**(1): 53-56
- BLAKE, D., A. M. HUTSON, P. A. RACEY, J. RYDELL and J. R. SPEAKMAN (1994). "Use of lamp lit roads by foraging bats in southern England." Journal of Zoology **234**(3): 453-462
- BOONMAN, A. M., M. BOONMAN, F. BRETSCHEIDER and W. A. V. D. GRIND (1998). "Prey detection in trawling insectivorous bats: duckweed affects hunting behaviour in Daubenton's bat, *Myotis daubentonii*." Behavioral Ecology and Sociobiology **44**: 99-107
- BRIGHAM, R. M., H. D. J. N. ALDRIDGE and R. L. MACKEY (1992). "Variation in Habitat Use and Prey Selection by Yuma Bats, *Myotis yumanensis*." Journal of Mammalogy **73**(3): 640-645
- BROWN, J. H. (1968). "Activity Patterns of Some Neotropical Bats." Journal of Mammalogy **49**(4): 754-757
- BROWN, J. S. (1988). "Patch use as an indicator of habitat preference, predation risk, and competition." Behavioral Ecology and Sociobiology **22**(1): 37-47
- BUCHLER, E. R. (1980). "The Development of Flight, Foraging, and Echolocation in the Little Brown Bat (*Myotis lucifugus*)." Behavioral Ecology and Sociobiology **6**(3): 211-218
- BUTCHER, S. E. (1988). Environmental factors and the water regime of De Hoop Vlei. Environmental Studies. Cape Town, University of Cape Town. **Masters**: 140.
- CATTO, C. M. C., P. A. RACEY and P. J. STEPHENSON (1995). "Activity patterns of the serotine bat (*Eptesicus serotinus*) at a roost in southern England." Journal of Zoology (London) **235**(635-644): 635
- CIECHANOWSKI, M., T. ZAJĄC, A. BIŁAS and R. DUNAJSKI (2007). "Spatiotemporal variation in activity of bat species differing in hunting tactics: effects of weather, moonlight, food abundance, and structural clutter" Canadian Journal of Zoology **85**(12): 1249-1263
- CLARK, B. S., B. K. CLARK and J. DAVID M. LESLIE (2002). "Seasonal Variation in Activity Patterns of the Endangered Ozark Big-Eared Bat (*Corynorhinus townsendii ingens*)." Journal of Mammalogy **83**(2): 590-598
- CLARK, B. S., J. DAVID M. LESLIE and T. S. CARTER (1993). "Foraging Activity of Adult Female Ozark Big-Eared Bats (*Plecotus townsendii ingens*) in Summer." Journal of Mammalogy **74**(2): 422-427
- CUMMING, G. S. and R. T. F. BERNARD (1997). "Rainfall, food abundance and timing of parturition in African bats." Oecologia **111**: 309-317
- DE JONG, J. and I. AHLEN (1991). "Factors Affecting the Distribution Pattern of Bats in Uppland, Central Sweden." Holarctic Ecology **14**(2): 92-96
- DEMETER, A. (1982). "Prey of the Spotted Eagle-Owl *Bubo africanus* in the Awash National Park, Ethiopia." Bonner zoologische Beiträge **33**(2-4): 283-292
- DIETZ, M. and E. K. V. KALKO (2006). "Seasonal changes in daily torpor patterns of free-ranging female and male Daubenton's bats (*Myotis daubentonii*)." **176**: 223-231
- DWYER, P. D. (1970). "Foraging behaviour of the Australian large-footed *Myotis* (Chiroptera)." Mammalia **34**(1): 76-80
- EIDE, N. E., J. U. JEPSEN and P. PRESTRUD (2004). "Spatial organization of reproductive Arctic foxes *Alopex lagopus*: responses to changes in spatial and temporal availability of prey." Journal of Animal Ecology **73**: 1056-1068
- ENCARNAÇÃO, J. A. and M. DIETZ (2006). "Estimation of food intake and ingested energy in Daubenton's bats (*Myotis daubentonii*) during pregnancy and spermatogenesis." European Journal of Wildlife Research **52**: 221-227
- ENTWISTLE, A. C., P. A. RACEY and J. R. SPEAKMAN (1996). "Habitat Exploitation by a Gleaning Bat, *Plecotus auritus*." Philosophical Transactions: Biological Sciences **351**(1342): 921-931

- ERICKSON, J. L. and S. D. WEST (2002). "The influence of regional climate and nightly weather conditions on activity patterns of insectivorous bats." Acta Chiropterologica **4**(1): 17-24
- FAURE, P. A. and R. M. R. BARCLAY (1994). "Substrate gleanng versus aerial hawking: plasticity in the foraging and echolocation behaviour of the long-eared bat, *Myotis evotis*." Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology **174**(5): 651-660
- FENTON, M. B. (1970). "A technique for monitoring bat activity with results obtained from different environments in southern Ontario." Canadian journal of zoology **48**: 847-851
- FENTON, M. B. (1989). "The foraging behavior and ecology of animal-eating bats. ." Canadian Journal of Zoology **68**: 411-422
- FENTON, M. B. (1997). "Science and the Conservation of Bats." Journal of Mammalogy **78**(1): 1-14
- FENTON, M. B., D. AUDET, D. C. DUNNING, J. LONG, C. B. MERRIMAN, D. PEARL, D. M. SYME, B. ADKINS, S. PEDERSEN and T. WOHLGENTANT (1993). "Activity Patterns and Roost Selection by *Noctilio albiventris* (Chiroptera: Noctilionidae) in Costa Rica." Journal of Mammalogy **74**(3): 607-613
- FENTON, M. B. and W. BOGDANOWICZ (2002). "Relationships between external morphology and foraging behaviour: bats in the genus *Myotis*." Canadian Journal of Zoology **80**: 1004–1013
- FENTON, M. B., N. G. H. BOYLE, T. M. HARRISON and D. J. OXLEY (1977). "Activity Patterns, Habitat Use, and Prey Selection by Some African Insectivorous Bats." Biotropica **9**(2): 73-85
- FENTON, M. B., C. M. SWANEPOEL, R. M. BRIGHAM, J. CEBEK and M. B. C. HICKEY (1990). "Foraging Behavior and Prey Selection by Large Slit-Faced Bats (*Nycteris grandis*; Chiroptera: Nycteridae)." Biotropica **22**(1): 2-8
- FENTON, M. B. and D. W. THOMAS (1980). "Dry-Season Overlap in Activity Patterns, Habitat Use, and Prey Selection by Sympatric African Insectivorous Bats." Biotropica **12**(2): 81-90
- FINDLEY, J. S. (1972). "Phenetic Relationships Among Bats of the Genus *Myotis*." Systematic Zoology **20**(1): 31-52
- FUHRMANN, M. and A. SEITZ (1992). Nocturnal activity of the brown long-eared bat (*Plecotus auritus* L., 1758): data from radio-tracking in the Lenneberg forest near Mainz (Germany). Wildlife Telemetry. Priede and Swift.
- GITTLEMAN, J. L. and S. D. THOMPSON (1988). "Energy Allocation in Mammalian Reproduction." American Zoologist **28**(3): 863-875
- HANWELL, A. and M. PEAKER (1977). "Physiological effects of lactation on the mother." Symposia of the Zoological Society , London **41**: 297-312
- HAYES, J. P. (1997). "Temporal Variation in Activity of Bats and the Design of Echolocation-Monitoring Studies." Journal of Mammalogy **78**(2): 514-524
- HECKER, K. R. and R. M. BRIGHAM (1999). "Does Moonlight Change Vertical Stratification of Activity by Forest-Dwelling Insectivorous Bats?" Journal of Mammalogy **80**(4): 1196-1201
- HEITHAUS, E. R., T. H. FLEMING and P. A. OPLER (1975). "Foraging Patterns and Resource Utilization in Seven Species of Bats in a Seasonal Tropical Forest." Ecology **56**(4): 841-854
- HOOD, W. R., O. T. OFTEDAL and T. H. KUNZ (2006). "Variation in body composition of female big brown bats (*Eptesicus fuscus*) during lactation." Journal of Comparative Physiology B **176**: 807–819
- HOPCRAFT, J. G. C., A. R. E. SINCLAIR and C. PACKER (2005). "Planning for success: Serengeti lions seek prey accessibility rather than abundance." Journal of Animal Ecology **74**: 559-566
- HOSKING, G. P. (1979). "Trap comparison in the capture of flying Coleoptera." New Zealand Entomologist **7**(1): 87-92
- HOUSTON, R. D., A. M. BOONMAN and G. JONES (2004). Do Echolocation signal parameters restrict bats' choice of prey? Echolocation in bats and dolphins. J. A. Thomas, C. Moss and M. Vater. Chicago, University of Chicago Press: 339-345.
- HUGHES, J. J. and D. WARD (1993). "Predation risk and distance to cover affect foraging behaviour in namib Desert gerbils." Animal Behaviour **46**: 1243-1245

- IWASA, Y., M. HIGASHI and N. YAMAMURA (1981). "Prey Distribution as a Factor Determining the Choice of Optimal Foraging Strategy." The American Naturalist **117**(5): 710-723
- 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**(1): 93-103
- JACOBS, D. S. (2000). "Community level support for the allotonic frequency hypothesis." Acta chiropterologica **2**(2): 197-207
- JACOBS, D. S. and R. M. R. BARCLAY (2009). "Niche Differentiation in Two Sympatric Sibling Bat Species, *Scotophilus Dinganii* and *Scotophilus Mhlanganii*." Journal of Mammalogy **90**(4): 879-887
- JACOBS, D. S., R. M. R. BARCLAY and M. H. WALKER (2007). "The allometry of echolocation call frequencies of insectivorous bats: why do some species deviate from the pattern?" Oecologia **152**(583-594)
- JACOBS, D. S., J. M. RATCLIFFE and J. H. FULLARD (2008). "Beware of bats, beware of birds: the auditory responses of eared moths to bat and bird predation." Behavioral Ecology **19**(6): 1333-1342
- JONES, G. (1990). "Prey Selection by the Greater Horseshoe Bat (*Rhinolophus ferrumequinum*): Optimal Foraging by Echolocation?" Journal of Animal Ecology **59**(2): 587-602
- JONES, G. and T. KOKUREWICZ (1994). "Sex and age variation in echolocation calls and flight morphology of Daubenton's bats *Myotis daubentonii*." Mammalia **58**(1): 41-50
- JONES, G. and J. M. V. RAYNER (1988). "Flight performance, foraging tactics and echolocation in free-living Daubenton's bats, *Myotis daubentoni* (Chiroptera: Vespertilionidae)." Journal of Zoology, London **215**: 113-132
- JONES, G. and J. M. V. RAYNER (1991). "Flight performance, foraging tactics and echolocation in the trawling insectivorous bat *Myotis adversus* (Chiroptera: Vespertilionidae)." Journal of Zoology, London **225**: 393-412
- JONES, G. and J. RYDELL (1994). "Foraging Strategy and Predation Risk as Factors Influencing Emergence Time in Echolocating Bats." Philosophical Transactions: Biological Sciences **346**(1318): 445-455
- KALCOUNIS, M. C. and R. M. BRIGHAM (1995). "Intraspecific variation in wing loading affects habitat use by little brown bats (*Myotis lucifigus*)." Canadian Journal of Zoology **73**: 89-95
- KALKO, E. K. V. and H.-U. SCHNITZLER (1989). "The Echolocation and Hunting Behavior of Daubenton's Bat, *Myotis daubentoni*." Behavioral Ecology and Sociobiology **24**(4): 225-238
- KARLSON, B.-L., J. EKLOF and J. RYDELL (2002). "No lunar phobia in swarming insectivorous bats (family Vespertilionidae)." Journal of Zoology, London **256**: 473-477
- KATO, M., T. ITIOKA, S. SAKAI, K. MOMOSE, S. YAMANE, A. A. HAMID and T. INOUE (2000). "Various population fluctuation patterns of light-attracted beetles in a tropical lowland dipterocarp forest in Sarawak." Population Ecology **42**(1): 97-104
- KELM, D. H. and O. V. HELVERSEN (2007). "How to budget metabolic energy: torpor in a small Neotropical mammal." Journal of Comparative Physiology B **177**: 667-677
- KOTLER, B. P., J. S. BROWN and O. HASSON (1991). "Factors Affecting Gerbil Foraging Behavior and Rates of Owl Predation." Ecology **72**(6): 2249-2260
- KRULL, D., A. SCHUMM, W. METZNER and G. NEUWEILER (1991). "Foraging Areas and Foraging Behavior in the Notch-Eared Bat, *Myotis emarginatus* (Vespertilionidae)." Behavioral Ecology and Sociobiology **28**(4): 247-253
- KUNZ, T. H. (1973). "Resource Utilization: Temporal and Spatial Components of Bat Activity in Central Iowa." Journal of Mammalogy **54**(1): 14-32
- KUNZ, T. H. (1974a). "Feeding Ecology of a Temperate Insectivorous Bat (*Myotis Velifer*)." Ecology **55**(4): 693-711
- KUNZ, T. H. (1974b). "Reproduction, Growth, and Mortality of the Vespertilionid Bat, *Eptesicus fuscus*, in Kansas." Journal of Mammalogy **55**(1): 1-13

- KUNZ, T. H. (2009). Methods of assessing the availability of prey to insectivorous bats. Ecological and behavioural methods for the study of bats. T. H. Kunz and S. Parsons. Baltimore, Maryland, U.S.A., Johns Hopkins University Press: 920.
- KUNZ, T. H., J. A. WRAZEN and C. D. BURNETT (1998). "Changes in body mass and fat reserves in pre-hibernating little brown bats (*Myotis lucifugus*)." Ecoscience **5**(1): 8-17
- KURTA, A., G. P. BELL, K. A. NAGY and T. H. KUNZ (1989). "Energetics of Pregnancy and Lactation in Free-ranging Little Brown Bats (*Myotis lucifugus*)." Physiological Zoology **62**(3): 804-818
- KURTA, A., T. H. KUNZ and K. A. NAGY (1990). "Energetics and water flux of free-ranging big brown bats (*Eptesicus fuscus*) during pregnancy and Lactation." Journal of Mammalogy **71**(1): 59-65
- LACKI, M. J. (1984). "Temperature and humidity-induced shifts in the flight activity of little brown bats." OHIO J. SCI. **84**(5): 264-266
- LANG, A. B., E. K. V. KALKO, H. R. MER, C. BOCKHOLDT and D. K. N. DECHMANN (2006). "Activity levels of bats and katydids in relation to the lunar cycle." Oecologia **146**: 659-666
- LEWIS, T. and G. C. DIBLEY (1970). "Air Movements near windbreaks and a hypothesis of the mechanism of the accumulation of airborne insects." Annals of Applied Biology **66**: 477-484
- LEWIS, T. and J. W. STEPHENSON (1966). "The permeability of artificial windbreaks and the distribution of flying insects in the leeward sheltered zone." Annals of Applied Biology **58**(3): 355-363
- MACARTHUR, R. H. and E. R. PIANKA (1966). "On Optimal Use of a Patchy Environment." The American Naturalist **100**(916): 603-609
- MACKIE, I. J. and P. A. RACEY (2007). "Habitat use varies with reproductive state in noctule bats (*Nyctalus noctula*): Implications for conservation." Biological Conservation **140**: 70-77
- MADSEN, H., H. SPLIID and P. THYREGOD (1985). "Markov models in discrete and continuous time for hourly observations of cloud cover." Journal of Climate and Applied Meteorology **24**: 629-639
- MAIER, C. (1992). "Activity Patterns of pippistrelle bats (*Pipistrellus pipistrellus*) in Oxfordshire." Journal of Zoology (London) **228**: 69-80
- MASON, M. K., D. HOCKMAN, D. S. JACOBS and N. ILLING (2010). "Evaluation of maternal features as indicators of asynchronous embryonic development in *Miniopterus natalensis*." Acta Chiropterologica **12**(1): 161-171
- MCDONALD, J., I. RAUTENBACH and J. NEL (1990). "Foraging ecology of bats observed at De Hoop Provincial Nature Reserve, southern Cape Province. ." South African Journal of Wildlife research **20**(4): 133-145
- MCNAB, B. K. (1982). Evolution alternatives in the physiological ecology of bats. Ecology of Bats.
- MEEUS, J. (1998). Astronomical Algorithms. Richmond, Virginia, USA, Willmann-Bell Inc.
- MEYER, C. F. J., M. WEINBEER and E. K. V. KALKO (2005). "Home-range size and spacing patterns of *Macrophyllum macrophyllum* (Phyllostomidae) foraging over water." Journal of Mammalogy **86**(3): 587-598
- MILNE, D. J., A. A. FISHER, I. RAINEY and C. R. PAVEY (2005). "Temporal Patterns of bats in the top end of the Northern Territory, Australia." Journal of Mammalogy **86**(5): 909-920
- MINNIS, P., D. R. DOELLING, V. CHAKRAPANI, D. A. SPANGENBERG, T. UTTAL, R. F. ARDUINI and M. SHUPE (2001). "CLOUD COVERAGE AND HEIGHT DURING FIRE ACE DERIVED FROM AVHRR DATA." Journal of Geophysical Research **106**(15): 215-233
- NEGRAEFF, O. E. and R. M. BRIGHAM (1995). "The influence of moonlight on the activity of little brown bats (*Myotis lucifugus*)." Zeitschrift für Säugetierkunde **60**: 330-336
- NEUWEILER, G. (2000). Reproduction and Development. The Biology of bats. G. Neuweiler. Oxford, GB, Oxford University Press: 241-248.
- NORBERG, U. M. (1990). Vertebrate Flight: mechanics, physiology, morphology, ecology and evolution. Berlin, Springer-Verlag.
- NORBERG, U. M. and J. M. V. RAYNER (1987). "Ecological Morphology and Flight in Bats (Mammalia; Chiroptera): Wing Adaptations, Flight Performance, Foraging Strategy and Echolocation."

- Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences **316**(1179): 335-427
- O'DONNELL, C. F. J. (2000). "Influence of season, habitat, temperature, and invertebrate availability on nocturnal activity of the New Zealand long-tailed bat (*Chalinolobus tuberculatus*)."  
New Zealand Journal of Zoology **27**: 207-221
- O'DONNELL, C. F. J. (2001). "Home range and use of space by *Chalinolobus tuberculatus*, a temperate rainforest bat from New Zealand." Journal of Zoology, London **253**: 253-264
- O'FARRELL, M. J. and W. G. BRADLEY (1970). "Activity Patterns of Bats over a Desert Spring." Journal of Mammalogy **51**(1): 18-26
- O'FARRELL, M. J., W. G. BRADLEY and G. W. JONES (1967). "Fall and Winter Bat Activity at a Desert Spring in Southern Nevada." The Southwestern Naturalist **12**(2): 163-171
- OFTEDAL, O. T. (1984). "Milk composition, milk yield and energy output at peak lactation: a comparative review." Symposia of the Zoological Society, London **51**: 33-85
- OXBERRY, B. A. (1979). "Female reproductive patterns in hibernating bats." Journal of Reproduction and Fertility **56**(1): 359-367
- PAIGE, K. N. (1995). "Bats and Barometric pressure: conserving limited energy and tracking insects from the roost." Functional Ecology **9**: 463-467
- PARSONS, K. N., G. JONES and F. GREENAWAY (2003). "Swarming activity of temperate zone microchiropteran bats: effects of season, time of night and weather conditions." Journal of Zoology (London) **261**: 257-264
- RACEY, P. A. (1973). "Environmental factors affecting the length of gestation in heterothermic bats." Journal of Reproduction and Fertility Supplement **19**: 175-189
- RACEY, P. A. (1988). Reproductive assessment in bats. Ecological and Behavioral Methods for the Study of Bats. T. H. Kunz and S. Parsons. Baltimore, Maryland, Johns Hopkins Press. **2**: 920.
- RACEY, P. A. and A. C. ENTWISTLE (2003). Conservation Ecology of Bats. Bat Ecology. T. H. Kunz and M. B. Fenton. Chicago, USA, University of Chicago Press. **2**: 209-253.
- RACEY, P. A. and J. R. SPEAKMAN (1987). "The energy costs of pregnancy and lactation in heterothermic bats." Symposia of the Zoological Society, London **57**: 107-125
- RATCLIFFE, J. M. and J. W. DAWSON (2003). "Behavioural flexibility: the little brown bat, *Myotis lucifugus*, and the northern long-eared bat, *M. septentrionalis*, both glean and hawk prey." Animal Behaviour **66**: 847-856
- RAYNER, J. M. V. (1991). "On the Aerodynamics of Animal Flight in Ground Effect." Philosophical Transactions: Biological Sciences **334**(1269): 119-128
- ROBINSON, S. K. and R. T. HOLMES (1982). "Foraging Behavior of Forest Birds: The Relationships Among Search Tactics, Diet, and Habitat Structure." Ecology **63**(6): 1918-1931
- RUEDI, M. and F. MAYER (2001). "Molecular Systematics of Bats of the Genus *Myotis* (Vespertilionidae) Suggests Deterministic Ecomorphological Convergences." Molecular Phylogenetics and Evolution **21**(3): 436-448
- RUSS, J. M., M. BRIFFA and W. I. MONTGOMERY (2003). "Seasonal patterns in activity and habitat use by bats (*Pipistrellus* spp. and *Nyctalus leisleri*) in Northern Ireland, determined using a driven transect." Journal of Zoology, London **259**: 289-299
- RYDELL, J. (1989). "Feeding Activity of the Northern Bat *Eptesicus nilssoni* during Pregnancy and Lactation." Oecologia **80**(4): 562-565
- RYDELL, J. (1991). "Seasonal Use of Illuminated Areas by Foraging Northern Bats *Eptesicus nilssoni*." Holarctic Ecology **14**(3): 203-207
- RYDELL, J. (1993). "Variation in Foraging Activity of an Aerial Insectivorous Bat during Reproduction." Journal of Mammalogy **74**(2): 503-509
- RYDELL, J., A. ENTWISTLE and P. A. RACEY (1996). "Timing of Foraging Flights of Three Species of Bats in Relation to Insect Activity and Predation Risk." Oikos **76**(2& 6): 243-252
- SAUNDERS, M. B. and R. M. R. BARCLAY (1992). "Ecomorphology of Insectivorous Bats: A Test of Predictions Using Two Morphologically Similar Species." Ecology **73**(4): 1335-1345

- SCHNITZLER, H.-U. and E. KALKO (2001). "Echolocation by Insect-Eating Bats." BioScience **51**(7): 557-569
- SCHNITZLER, H.-U., C. F. MOSS and A. DENZINGER (2003). "From spatial orientation to food acquisition in echolocating bats." TRENDS in Ecology and Evolution **18**(8): 386-394
- SCHOEMAN, M. C. and D. S. JACOBS (2003). "Support for the allotonic frequency hypothesis in an insectivorous bat community." Oecologia **134**: 154–162
- SCHOEMAN, M. C. and D. S. JACOBS (2010). "The relative influence of competition and prey defences on the trophic structure of animalous bat ensembles." Oecologia 10.1007/s004442-010-1854-3.
- SEIDMAN, V. M. and C. J. ZABEL (2001). "Bat Activity along Intermittent Streams in Northwestern California." Journal of Mammalogy **82**(3): 738-747
- SHIEL, C. B. and J. S. FAIRLEY (1998). "Activity of Leisler's bat *Nyctalus leisleri* (Kuhl) in the field in South-East County Wexford, as revealed by a bat detector." Biology and Environment: Proceedings of the Royal Irish Academy **98B**(2): 105–112
- SHIEL, C. B. and J. S. FAIRLEY (1999). "Evening emergence of two nursery colonies of Leisler's bat (*Nyctalus leisleri*) in Ireland." Journal of Zoology, London **247**: 439-447
- SHIEL, C. B., R. E. SHIEL and J. S. FAIRLEY (1999). "Seasonal changes in the foraging behaviour of Leisler's bats (*Nyctalus leisleri*) in Ireland as revealed by radio-telemetry." Journal of Zoology, London **249**: 347-358
- SIEMERS, B. M., K. BEEDHOLM, C. DIETZ, I. DIETZ and T. IVANOVA (2005a). "Is species identity, sex, age or individual quality conveyed by echolocation call frequency in European horseshoe bats?" Acta Chiropterologica **7**(2): 259-274
- SIEMERS, B. M., P. STILZ and H.-U. SCHNITZLER (2001). "The acoustic advantage of hunting at low heights above water: behavioural experiments on the European 'trawling' bats *Myotis capaccinii*, *M. dasycneme* and *M. daubentonii*." The Journal of Experimental Biology **204**: 3843–3854
- SIEMERS, B. O., E. BAUR and H.-U. SCHNITZLER (2005b). "Acoustic mirror effect increases prey detection distance in trawling bats." Naturwissenschaften **92**: 272–276
- SIMMONS, N. B. (2004). Order: Chiroptera. Mammal species of the World: A taxonomic and geographic reference. D. E. Wilson and D. M. Reeder. Washington, D.C., Smithsonian Institution Press.
- SKINNER, J. D. and R. H. N. SMITHERS (1990). The mammals of the Southern African subregion. Pretoria, University of Pretoria.
- SPEAKMAN, J. R. and D. W. THOMAS (2003). Physiological Ecology and energetics of bats. Bat Ecology. T. H. Kunz and M. B. Fenton. Chicago, USA, University of Chicago Press.
- STADELMANN, B., D. S. JACOBS, C. SCHOEMAN and M. RUEDI (2004). "Phylogeny of African *Myotis* bats (Chiroptera, Vespertilionidae) inferred from cytochrome b sequences." Acta Chiropterologica **6**(2): 177–192
- STOFFBERG, S. and D. S. JACOBS (2004). "The influence of wing morphology and echolocation on the gleaning ability of the insectivorous bat *Myotis tricolor*." Canadian Journal of Zoology **82**: 1854–1863
- SWIFT, S. M. (1980). "Activity patterns of Pipistrelle bats (*Pipistrellus pipistrellus*) in North-east Scotland." Journal of Zoology, London **190**(3): 285-295
- TAYLOR, L. R. (1963). "Analysis of the Effect of Temperature on Insects in Flight." Journal of Animal Ecology **32**(1): 99-117
- TAYLOR, P. J. (2000). Bats of Southern Africa; guide to biology, identification and conservation. Scottsville, University of Natal Press.
- THIES, W., E. K. V. KALKO and H.-U. SCHNITZLER (2006). "Influence of environment and resource availability on activity patterns of *Carollia castanea* (Phyllostomidae) in Panama." Journal of Mammalogy **87**(2): 331

- THOMAS, S. P. (1975). "Metabolism During Flight In Two Species Of Bats, *Phyllostomus Hastatus* And *Pteropus gouldji*." Journal of Experimental Biology **63**: 273-293
- THOMAS, S. P. (1987). The physiology of bat flight. Recent Advances in the Study of Bats. M. B. Fenton, P. A. Racey and J. M. V. Rayner. Cambridge, Cambridge University Press: 75-99.
- TODD, V. L. G. and D. A. WATERS (2007). "Strategy-switching in the gaffing bat." Journal of Zoology **273**: 106–113
- UK-METEOROLOGICAL-OFFICE. (2006). "MIDAS Land Surface Stations data (1853-current)." Retrieved June, 2008, 2008.
- VAUGHAN, N., G. JONES and S. HARRIS (1997). "Habitat Use by Bats (Chiroptera) Assessed by Means of a Broad-Band Acoustic Method." The Journal of Applied Ecology **34**(3): 716-730
- WAI-PING, V. and M. B. FENTON (1989). "Ecology of Spotted Bat (*Euderma maculatum*) Roosting and Foraging Behavior." Journal of Mammalogy **70**(3): 617-622
- WALKER, E. P. (1964). Mammals of the world. Baltimore, Maryland, U.S.A., John Hopkins University Press.
- WALSH, A. L. and S. HARRIS (1996). "Factors Determining the Abundance of Vespertilionid Bats in Britain: Geographical, Land Class and Local Habitat Relationships." The Journal of Applied Ecology **33**(3): 519-529
- WARREN, R. D., D. A. WATERS, J. D. ALTRINGHAM and D. J. BULLOCK (2000). "The distribution of Daubenton's bats (*Myotis daubentonii*) and pipistrelle bats (*Pipistrellus pipistrellus*) (Vespertilionidae) in relation to small-scale variation in riverine habitat." Biological Conservation **92**: 85-91
- WIBIG, J. (2008). "Cloudiness variations in Łódź in the second half of the 20th century." International Journal Of Climatology **28**: 479–491
- WILDE, C. J., C. H. KNIGHT and P. A. RACEY (1999). "Influence of torpor on milk protein composition and secretion in lactating bats." Journal of Experimental Zoology **284**(1): 35-41
- WILKINSON, G. S. and J. W. BOUGHMAN (1998). "Social calls coordinate foraging in greater spear-nosed bats." Animal Behaviour **55**: 337–350
- WILLIAMS, C. B. (1961). "Studies in the Effect of Weather Conditions on the Activity and Abundance of Insect Populations." Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences **244**(713): 331-378
- WORLD-METEOROLOGICAL-ORGANISATION (1972, 1974). Manual on codes. WMO. Geneva, Switzerland, WMO. **1 and 2**.

**Report back on Examiners comments on M.Sc Dissertation:**

**Stacey Jordaan: JRDSTA001**

**'Factors affecting the activity patterns of *Myotis tricolor* (Chiroptera: Vespertilionidae)'**

**EXAMINER 1:**

**COMMENT:**

**Abstract**

Although describing the study, the abstract is somewhat lacking in detail and should include some indication of when and where the study was conducted and in what year and should also include some numerical results (of the most significant findings).

Pg iv, Line 5: Not clear if six bats in total were radio tagged, or six in each of the categories (early pregnancy, late pregnancy, lactation), and how often during the year.

Pg iv, line 10: During what year? September is not definitive.

RESPONSE: Changes have been made to make these issues clearer.

COMMENT: It is not usual to use first person (I, we, us etc.) in scientific writing. I would urge the rewording of all sentences written in first person-this applies throughout the dissertation.

RESPONSE: I feel that this is a subjective view and that writing in the first person is acceptable as long as it is used where and how appropriate. I have, however, amended the use of "I" and "we" interchangeably, substituting "we" for "I".

**Introduction:**

COMMENT: As personal preference I would not add hypotheses as part of the literature review, but would instead list them at the end of the chapter, as the reader would understand that they were drawn from the previous studies mentioned in the literature review. They disappear and have less obvious impact when mixed between the literature.

RESPONSE: In fact, my last paragraph at the end of the chapter lists my hypothesis and predictions. This has just been written in a manner that flows as a paragraph, rather than a list.

COMMENT: As a conclusion to chapter one, a short paragraph giving a brief outline of the rest of the dissertation to follow could be included.

RESPONSE: I feel this is a suggestion and is based on the author's writing style, therefore I have chosen not to do this.

## Methods:

### COMMENT:

A map of the study area in relation to South Africa, as well a close-up map of the De Hoop vlei and the proximity of Hothole Cave would be useful to the reader.

RESPONSE: For the sake of brevity I have not included this map. In any case such a map would not provide the reader with much extra insight.

COMMENT: Table 1- the header of table 1 needs to refer specifically to bats.

RESPONSE: This has been amended; the specific species used to produce the table has now been indicated.

COMMENT: Pg 22, line 1: When starting a sentence with a species name it is usual to write the genus name in full, not abbreviated.

RESPONSE: The full genus name has been inserted at this point.

COMMENT: Pg 22, line 16: The moonlight index might be explained a bit more by inclusion of a table or calculation.

RESPONSE: This has been more clearly explained by the inclusion of an example calculation.

COMMENT: Pg 22, line 17: Was the visual division of the sky done from the same point each day and by the same person? Illustrations could also be useful.

RESPONSE: This information has been added.

## Results:

### COMMENT:

When discussing the results, the year date should be included every time a certain month of study is discussed. It is confusing to the reader, who will not remember the details as well as the author. So

for instance, September, October, November, March could all be in the same year, so it needs to be indicated every time in what year the specific month occurred.

RESPONSE: This has been amended. The year has been included where necessary.

COMMENT:

Pg 29, Figure 1: The legend contains a bit of discussion that should be removed. Also, perhaps I misunderstood, but the box and whisker plots indicate September, but in the results discussion all the months are also mentioned, so it is assumed that the reader knows when bats are pregnant etc. The 'rules' of figures and their legends is that they should 'stand alone' and should be able to be complete, without the need for the reader to read the text. It is also important to indicate the meaning any abbreviations used. In fact this holds true for all figure legends and table headers throughout the dissertation. They should have some indication of what the study was about, when and where it took place and what exactly is being represented.

RESPONSE: All the information in the Figure 1 legend is needed to sufficiently understand the figure and allows the figure to 'stand alone' as the examiner instructs. Information has been added to the legends of other figures to correct this and all abbreviations have been explained.

COMMENT:

Pg 31, 32: Figures have no figure legends! One should always have a figure legend below a figure, even if it means making the figure a bit smaller to fit. Same for pages 36, 37, 40, 41.

RESPONSE: This has been corrected. Figure legends are no longer on the following page after a figure.

COMMENT:

Pg 42, Figure 7 legend: As it currently stands, the figure legend could be for any place on earth and in any year. So it is important to say where and when the weather data was obtained from.

RESPONSE: All relevant information has been added.

COMMENT:

Pg 44, Table 2: The header needs more detail. What are GLZ's, whose activity patterns are they investigating? When, where?

RESPONSE: All relevant information has been added.

COMMENT:

Pg 45, 46, 47, 49, Figures 8, 9 & 10, 11: Again more detail in legend. What is the meaning of the numbers above the x-axis label 'Date'? It's a bit confusing, especially with such a sparsely descriptive legends.

RESPONSE: More information has been added to figure legends to clarify these issues.

Discussion:

COMMENT:

Emphasis again should be made on the use of third person, rather than first person whilst discussing results.

RESPONSE: I have not changed this. See response to this issue above.

COMMENT:

References

The following references were omitted in the list:

Jacobs (1999) pg4  
Lacki (1998) pg 5  
MacDonald et al 1990 pg 7  
Walker (1964) pg12  
Skinner & Smithers (1990) pg 13  
Taylor (2000). pg 13  
Fenton (1990) pg 14  
Jacobs (2007) pg 16  
Hoskin (1979) pg 21  
Kato et al (2000) pg 21

RESPONSE: These references have been added.

**EXAMINER 2:**

COMMENT: The candidate vacillates throughout between the use of "I" and "we". Choose one and stick to it. I'd advise the use of "I".

RESPONSE: Changes have been made: all "we" have been changed to "I".

Introduction:

COMMENT:

Page 4, throughout:

I do not agree that wing morphology and echolocation call structure "largely determine bat flight and foraging capabilities" and suggest this section starts with a less dogmatic tone. For one, models, such as those of Norberg and Rayner and Aldridge and Rautenbach, about flight based on wing measurements used fixed wing aerodynamics as their basis for making predictions about bats' behavioural capabilities. We know now that these models inadequately explain much of what we now understand about how bats fly. For two, the majority of echolocating bats exhibit some degree of plasticity in echolocation call design; among the most flexible, in this respect, are the myotis.

RESPONSE: I have changed the wording of this paragraph to indicate that this is a hypothesis with a level of uncertainty, rather than a “rule”.

COMMENT:

Page 11, bottom third of page:

Here and elsewhere, the candidate sometimes introduces a species using only its Latin binomial. In this case it is a New World mouse that, given the context, might to the uninitiated be thought to be a bat. In other instances the candidate jumps between congeneric species, and species within and between bat families in a single paragraph without indicating as much. I suggest using common names and Family/Order designations on the first mention of each species.

RESPONSE: These changes have been made.

COMMENT:

Page 12, last paragraph:

There are now more than 100 identified species of *Myotis*. References should be more up to date than the ones cited here, none of which are less than ten years old. In most other instances, however, I should say that I was duly impressed with the scholarship of the candidate’s thesis.

RESPONSE: More up to date references have been added and the information in this paragraph suitably revised.

COMMENT:

Page 14, fifth line from top:

Ratcliffe and Dawson (2003) did not consider *Myotis nattereri*. We considered *Myotis lucifugus* and *M. septentrionalis* and demonstrated that both could glean and hawk prey. To my knowledge, we were the first to refer to such plasticity in foraging strategy in predatory bats – explicitly at least - as “behavioural flexibility”.

RESPONSE: This mistake has been amended.

Methods:

COMMENT:

Page 19, second sentence under “Radio telemetry”

The candidate should remind the reader which three reproduction stages are being discussed - those outlined in Table 1, or nulliparous/pregnant/lactating?

RESPONSE: The reproductive states being investigated has been inserted here.

COMMENT:

Page 20:

It is not 100% clear to me whether the candidate knew, at all times, if a radio-tagged bat was inside or outside the roost. Could it be possible that a bat returning to the roost could have been mistaken for one leaving and/or vice versa? If not, I would suggest making this crystal clear as it is a strength.

RESPONSE: I did not know, at all times, if a radio-tagged bat was inside or outside the roost but rather had to infer this from all available information. Thus I cannot add this into the methods.

COMMENT:

Page 22:

Does % moon illumination account for the potential effect(s) of the moon being present/absent at different times on different nights (i.e. different times of the month, year)?

RESPONSE: Yes it does. The calculation for % moon illumination has now been included in the methods to clearly illustrate that I control for the time that the moon was up.

COMMENT:

Page 23:

“All measures were made by the same observer”. Was qualitative to quantitative wind rating calibrated and, if so, how? The “same observer” should be identified.

RESPONSE: The qualitative wind rating was not calibrated to a quantitative measure. The “same observer” has been identified.

COMMENT:

Page 24:

Under “Insect Abundance”, that differences between habitats were not being investigated is not a statistically defensible rationale for data pooling. If there were differences, an explanation/justification as to why data were still subsequently pooled should be provided.

RESPONSE: There were no significant differences in the total insect numbers and biomass between the two habitat types, indicating that pooling the data was not invalid. This has been indicated in the text.

COMMENT:

Pages 24/25:

Check spelling: “lilliefors” versus “Lillifors”

RESPONSE: This has been corrected.

## Results:

### COMMENT:

Page 34:

Under “Insect Abundance ...”, here and elsewhere it might be helpful to remind/define exactly what was compared and of how many hours after dusk “early evening” comprised.

RESPONSE: I have clarified what is being compared in this paragraph.

### COMMENT:

Figure 4:

While I agree breakpoints are useful, they make interpreting some of the ranges difficult (e.g., Biomass, September – is the 75% quartile at 600 or 1000?).

RESPONSE: I have removed this scale break and resized the graph to make it clearer.

### COMMENT:

Page 39:

Last sentence, while the median for all three months can be zero, it seems unlikely that the mean was zero in September and January, especially for September. This needs to be rechecked. Also, a reference is needed to support the contention that a Kruskal-Wallis test can give a significant result impenetrable to post-hoc tests.

RESPONSE: The mean was not zero for all three months (it was for November) and this has been amended in the text. The statement about the strength of the Kruskal-Wallis test has been removed from the text.

### COMMENT:

Page 43:

Again a quick reminder would be helpful as to how exactly emergence time is related to total rain per night. Figure 11 does not make the relationship between the two variables clear.

RESPONSE: In the text it states: “emergence time was significantly positively correlated with total rain per night”. I am not sure how to quantify this relationship further.

### COMMENT:

Figure 8:

This and other figures of this multi-variable/split y-axis design are difficult to grasp. Also, in general, figures could do with proper figure headings rather than short title/descriptor combinations.

RESPONSE: The figure legends have been augmented to better explain the figures.

Discussion:

COMMENT:

Page 49 (1<sup>st</sup> page of Discussion), first sentence:

What does “advanced pregnancy” mean given the scheme to categorize bats described in Table 1 has no such category (only early and mid)?

RESPONSE: This has been ammended. “In advanced pregnancy” has been changed to “in mid-pregnancy when first captured (thus advancing from mid- to late-pregnancy over the three weeks of study) in early November 2008”. Table 1 comes from a study (Mason *et al.*, 2010) which only captured bats up to mid pregnancy, as late pregnancy bats were not needed for further analysis. Likewise, I wanted to catch bats that would continue being pregnant for the period of radio-tracking and thus did not want to catch any bats during late pregnancy.

COMMENT:

Page 49, last sentence:

“emerged later”, in absolute terms or with respect to daily sunset?

RESPONSE: This is a later emergence time with respect to sunset time, which has been indicated in the text.

COMMENT:

Page 55:

Is it possible to disentangle the relative importance of temperature versus insect abundance?

RESPONSE: I attempted to do this by running a generalized linear/non-linear model (GLZ) on the number of foraging bouts to investigate what parameters (including temperature, insect numbers and insect biomass) influence this activity variable and how they interact. This indicated that temperature is affecting the activity more than the insect abundance. I could not disentangle this relationship further but discussed the possible relative significance of these two factors in the discussion.

COMMENT:

Page 57:

First sentence, I am not sure what the candidate is trying to say. Sound attenuates in intensity with respect to frequency and distance, while the speed of sound is effectively a constant, depending to a relatively small degree on temperature and humidity.

RESPONSE: “When hunting at the edge of the vegetation (‘clutter-edge forager’; Stoffberg & Jacobs, 2004) the low frequency calls of *M. tricolor*, which attenuate slowly through the vegetation, allow eared moths to hear them with enough time to manoeuvre and avoid capture (Jacobs *et al.*, 2008).” Here I am not referring to the speed of the sound, but the fact that the sound will not attenuate through the vegetation as much for a clutter-edge forager than for a clutter-forager. This has been changed to: “... the low frequency calls of *M. tricolor*, which attenuate less through the vegetation (than would a higher frequency call or the calls of a ‘clutter-forager’), allow eared moths to hear them with enough time to manoeuvre and avoid capture (Jacobs *et al.*, 2008).”

COMMENT:

Page 57 and elsewhere in the Discussion:

**It would be helpful if figures were cited at relevant points throughout the discussion.**

RESPONSE: References to figures have been inserted into the discussion, where relevant, to facilitate comprehension of the results and interpretation.

COMMENT:

Page 58, second sentence:

Perhaps replace “augment” with “increase”.

RESPONSE: This change has been made.

COMMENT:

Page 58, second to last sentence:

“foraging duration” is reference to bout duration, total time spent foraging, or number of bouts?

RESPONSE: “Foraging duration” is referring to the duration of foraging bouts throughout the dissertation.

COMMENT:

Page 59, whole page:

Like the rest of the candidate's thesis, I enjoyed this section. But here I have some questions of my own and some alternative ways of testing the candidate's proposals. Here goes:

(1) How do you know that the bats do not hear the rain or simply make exploratory flights to the entrance, get a bit wet, and then fly back to roost? Having been to the roost a few times myself, this seems as likely an explanation as the ability to detect humidity (or, indeed, a fine way to test for humidity!).

(2) What evidence, if any, is there that *Myotis tricolor* or any other bats can "ascertain information on any particular night, without exiting the roost" or that there are bats that act as "pioneering conspecifics" who "explore conditions". The latter explanation, especially, seems unlikely.

(3) Last, one way to test the hypothesis that rain has detrimental effects on bats' abilities to echolocate (which seems quite probable to me) would be to investigate whether or not non-echolocating pteropodids and/or birds show no such aversion to flying in rain. Alternatively, it could be that rain makes flight itself difficult (which seems to me more likely still).

RESPONSE: 1: It is possible that the bats can hear the rain, and this has been added to the text. However, I know that the bats did not make exploratory flights as they were detected by the automatic radio receiver as soon as they were near the entrance to the cave. In fact, a bat circling low within the cave, but below the entrance (sink-hole cave) was always picked up by the receiver.

2: There is no evidence of these phenomena. I am merely discussing them as possibilities to explain my results but will alter my wording to indicate my uncertainty of these suggestions.

3: This suggestion will be taken into consideration when (and if) the dissertation is written up for publication.

**EXAMINER 3:**

However, for the sake of the planning of future studies or a potential publication I do have some comments

1

COMMENT:

I think the best comparison would have been to look at non-reproductive individuals during the SAME season, only this would have shown you an effect of reproduction, teased apart from the effects of season and other environmental variables.

RESPONSE: I acknowledge that this would have been the most optimal experimental design, however the number of bat radio-tagged was limited by practicality and the cost of the radio-tags, and therefore this was not possible.

COMMENT:

Insect abundance: you are not really assessing insect abundance that is relevant for this particular species. I would definitely have done some faecal analysis to find out which Coleoptera, Diptera etc were consumed as especially in the former bats can be quite choosy and thus you may not have assessed actual food availability. There may also be a seasonal switch in foraging strategy/food choice correlated with reproductive state or season, which can result in the differences in numbers of foraging bouts etc that you see and which would be very relevant for the interpretation of your results. There's the additional problem of using light traps, which I'm sure you're aware of as they attract insects and thus affect abundance, while not attracting all insects equally. That may not have been feasible to change logistically, but should at least be acknowledged

RESPONSE: I did not do faecal analysis as this has been done for my study population at the study location. Insect remains from faecal pellets were only identified to order level, and this is why I analysed insect prey availability to this level. The limitation of using light traps has been acknowledged.

COMMENT:

Radiotelemetry: I'm sure there is a reason why (maybe someone else was doing that) but having transmitters on the bats and not at least getting an impression of where exactly they go and which niche (edge/open-air...) they use seems a shame. You did not really look at foraging behaviour, but at activity patterns (title!)

RESPONSE: I did attempt to do this, but at the speed that the bats were leaving the roost I was not always able to ascertain their direction. And when I was, I was never able to follow them. I suspect that the landscape and the accessibility of the Reserve where the work was conducted are the reasons for this.

COMMENT:

Abstract (and title): in my opinion you looked at activity patterns not foraging behaviour

..thus females may use torpor during this time... that is an assumption. I would rather say „may use compensation, such as torpor or a switch in diet...“

RESPONSE: “Females may use torpor during this time” has been changed to “females may use compensation, such as torpor, during this time.” The title has been changed from “foraging behaviour” to activity patterns”.

Introduction:

COMMENT:

Page 3, 3rd para: Furthermore many (or even most) insectivorous bats... there are quite a lot that are not opportunistic and also not very flexible for example an extreme open-air forager like a free-tailed bat can most likely not forage in any other niche due to morphology. But it is true for the many species with intermediate morphology. Just a question of wording

RESPONSE: I have taken “(or even most)” out of this paragraph.

COMMENT:

Page 5, 2nd para: „Low temperatures are hypothesized to reduce activity levels in bats“ that is true the literature says that, but is most likely and indirect effect of food availability, which would also explain your results. For example in the two examples you list further down it may be that food availability is not affected by the low temps. I've seen bats forage over the snow in January...when there were insects around.

RESPONSE: I feel I have addressed this because I end this same sentence with: “and because of low prey (insect) activity levels at low ambient temperatures.” And I discuss the relative importance of a direct effect of temperature and the effect via insect availability 4 paragraphs after this.

COMMENT:

Page 6, 1st para: Light levels never directly influence bats, but always indirectly via food availability and predation pressure. There are many species of bats that do not show lunar phobia: *Carollia* forages in the understory where moonlight does not penetrate and *Anthrozous*' food (skorpions etc) may not be affected by moonlight in their activity.

RESPONSE: “Increased light levels have also been reported to result in decreased activity” has been changed to “...reported to be associated with decreased activity”. The remainder of this paragraph discusses that light levels may affect behaviour through food availability and predation pressure and the fact that these results are far from consistent across species.

COMMENT:

Page 6, 2nd para: Rain is a similar case, a flying bat probably generates enough heat to be able to sustain rain, but a) food may not be around and b) echolocation is more difficult for bats foraging for small insects. *Corynorhynchus* is a gleaner that is less likely to be affected and *Carollia* is specialized on Piper fruit, which also occur regardless of the (short local) rainfall. It's more likely a trade-off between foraging efficiency (and thus energy spent during flight) and food availability than a direct effect of the rain. In *Myotis* however, an actively echolocating forager, rain would make the detection of food very difficult and it's fair to assume an effect there.

RESPONSE: I have acknowledged in the text that the lack of effect of rain on these two species is likely because they do not use echolocation to locate their food and that rain most likely affects bats through impairing echolocation. I have suggested that this necessitates investigation into the effect of rain, because the study species uses echolocation to actively search for insect prey.

COMMENT:

Page 11, last sentence: ...increased foraging time or switches in foraging strategy or food type...

RESPONSE: This has been added to the text.

COMMENT:

**Page 12, 1st para: see also papers published by Kamran Safi for these sex specific differences**

RESPONSE: I was not investigating differences between sexes but rather between reproductive classes in females. Therefore only data on the foraging behaviour of females in various reproductive states is relevant to my study.

Methods:

COMMENT:

**Page 21, 2nd para: ...a beetle will weigh more than a similar sized moth...yes, but may not provide more food as it's mainly chitin!**

RESPONSE: Biomass is still an important measure of insect availability as it accounts for differences in size. Also, the increased weight of beetles was used only as an example to explain what was meant by "mass differences between orders due to body composition".

COMMENT:

**Page 23: citation for BCI: I'm pretty sure that Björn Siemers as ingenious as he is did not invent the BCI!!**

RESPONSE: This reference is not suggesting Siemers (2005a) invented BCI as it is a widely used concept and I'm not sure if its first use can be traced. This is simply a reference to indicate that this method has been used before and to indicate whose methods I followed in deciding to use BCI.

COMMENT:

**Activity Patterns (page 24): emergence time is in hours in the graphs**

RESPONSE: While emergence time was analysed as minutes after sunset, the graphs were converted to hours after sunset to make interpretation of the graphs easier.

COMMENT:

**Page 26, 1st para: the last part is not clear to me, why did the other variables result in errors**

RESPONSE: I could not determine the exact problem here but it was most likely due to a high prevalence of zero's in the data that could not be included. This did not affect the interpretation of the data as the total insect abundance had already been investigated.

Results:

COMMENT:

**Missing: actual numbers of bats, actual weights. N-numbers vary between tests and it's not easy to follow sample sizes**

RESPONSE: This has been inserted as a new table 2.

COMMENT:

The low BCI in conjunction with the higher number of foraging bouts may indicate that the period before September may have been the limiting one and they may be compensating for that in September and that this effect (maybe low insect availability before September) may overrule the effect of pregnancy/lactation later on.

RESPONSE: The bats are certainly in a state of recovery during September as they have just returned from migration. The low BCI could be a result of this, which is discussed in the text.

COMMENT:

Activity patterns: When (actual hour) was sunset during the different months and when did the bats actually emerge? Did they emerge at the same time always, and it was only the timing of sunset that changed? Also: sunset according to an online algorithm may not be when it actually gets dark. This should be at least discussed as the nights in September, when there are more foraging bouts, are apparently longer.

RESPONSE: As stated in the text, emergence time was measured as minutes after sunset. Therefore both the sunset time and the emergence time with respect to sunset changed. Since sunset time was calculated in the same way for all months, whether it represents when it actually gets dark (which is relative and very difficult to measure) or when the sun just falls below the horizon should not matter as the same point in the sunset process is being used as a reference across months. It is the relative difference between months that is important to the analysis, not the actual difference.

COMMENT:

Also: how evenly were foraging bouts spread over the night, again times would help. As mentioned above the differences in number and/or duration of foraging bouts may be caused by a switch in diet, where foraging all of a sudden becomes more efficient because a certain food source is more available (such as swarming insects as known from temperate bats, whose parturition coincides with high occurrence of insect swarms). Another explanation could be that they have to fly farther during certain times of the year. All of this you cannot verify without following the bats when they forage.

RESPONSE: If the dissertation is written up for publication the actual times of foraging bouts will be included. Including them at this stage would not be feasible given the time constraints. These additional explanations for an increase in the number of foraging bouts have been added to the text.

COMMENT:

Graphs on page 32: in the beginning of the methods you say that „emergence“ refers to any emergence event in case of multiple ones per night. But in these graphs and also some of the analyses I think you are talking about the first emergence, right? That is a bit confusing. Or is it actually the mean (which would explain much later emergence in September when there are more foraging bouts), which would not be very informative I think.

RESPONSE: Unless explicitly stated I am not referring to just the initial emergence. These graphs are displaying the mean emergence time per bat for each month. Therefore bats with an early and a late emergence would have a later mean emergence than those with just an early emergence.

COMMENT:

**Page 33, Insect abundance: this, too, indicates that September may be a particularly difficult month (preceeding dry periods? Cold period?) which the bats have to compensate for and the effect of which may be stronger than that of reproduction**

RESPONSE: I discuss in detail in the discussion that the weather conditions were poor in September and discuss that the effects of this may override those of reproduction.

COMMENT:

**Figure 8 to 11: you have to interrupt the lines whenever there is a gap in the data. In this particular figure you do it for „duration“ between September and November, but not anywhere else**

RESPONSE: The lines are connected in these figures, even though many of the measurements are not sequential, because this aids in clarifying the figures and helps the reader visualise the trends being displayed.

Discussion:

COMMENT:

**1st para: and then it makes sense that the can afford to forage less.**

RESPONSE: This comment has been noted.

COMMENT:

**Page 50, 1st para: this seems to indicate that emergence times presented in the results are mean emergence times? I don't really see what we learn from that. See comments in results**

RESPONSE: See response to comment about graphs on page 32 in results section.

COMMENT:

**Page 51, 2nd para: well yes, they were pregnant! That is not really their body mass although it may end up meaning the same.  
If bats gain mass AND do not forage longer they may simply not have a problem, or only during pregnancy, see comments above.**

RESPONSE: This paragraph is not discussing fat storage during pregnancy but saying that since the BCI of lactating bats was not significantly different from that of pregnant bats, lactating bats may be using storage.

COMMENT:

Page 52, 1st para: ...would preclude major mass gain...probably true, but nonetheless an assumption unless you have a citation for it.

RESPONSE: Citations have been added.

COMMENT:

Page 53, 2nd para: again see earlier comments, maybe conditions were particularly bad during or before September, which is info you don't have (discuss)

RESPONSE: As mentioned above, the bats are certainly recovering during September as they have just returned from migration after a winter-long hibernation.

COMMENT:

Page 54: In our study, during September, the insect numbers....you were just talking about someone else's study

RESPONSE: This has been corrected in the text.

COMMENT:

Page 55 (see earlier comments): low temps are more likely to affect insects rather than the bats directly (which you state in the next para)

RESPONSE: I feel that I address this issue adequately enough. These effects are very difficult to disentangle.

COMMENT:

Page 56, top: order may just not be accurate enough, at least morphotype or some other finer determination might have helped

RESPONSE: I acknowledge that this may have been helpful and will use it to inform future research. The dietary data for *Myotis tricolor* was based on data study done on my study population at the study location. Insect remains from faecal pellets were only identified to order level in this study, and this is why I analysed insect prey availability to this level.

COMMENT:

Page 58: lack of effect of moonlight: was there an effect of moonlight on the insects? This may be hard to say because you used light traps, but if there was no effect of moonlight on insects...

RESPONSE: I did not analyse the effect of moonlight on the insect availability.

COMMENT:

2nd para: ...since foraging duration is not limited within a night...except by insect availability

RESPONSE: As stated in the text, insect availability did not appear to be limiting as insect abundance had no effect on any activity patterns parameters.

COMMENT:

Page 62: ...indicating the females may also use fat storage... and further down...prey abundances may not be limiting...this is contradictory

RESPONSE: This is not necessarily contradictory because the time available for foraging may be limited during lactation as the lactating females may need to spend time nursing and grooming the young.

**Supervisor:** Assoc. Prof. David Jacobs:

Signed \_\_\_\_\_

Date: \_\_\_\_\_

**HOD:** Assoc. Prof. John Hoffman:

Signed \_\_\_\_\_

Date: \_\_\_\_\_

University of Cape Town