

# CHAPTER 1

## General Introduction and Aims

In the following literature review I will discuss the relevant physiological and behavioural aspects of the ecology of a small, cavity roosting, insectivorous bird, including metabolic rate, thermoregulation and torpor use, roost selection, diet and home range. Topics will be presented generally followed by a specific discussion of each topic with respect to the Order Caprimulgiformes (nightjars) and the family Aegothelidae (owlet-nightjars).

### Ecological Energetics

A study of the ecological energetics of a species involves the examination of many aspects of its behavioural ecology and physiology, and how they are related to the energetic demands of the animal. An animal's capacity to survive in its natural environment relies on its ability to balance its energy budget, including all sources of energy gain, storage, and loss, in order to maintain physiological processes (Withers, 1992). Energy is supplied to an individual in the form of chemical bond energy from macronutrients such as fats, carbohydrates and protein (energy production). Energy is lost via elimination of faeces and urine, activity, and metabolic energy dissipated to the environment as heat (respiration). Energy loss through elimination is minor compared to losses through activity and metabolic processes. Much of an animal's energy is expended through activities and behaviours necessary to maintain fitness, including locomotion, foraging, breeding, defending territories, reproduction, and raising and defending offspring. Metabolic processes, including digestion, oxidation, respiration, growth, tissue repair, thermoregulation, and excretion of undigested food and metabolic wastes, result in energy being expended as heat or stored as potential energy. The sum of all physical and chemical reactions occurring in an organism over time is widely referred as its metabolic rate (MR).

### Metabolic Rate

The rate of metabolism is a critical part of an animal's physiology and is highly variable. The MR of an animal must match the energetic cost of all of its activities and typically varies with ambient temperature ( $T_a$ ), diet quality, pregnancy, lactation, time of day and year, sex, age, posture and many other factors (Bartholomew, 1982b). Resting metabolic rate (RMR) is generally measured for an individual under the least physiologically demanding conditions during the animal's natural rest phase. The minimum RMR occurs when a fasting animal is at rest in its thermoneutral zone (TNZ), the range of temperatures at which energy metabolism is

lowest as no heat is produced specifically for thermoregulation, and is referred to as its basal metabolic rate (BMR; Bartholomew, 1982b). MRs are highly temperature-dependant and will increase outside of an animal's TNZ. Thus, the microclimate in which an animal spends the majority of its time during its rest phase is relevant for energy conservation. When standardized for body mass, BMRs allow for a comparison of the adaptive efficiencies of animal physiology and energy metabolism amongst species.

The BMR of whole animals increases with body size (Brody, 1945; Scholander et al., 1950). Originally, Brody (1945) determined the relationship between body mass (BM) and BMR for birds:  $BMR \text{ (kcal day}^{-1}\text{)} = 89 \text{ BM (kg)}^{0.64}$ . Later it was concluded that the mass-specific BMR of non-passerine birds was slightly lower than that of passerine birds and separate equations were developed for each group (Lasiewski & Dawson, 1967; Aschoff & Pohl, 1970; Bartholomew, 1982b; McKechnie et al., 2006). More recently, statistical analysis has shown that the difference in mass-specific BMR between passerines and non-passerines was negligible and one equation is now recommended for both groups (Reynolds & Lee, 1996; Rezende et al., 2002). However, McKechnie et al. (2006) reported significant differences in the BM to BMR relationship between captive-raised and wild-caught birds.

Whereas the whole animal BMR of birds increases with size, the mass-specific BMR ( $\text{ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$ ) increases steeply with decreasing size and consequently, energy expenditure per unit mass in small birds is much higher than in large birds. The reason for this relationship is still not fully understood, but may be related to overheating in large species or a greater proportion of inactive tissues in larger than in small species (Schmidt-Nielsen, 1997).

### **Seasonal Variation in Metabolic Rate**

BMRs are not constant and are affected by physical changes of the animal, such as increases in fat stores with seasonal changes in  $T_a$ . In temperate climates, it has been hypothesized that large changes in seasonal  $T_a$  are compensated for by changes in insulation (such as fur and feathers) and fat deposits by birds and mammals. Animals with adequate insulation should be able to maintain a constant body temperature ( $T_b$ ) without increasing MR above BMR (Scholander et al., 1950). However, species differ in their capacity to increase fat stores and insulation during winter, an effect which appears to be correlated with the climate the species inhabits (Dawson & Marsh, 1989; Swanson, 1991; Liknes et al., 2002). There are also small-body-size constraints associated with carrying extra mass, and constraints imposed by requirements for flight (Scholander et al., 1950). Physiological adjustments to BMR may be

required to cope with low  $T_{as}$  for some species. Yet there is still considerable controversy about whether the BMR of birds should be higher in winter to maintain  $T_b$  at low  $T_{as}$  (Weathers & Caccamise, 1978), or lower to reduce energy expenditure for thermoregulation (King, 1974). Masman et al. (1986) discussed two alternative hypothesis concerning seasonal energy patterns in birds. The ‘increased demand hypothesis’ suggests that reproduction results in a substantial increase in adult energy demand leading to an increase in BMR during the breeding season. (Note however, BMR is generally measured in non-reproductive individuals). The ‘reallocation hypothesis’ proposes that abundant food and moderate temperatures during the breeding season offset the energy costs associated with breeding, resulting in little seasonal variation in BMR.

Seasonal measurements of BMR in the laboratory support the fact that species use different strategies for coping with low winter  $T_{as}$ . Maddocks & Geiser (2000) found that for a small Australian passerine, the Australian silver-eye (*Zosterops lateralis*), the mass-specific BMR of winter-acclimatized birds was 20% lower than that of summer-acclimatized birds. Below the TNZ, the difference in RMR and mass-specific thermal conductance between winter and summer birds progressively increased with decreasing  $T_a$ . Body mass did not differ between summer and winter, suggesting that the ability of winter birds to tolerate low  $T_a$  with a smaller increase in RMR was due more to increased insulating plumage than winter fat stores. Increased plumage would reduce thermal conductance and enable birds to maintain  $T_b$  at a lower energetic costs. However, for resident American goldfinches (*Carduelis tristis*) in South Dakota, USA, winter-acclimatized birds had significantly higher mass-specific BMRs (by 23%) than summer-acclimatized birds (Liknes et al., 2002). Winter birds were also 12% heavier than summer birds and Liknes et al. (2002) suggested that the increased size of the large pectoralis muscle and increased fat stores in Nearctic zone birds during winter provides them with a larger energy reservoir to draw upon during cold exposure. Thus, a higher winter BMR can be accommodated for.

Variation in the severity of winter temperatures may have influenced the results of these studies and the disparity between findings suggests that birds may use dissimilar physiological strategies in different climates and/or regions. Increased insulation may provide adequate protection from cold exposure in the moderate winter climates of Australia (0 to 13°C in Maddocks & Geiser, 2000), but may not be sufficient in the colder temperate climates of northern North America (winter mean = -8.2°C in Liknes et al., 2002). Moreover, different populations of a species distributed over a wide geographic range may differ in the extent of

their seasonal variation in BMR. For example, house finches (*Carpodacus mexicanus*) in California which experience mild winters exhibit little seasonal BMR variation, whereas those in Colorado, where winters are more severe, increase fat deposits as well as BMR (Dawson et al., 1983; Dawson & Marsh, 1989). Thus, birds in temperature regions may need to increase energy reserves and BMR during winter more than their southern counterparts to survive colder conditions.

Studies of seasonal changes in field metabolic rate (FMR) on free-living birds have also produced conflicting results. Some species exhibit substantial differences between winter and breeding season FMR, while others do not. Clearly, energy allocation patterns differ among species. In a review of FMR of free-living birds measured during winter and during various stages of the breeding cycle, Weathers & Sullivan (1993) found that strategies differed between species and even sexes. As suggested by the increased demand hypothesis, three species of birds increased FMR during summer. However, for two species there was no seasonal difference in FMR, in three species there were different strategies between the two sexes, and one species decreased FMR. More recently the very small 6.5 g Verdins (*Auriparus flaviceps*) and 10 g Carolina chickadees (*Poecile carolinensis*) have both been found to have higher energy requirements, and thus higher FMR, during winter (Webster & Weathers, 2000; Doherty et al., 2001). Weathers & Sullivan (1993) proposed that seasonal FMR differences may be due to diet. FMR is expected to increase more during the breeding season in species that feed on difficult to capture prey, such as insectivores and carnivores.

### **Thermoregulation and Torpor Use**

Homeothermic thermoregulation means that the body provides a constant internal environment that optimizes physiological functions (Withers, 1992). However, this type of thermoregulation is energetically expensive, especially for small animals, which lose substantial amounts of endogenously-produced heat because of their large surface area to body mass ratio (Bartholomew, 1982b; Chown & Gaston, 1997; Bartels et al., 1998; Geiser, 1998). The high MR of endothermic animals has favored the evolution of a variety of means to minimize energy expenditure and cope with periods of food shortage (Withers, 1977; Brigham, 1992a; Geiser & Ruf, 1995). For some endotherms, torpor has evolved as a facultative means to lower the thermoregulatory  $T_b$  set point, resulting in a drop in  $T_b$  and MR and reduced activity (Hohtola et al., 1991; Geiser & Ruf, 1995; Wang & Wolowyk, 1988; Schleucher, 2004). Although viewed as a primitive trait in the past, torpor is now recognized as a sophisticated adaptation by some endotherms to local environmental conditions

(Bartholomew, 1982b; Geiser & Ruf, 1995). To survive and reproduce, animals must ultimately balance energy use with energy accumulation. Thus, the ability to employ torpor is a means by which some animals lessen the impacts of food shortages, especially during periods with low  $T_a$ , on a daily and seasonal basis.

Temperate zone endotherms may periodically face energetic constraints due to extreme climatic conditions and ephemeral food supplies. The current literature suggests that torpor is employed during periods of prey shortage due to seasonal drought, even when not accompanied by cold temperatures (Bartels et al., 1998; Dausmann et al., 2005). In birds, torpor appears to be used mainly by insectivorous and nectarivorous species that regularly experience food shortages. Insectivores, especially aerial feeders such as bats, swifts, swallows and nightjars, which rely on activity by their prey, are among those most strongly affected by temperature dependent food availability (Racey & Swift, 1985). Laboratory studies of torpor on hummingbirds (Calder, 1973; Carpenter, 1974; Hainsworth et al., 1977; Hiebert, 1992) and common poorwills (Bartholomew et al., 1957) indicate that one or a combination of food shortage, reduced energy reserves, and cold or drought, can induce torpor. Recent field studies indicate that heterothermic responses may be a routine means of balancing energy requirements in several species, and that energy emergencies are not always necessary for torpor induction (Reinertsen, 1983; Brigham, 1992a; Körtner et al., 2001; Turbill et al., 2003).

Although torpor results in a substantive reduction of energy expenditure, the animal must terminate torpor by rewarming before activity can commence. Arousal is an energetically expensive process, however recent studies have found that a number of heterothermic endotherms may rely on passive rewarming to arouse from bouts of torpor (Lovegrove et al., 1999; Geiser & Drury, 2003; Geiser et al., 2004). Lovegrove et al. (1999) found that exogenous heating from increasing ambient  $T_a$  reduced the cost of arousal from 27-52% of the total energy expenditure during torpor bouts in the marsupial (*Sminthopsis macroura*). Other animals may use solar radiation to warm from torpor through basking. Geiser & Drury (2003) determined that the average arousal cost for *S. macroura* by passively rewarming from torpor using radiant heat was only about 70% of its BMR. At these low metabolic rates any level of torpor would result in a reduction in energy expenditure provided there was access to sufficient external heat. In contrast, the average energy expenditure to actively arouse from torpor was 340% of BMR (Geiser & Drury, 2003). Passive rewarming by basking in the sun has been observed by both free-ranging mammals (*Pseudantechinus macdonnellensis*, Geiser

et al., 2002; *Sminthopsis crassicaudata*, Warnecke et al., 2008) and birds (*Chordeiles acutipennis*, Marshall, 1955; *Podargus strigoides*, Körtner et al., 2001; *P. nuttallii*; Woods, 2002).

## **Roosting**

Since  $T_a$  has such a profound effect on MR, the use of cavity roosts by birds is a key factor in energy conservation. Birds using cavities as roost and nest sites benefit from increased protection from predators, better thermal buffering from temperature extremes, and reduced energy requirements as nest construction is often not necessary (Gibbons & Lindenmayer, 2002). The benefits of roosting in a cavity to avoid predation are clear. Birds in hollows are more difficult to detect, hollows are generally dark and visually orientated predators likely have trouble finding their prey, and cavities higher in trees may discourage non-arboreal predators (Nilsson, 1984; Rendell & Robertson, 1989).

Several studies on both bats and birds have confirmed that roost microclimate is important for roost selection (Walsberg, 1985; Chruszcz & Barclay, 2002; Lausen & Barclay, 2006). During cold conditions, birds may experience significant thermoregulatory stress during their resting phase when daily fasting occurs. For diurnal birds, this rest phase occurs at night, when  $T_a$  is generally lower. Data for three species occupying cavities or domed nests indicate that nocturnal energy consumption is reduced by up to 43% compared to that expected for birds roosting in exposed sites (Walsberg, 1985). For birds roosting in cavities, a major source of energy savings is an increase in  $T_a$  in the cavity due to the retention of metabolically produced heat (White et al., 1975; 1978). Cavity roosts also offer thermal protection during hot weather. Generally, cavities that are deeper, with thicker walls have better thermal insulation and remain warmer on cold days and cooler on hot days (Gibbons & Lindenmayer, 2002).

Worldwide, 257 species of birds have been recorded to nest in hollows, but few roost in hollows year round (Gibbons & Lindenmayer, 2002). In Australia, 94 species use hollows for nesting, but year round cavity users may be limited to just four species, the masked owl (*Tyto novaehollandia*), sooty owl (*Tyto tenebricosa*), white-throated treecreeper (*Cormobates leucophaea*), and Australian owl-nightjar (*Aegotheles cristatus*; Gibbons & Lindenmayer, 2002). Species roosting in hollows should accrue substantial thermoregulatory advantages year round by avoiding extreme  $T_a$ s during their rest phase. Hummingbirds (Trochilidae) experience high energetic costs due to their small size, high rate of activity, and seasonal food

supply, and most species regularly use cavities which provide thermal benefits. Hillstar hummingbirds (*Oreotrochilus estella*) in the high Andes use caves to avoid extreme cold, and the blue-throated (*Lampornis clemenciae*), Hillstar (*Oreotrochilus chimborazo*) and Calliope (*Stellula calliope*) hummingbirds nest in rocks or tree limbs to avoid direct solar radiation (Calder, 1973; Calder & Booser, 1973). Desert birds regularly use the burrows of other species to avoid extreme heat. Williams et al. (1999) found that Hoopoe Larks (*Alaemon alaudipes*) in the Arabian Desert can potentially reduce water loss by up to 81% by sheltering in lizard burrows during the hottest part of the day.

### **Territoriality and Home Range**

Whereas the type of roost will affect the energy expenditure of birds during rest, the use of a known territory will have energy implications during the active phase. Territoriality is defined as the establishment of an area by an animal or animals from which other individuals are partially or totally excluded (Howard, 1920; Begon et al., 1996). To be considered territorial, a species must defend a physical space from other animals for at least part of its annual cycle. Animals may defend territories to protect food resources or breeding sites. The defense of any area requires the expenditure of time and energy in aggressive or display behaviour, thus, in order to justify defending a territory, survival and/or reproductive success must be enhanced (Orlans, 1971). Furthermore, the increased risk of predation due to more frequent vocalizations and conspicuous behaviour often associated with territorial behaviour increases the costs of territoriality. Thus, territoriality is only advantageous when there is a limited supply of potentially exhaustible resources, such as food or safe roost/nest sites. In this case, it is advantageous for individuals to confine activities to a more or less permanent area because the best foraging sites and refuges become familiar. Territorial behaviour can be flexible, reflecting the balance between cost and benefits. For example, great tits (Paridae) abandon defense of their winter territories on cold days to save essential energy (Hinde, 1956).

Territoriality is more common in species whose prey are distributed uniformly, as a patchily distributed food supply is usually not defensible (Brown, 1964; Orlans, 1971). Resources that rapidly change invite opportunistic use, not site specific commitment. Thus, when food availability is patchy or shifts frequently (e.g. fruit) territoriality should not be exhibited. There is also a strong correlation between territory size, body mass, and diet in species of birds (Schoener, 1968). Predators tend to have larger territories than omnivores or herbivores of the same size, and territory or home range size increases more rapidly with body mass for predators (Schoener, 1968). Nonetheless, territory size should be correlated with food

availability in different habitats (Orians, 1971). Thus, species will defend larger territories where food resources are lower (Cody, 1985). Territory size can increase with decreasing food supplies only to a limited degree, beyond which a habitat should become unacceptable to the bird (Cody, 1985). Low food densities are not worth defending. Territory size will also depend on the density of competitors for the available space, and may decrease when intraspecific densities are high (Hixon, 1980).

An area that an animal occupies, but does not defend is known as its home range (Alcock, 1993). Many territorial species defend space for only part of the annual cycle, typically the breeding season, becoming non-territorial occupants of a home range for most of the year. Another strategy is to defend a core area, but use a much larger area for foraging. For example, many species of owls defend a territory around a breeding site, but hunt over a much wider home range (Martin, 1990). Not surprisingly, food based territories are typically much larger than breeding territories (Alcock, 1993). When resources, such as roosts/dens or food supply, are abundant, no territoriality may occur (Gibbons & Lindenmayer, 2002).

### **The Order Caprimulgiformes**

Caprimulgiformes are nocturnal, cryptically-coloured, primarily insectivorous birds found in a variety of habitats worldwide. The classification of the birds in this order has changed throughout history and taxonomists have included them in the Order Picariae, with the swifts, hoopoes and hummingbirds, and more recently in the Order Strigiformes with the owls (Holyoak, 2001). Currently, they are recognized as a separate order consisting of 107 species divided into 5 families with distinct morphological and behavioural differences. The family Steatornithidae is represented by a single species, the Oilbird (*Steatornis caripensis*), found in Central and South America. This family/species is unique from the other Caprimulgiformes in that it is fruit-eating, nests in caves, and is one of only two species of bird known to echolocate. The Caprimulgidae, or true nightjars and nighthawks, form the most diverse and widespread group (89 species), with species found on all continents except Antarctica. Birds in this family have small bills and weak feet relative to the other families of Caprimulgiformes and typically roost exposed on open ground during the day. The potoos (Nyctibiidae; 7 species) of Central and South America possess the same weak bill and feet as the Caprimulgidae, and like the Frogmouths (Podargidae) of the Asia-Pacific region, roost diurnally in an upright posture in trees and freeze in position to mimic the surrounding branches if disturbed. Podargidae (12 species) have stronger bills than the other families and are known to occasionally eat small vertebrates. They are the only family of the order known

to build nests. The Aegothelidae, or owl-nightjars (9 species), are unique within the Caprimulgiformes in that they roost in cavities. Aegothelidae are owl-like with large eyes, an ability to rotate their head 270°, and are typically smaller in body size (28 to 79 g) than the other families (32 to 624 g). Aegothelidae occur in Australia (1 species), Papua New Guinea (7 species), and New Caledonia (1 species).

### **Metabolic Rate of Caprimulgiformes**

In comparison to other non-passerine birds, the BMR of Caprimulgiformes is lower than expected based on body size (McNab & Bonaccorso, 1995; Bennett & Harvey, 1987). Bartholomew et al. (1962) predicted the metabolism of a 40 g bird to be 2.5 ml O<sub>2</sub> g<sup>-1</sup> h<sup>-1</sup>, based on Brody's (1945) equation. The BMR of 40 g common poorwills (*Phalaenoptilus nuttallii*) and whip-poor-wills (*Caprimulgus vociferus*), were 70% and 50% lower than this predicted value, respectively (Bartholomew et al., 1962; Lane et al., 2004b), and the BMR of the 88 g spotted nightjar (*Eurostopodus argus*) was 37% lower (Lasiewski & Dawson, 1967; Table 1). Mass-specific BMR of Caprimulgiformes generally decreases with increasing body mass as expected (McNab & Bonaccorso, 1995), but all species of nightjar examined to date have below average BMRs (Table 1).

Bennett & Harvey (1987) suggested that low BMRs are associated with nocturnal activity. In addition to the Caprimulgiformes, nocturnal owls (Strigiformes) and kiwis (Apterygidae), all had metabolic rates significantly lower than expected. Bennett & Harvey (1987) proposed that low BMR may be an adaptation to higher T<sub>a</sub> experienced during daytime when these birds are resting. As diurnal T<sub>a</sub> is typically warmer than nocturnal T<sub>a</sub>, the degree of thermoregulatory stress that nocturnal birds experience during their resting phase may be lower and the energy required to maintain high T<sub>b</sub> reduced compared to diurnal birds. These nocturnal species may also have an added advantage by being active during the colder periods of the night, when the activity of foraging would generate heat and reduce thermoregulatory costs (Webster & Weathers, 1990). During long, cold nights, diurnal birds are dependent on energy stores, and their ability to select nocturnal roost sites that minimize thermoregulatory stress costs becomes more crucial (Walsberg, 1985).

Nightjars have low BMR regardless of the latitude and/or habitat they occupy, from the tropics to the cold northern climates. The BMR of the pauraque (*Nyctidromus albicollis*), a tropical nightjar from Central and South America, was up to 40% less than predicted (Scholander et al., 1950), and the BMR of marbled and Papuan frogmouths (*Podargus*

*ocellatus* and *Podargus papuensis*) from the tropical northern regions of Australia were 60% less than predicted for non-passerine birds of their size (Lasiewski et al., 1970; Bech & Nicol, 1999; Table 1). Poorwills, whip-poor-wills, and common nighthawks (*Chordeiles minor*) from the cooler regions of western North America had BMRs 50 to 70% less than expected for their body size (Bartholomew et al., 1962; Lane et al., 2004b; Lasiewski & Dawson, 1964). A lower-than-normal BMR should be advantageous to an animal coping with both hot and cold temperature extremes (Bartholomew, 1982b). The combination of low BMR and the ability to enter torpor during cold periods (see next section) and cool through panting or gular fluttering (below) during heat stress makes Caprimulgiformes physiologically suited to deal with both environmental extremes of hot and cold.

In a hot environment, a reduced BMR minimizes the production of endogenous heat and reduces the need to lose heat (Bartholomew, 1982b). Caprimulgids tolerate high  $T_a$  ( $>35^\circ\text{C}$ ) without large increases in RMR as they are able to evaporate large quantities of water by gular fluttering. Gular fluttering is the process of fluttering the highly vascularized gular area, including the floor of the mouth and the anterior part of the esophagus, by muscle contraction or by movements of the hyoid apparatus (Bartholomew, 1982a). Gular fluttering has the advantage of requiring very little energy, and thus little heat production, and it does not result in alkalosis. In both poorwills and common nighthawks which employ gular fluttering, the increase in RMR at  $T_a > 35^\circ\text{C}$  was very gradual and never reached high levels (Lasiewski & Dawson, 1964). At temperatures above  $42^\circ\text{C}$  poorwills use gular fluttering to cool, but showed no rate increase even at temperatures above  $47^\circ\text{C}$  (Bartholomew et al., 1962). Poorwills can achieve an evaporative water loss to heat produced (EWL/HP) ratio of 3.5 with gular fluttering (Bartholomew, 1982a). Common nighthawks employ gular fluttering at  $T_a > 41^\circ\text{C}$  (Lasiewski & Dawson, 1964). However, frogmouths do not use gular fluttering but pant when exposed to high temperatures. For example, Papuan frogmouths pant to enhance evaporative cooling at  $T_a$ s above  $40^\circ\text{C}$  (Lasiewski et al., 1970). At a  $T_a$  of  $46.8^\circ\text{C}$  Papuan frogmouths showed a level of heat loss solely by panting that had previously only been seen in birds using gular fluttering (EWL/HP = 1.8; Lasiewski et al., 1970). However, panting does require more energy than gular fluttering (Bartholomew, 1982a).

### **Thermoregulation and Torpor Use in Caprimulgiformes**

The ability to enter torpor influences the energetics and behaviour of insectivorous caprimulgids. To date, torpor has been reported in at least one species from three of the five families of Caprimulgiformes including the Caprimulgidae (true nightjars), Podargidae

(frogmouths), and Aegothelidae (owlet-nightjars; reviewed in McKechnie & Lovegrove, 2002) and (Brigham et al., 2006).

The most remarkable and best known example of torpor use in a caprimulgid, or any bird, is by the common poorwill. Poorwills are known to enter prolonged states of inactivity lasting from several days to weeks and drop their  $T_b$  to as low as 4.3 °C (Jaeger, 1948; 1949; Bartholomew et al., 1957; Withers, 1977; Brigham, 1992a; Csada & Brigham, 1994; Woods, 2002). Common poorwills (35-50 g) occur in western North America and outside the nesting season typically enter short bouts of torpor at night for 8-12 h when  $T_a$  falls below 10°C and insect availability is low (Brigham, 1992a; Csada & Brigham, 1994; Woods, 2002; Woods & Brigham, 2004). Some individual poorwills may remain entirely inactive for 10 days or longer, using deep torpor daily, but passively rewarm on sunny days when exposed to solar radiation (Jaeger, 1948; 1949; Woods, 2002). These prolonged periods of inactivity have led to the suggestion that poorwills are capable of hibernation (Marshall, 1955; Jaeger, 1948; 1949; Woods & Brigham, 2004). Poorwills rarely enter torpor during the breeding season (Csada & Brigham, 1994). They have been recorded in torpor while incubating or brooding on only four instances (of 203 bird-nights recorded; Kissner & Brigham, 1993; Woods, 2002). This species has been found torpid in shallow rock crevices (Jaeger, 1948; 1949) and on rock ledges (Bartholomew et al., 1957), but they generally roost and enter torpor on open ground (Thorburg, 1953; Brigham, 1992a; Woods, 2002; Woods & Brigham, 2004). Torpor use by poorwills has been recorded in the field (Brigham, 1992a; Woods, 2002; Woods & Brigham, 2004) and in captivity (Marshall, 1955; Ligon, 1970; Bartholomew et al., 1957; Withers, 1977). The RMR of euthermic poorwills at a  $T_a$  of 20 °C was relatively low (0.72 to 1.9 ml<sup>-1</sup>g<sup>-1</sup>hr<sup>-1</sup>) and during torpor at a  $T_b$  of 4.8 °C oxygen consumption was less than 0.05 ml<sup>-1</sup>g<sup>-1</sup>hr<sup>-1</sup> (Bartholomew et al., 1957; Withers, 1977), a MR that is similar to that found in hibernating mammals (Geiser, 2004). The heart rate of poorwills declined more rapidly than  $T_b$  during entry into torpor (Bartholomew et al., 1962). Although birds regularly used passive rewarming from solar radiation in the wild (Woods, 2002) and when exposed to sun in captivity (Marshall, 1955), they are capable of actively rewarming from low  $T_b$  (7.5 °C) by shivering (Howell & Bartholomew, 1959; Bartholomew et al., 1962).

Occasional torpor use has been recorded for three other species of North American Caprimulgidae. Whip-poor-wills are slightly larger than poorwills (55 g) and occasionally enter torpor at dawn for an average of 6 h, lowering their  $T_b$  to 20 °C (Lane et al., 2004a; Brigham et al., 2006). Common nighthawks (80g) use torpor occasionally either at night or at

dawn, dropping  $T_b$  to 25°C under natural conditions (Fletcher et al., 2004). The torpid metabolic rate (TMR) of a common nighthawk forced into torpor by a reduced diet and severe mass loss was  $<0.2 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$  (BMR =  $1.1 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$ ) even though  $T_a$  was kept at  $\sim 20^\circ\text{C}$  (Lasiewski & Dawson, 1964; Table 1). However, torpor use by common nighthawks is rare and some authors have suggested that these birds are not physiologically adapted to enter torpor to conserve energy (Firman et al., 1993). Finally, one record exists of two lesser nighthawks (*Chordeiles acutipennis*; 50 g) in the southwestern United States entering torpor spontaneously with  $T_b$  falling to 19°C (Marshall, 1955).

Outside of North America, records for torpor use by caprimulgids are relatively sparse. One male European nightjar (*Caprimulgus europaeus*; 80 g) in Finland lowered its  $T_b$  to 19.3°C after 5 days of forced fasting in captivity and a reduction in body mass of  $>20\%$  (Peiponen, 1965). This individual exhibited two torpor bouts per day, the first entry occurring around midnight with arousal at dawn and a second entry at around 9:00 h (Peiponen, 1965). An Australian caprimulgid, the spotted nightjar (90 g), also appears capable of entering torpor. One of two captive individual spotted nightjars entered torpor after losing 12% of its mass (Dawson & Fisher, 1969). This bird lowered its  $T_b$  to 23.7 °C and its metabolic rate during torpor was  $0.40 \text{ ml O}_2 \text{ g}^{-1} \text{ hr}^{-1}$ , or 50% of euthermic values (Dawson & Fisher, 1969; Table 1). Freckled nightjars (*Caprimulgus tristigma*), 81 g African caprimulgids, entered torpor and lowered skin temperatures ( $T_{\text{skin}}$ ) to 12.8 °C, although  $T_{\text{skin}}$  was generally maintained  $>25^\circ\text{C}$  during torpor bouts (McKechnie et al., 2007). Freckled nightjars entered nocturnal torpor shortly after midnight and rewarmed shortly after sunrise.

The only species of Podargidae, and by far the largest bird known to use torpor, is the 500 g Tawny frogmouth (*Podargus strigoides*) found throughout Australia (Körtner et al., 2000; 2001). Tawny frogmouths are 6 to 10 times the size of other caprimulgids, but use torpor in the wild (Körtner et al., 2000; 2001). This species entered torpor when  $T_a$  was  $<9^\circ\text{C}$  and energy costs to undertake foraging were likely greater than the expected food intake (Körtner et al., 2001). Frogmouths commenced torpor bouts either during the night, ending at sunrise, or shortly before sunrise. Nocturnal torpor bouts were usually longer ( $\sim 7 \text{ h}$ ) than daytime bouts ( $\sim 3.5 \text{ h}$ ). The lowest  $T_b$  recorded was 29.1 °C and a  $T_b$  differential of  $>10^\circ\text{C}$  between normothermia and torpor was common.

Another Caprimulgiformes with a wide distribution in Australia is the Australian owlet-nightjar. Free-ranging Australian owlet-nightjars regularly entered torpor in eucalypt

woodlands on the Northern Tablelands of NSW between May and September (Brigham et al., 2000). Morning torpor bouts were the most common (60% of all bouts), but these were often paired with afternoon bouts (33%). Night bouts were rare (7%). The minimum  $T_{\text{skin}}$  during torpor was 19.6 °C, with mean minimum  $T_{\text{skin}}$  27 °C. Bouts varied in length depending on the time of day. Birds remained in torpor longer during dawn bouts (mean = 250 minutes), whereas afternoon bouts were relatively short (mean = 90 minutes). The longest bout duration was 540 minutes.

### **Use of Cavity Roosts by Aegothelidae**

Most true nightjars (Caprimulgidae) roost and nest on the ground and rely on cryptic plumage to avoid detection (Wang & Brigham, 1997; Brigham et al., 2000). Frogmouths (Podargidae) carefully select roosts in trees in which the bark matches plumage coloration, presumably to reduce chances of predation (Körtner & Geiser, 1999). The Aegothelidae is the only family of Caprimulgiformes that roost in cavities (Brigham et al., 1998; 2000). All species of Aegothelidae are thought to roost in cavities; however, little information is available for most species. Observations of feline owlet-nightjars (*Aegotheles insignis*) suggest that birds roost in tree hollows and in vine tangles 5-20 m high (Holyoak, 2001). One adult feline owlet-nightjar was observed at the entrance to a hole in a tree at 5 m height (Gilliard & LeCroy, 1961). Likewise, mountain owlet-nightjars (*A. albertisi*) occur in 'dark tangles of shrubbery and bamboo', and one was flushed from the hollow end of a broken off tree fern (Rand & Gilliard, 1967). Coates (1985) reported that mountain owlet-nightjars roosted in hollows in trees and tree ferns and that barred owlet-nightjars (*A. bennettii*) roost in tree hollows and hollow stumps. Aside from Australian owlet-nightjars, there are no other data on roosts of owlet-nightjars, but it is likely they all use hollows.

Australian owlet-nightjars are obligate cavity roosters and rarely occur in the open during the day. Australian owlet-nightjars are amongst the smallest species of Caprimulgiformes, and thus are likely more susceptible to predation. Predation rates on owlet-nightjars in a eucalypt woodland in eastern Australia were high (Brigham et al., 1999). Thus, the availability and quality of protective cavity roosts is likely important for avoiding predation while in torpor, as torpid birds do not readily respond to disturbance (Carpenter & Hixon, 1988), thus they possess little means for active defense against predators if discovered. Brigham et al. (1998) found that while owlet-nightjars preferred cavities in large trees with multiple hollows, they used hollows closer to the ground than expected by chance. Owlet-nightjars also selected roost trees significantly closer to another tree with a cavity, presumably for predator

avoidance. Owlet-nightjars have occasionally been found roosting in deep crevices in cliffs or banks, the roofs of buildings, termite mounds, fence posts, nest boxes, and abandoned babbler (*Pomatostomus*) nests (Higgins, 1999; Holyoak, 2001), and have been observed basking in the sun at the entrance to roost hollows (Schodde & Mason, 1980). It has been suggested that male/females roost separately, but close together throughout the year (Schodde & Mason, 1980).

### **Nocturnal Insectivores: Caprimulgiformes Foraging Tactics**

Aside from the three species of kiwi (Apterygidae), which rely entirely on scent and tactile cues to find prey on-or-underground, nocturnal insectivores are restricted to three orders of birds: the waders (Charadriiformes), owls (Strigiformes), and nightjars (Caprimulgiformes; Martin, 1990). Nocturnal Charadriiformes, including coursers, stone-curlews, and thick-knees, rarely fly when feeding and typically run across open ground in pursuit of prey using auditory and visual cues to detect them (Martin, 1990). Smaller insectivorous owls typically use ‘perch-and-pounce’ hunting techniques, catching prey with their talons.

Caprimulgiformes use two main hunting techniques: ‘sallying’, where the bird flies from a perch to catch each item of prey singly; and ‘hawking’ where the bird catches successive prey items while in continuous flight (Holyoak, 2001). Jackson (2003c) refers to these as the “perch-and-chase” and “sustained search” methods respectively. Hawking or sustained search is likely more efficient for exploiting insect swarms (Jackson, 2003c). Although these hunting methods are common in diurnal avian insectivores, Caprimulgiformes are the only nocturnal birds to employ these techniques, which require acute nocturnal vision.

Frogmouths, potoos and owlet-nightjars all forage by sallying, and some frogmouths and owlet-nightjars commonly sally to the ground for prey (Holyoak, 2001). Species of caprimulgids either hawk or sally for prey, and some species may use either technique depending on circumstances (Jackson, 2003c). For example, European nightjars sally when prey is scarce in cold weather and hawk when prey is plentiful or in locations with few perches (Holyoak, 2001). Most species of Afrotropical nightjars sally or “perch-and-chase” for food, and some may sally for aerial prey from a perch on the ground (Jackson, 2003b; 2003c). These different feeding methods likely contribute to the success of aerial nocturnal avian insectivores (Holyoak, 2001), for which insectivorous microbats offer the only competition. There are few confirmed records of Caprimulgiformes hunting on foot on the ground, which is not surprising given the short, weak legs and limited mobility of most species. In 722 stomachs collected from seven species of Afrotropical nightjars, only five

contained flightless prey items (Jackson, 2003c), supporting the hypothesis that caprimulgids rarely, if ever, forage on the ground. This may be to avoid predation (Holyoak, 2001).

All Caprimulgiformes possess a large, wide beak and have a unique arrangement of joints, flexible bones, and musculature involving the articulations of the upper and lower mandibles (see Martin, 1990). Thus, a characteristic of all species is the large gape that facilitates capturing prey on the wing. Jackson (2000b) found that the average gape size for Afrotropical nightjars was related to average prey size, with maximum prey size being 11 mm in diameter; however, there was considerable interspecific overlap in mean prey size taken. Prey are generally swallowed live and whole (Jackson, 2003c). Nightjars do not have a crop but do have powerful gizzards to break up food (Jackson, 2003c). Likely to direct insects towards the mouth, most species (including all Aegothelidae) have rictal bristles around the margin of the upper mandible (Jackson, 2003c). A third feature unique to nightjars is the absence of the horny sheath of the palate that is possessed by the majority of bird species. In the Caprimulgidae, the horny palate is replaced by a highly vascular membrane. Cowles (1967) suggested that this structure enables the bird to react quickly to prey striking the palate while in flight. Frogmouths and owlet-nightjars do not have this membrane, which supports the idea that they rely on ‘perch-and-pounce’ hunting techniques and potentially ground foraging.

Most Caprimulgiformes rely on visual acuity to detect prey. The eyes of all nightjars possess a large proportion of rods to enhance night vision and at least some of the caprimulgids have a tapetum lucidum in the retina (Rojas et al., 2004). The function of the highly reflective tapetum is to increase the chance that light will be intercepted by the photoreceptors, which increases the sensitivity of the eye. The location of the tapetum behind the photoreceptors roughly doubles the chance that light entering the eye will be detected (Martin, 1990). It is unknown whether frogmouths and owlet-nightjars possess a tapetum, but the lack of “eye shine” in owlet-nightjars implies they do not. The brain and Wulst morphology of frogmouths and owlet-nightjars is identical to that of owls (Iwaniuk & Wylie, 2006). The Wulst is an area of the brain homologous to the mammalian primary visual cortex. The hypertrophied visual Wulst of owls allows for excellent binocular vision (stereopsis). Thus, stereopsis is presumed to occur in both frogmouths and owlet-nightjars. In contrast, the potoos (Nyctibiidae) and true nightjars (Caprimulgidae) have smaller brains and Wulst volumes typical of similarly sized birds from other orders (Iwaniuk & Wylie, 2006).

The foraging activity by caprimulgids is likely constrained by visual acuity (Brigham & Barclay, 1995). With the exception of moonlit nights, crepuscular feeding seems to predominate among Caprimulgidae (e.g. poorwills, Brigham, 1992b; common nighthawks, Brigham & Fenton, 1991; Aldridge & Brigham, 1991). Common nighthawks have been observed to make two foraging bouts daily, one at dusk and another at dawn, and actively pursue or 'hawk' insects (Brigham & Fenton, 1991). Afrotropical nightjars feed intensively at dusk followed by a less intensive period of dawn foraging (Jackson, 2003c). Jetz et al. (2003) suggested that foraging occurs principally at dusk and dawn due to both greater prey availability and enhanced visibility. Many species adjust foraging behaviour with lunar condition. Afrotropical nightjars increase twilight foraging activity during new moons, but forage for longer on moonlit nights (Jackson, 2003c; Jetz et al., 2003). Whip-poor-wills and common poorwills, both which are primarily sally foragers, are active throughout the night when the moon is bright (Mills, 1986; Brigham, 1992b). However, common nighthawks, which hawk or forage during flight taking more than one prey item simultaneously, do not increase activity during moonlit periods of the true night (Aldridge & Brigham, 1991; Brigham & Fenton, 1991). Brigham et al. (1999) suggested that sallying may be possible in low light conditions, while hawking requires more light due to limitations on visual detection when both bird and prey are flying. Nonetheless, prey captured using both foraging methods may be restricted to larger insects due to the visual limitations in low light (Bayne & Brigham, 1995; Csada et al., 1992). Many nightjars, including several Afrotropical species, frequent roads at night. The open canopy cover above roadways may enable them to better see and catch flying insects backlit against the sky (Jackson, 2003b) or artificial lights (Jackson, 2003a).

Caprimulgids may be limited to detecting prey >5 mm long. Based on diet information, common poorwills appear to have a detection threshold for aerial insects with minimum body-lengths of 5 mm (Bayne & Brigham, 1995). Likewise, the minimum size of prey eaten by common nighthawks was 5 mm (Brigham & Barclay, 1995). Despite high availability, no chironomids, an abundant insect in the study area, were found in the diet of common nighthawks, suggesting that the birds fast flight speed and lower agility make it impossible to capture small insects (Brigham, 1990; Brigham & Fenton, 1991).

### **Diet of Caprimulgiformes**

Some information on diet has been published for the majority of Caprimulgiformes (Holyoak, 2001). With the exception of the fruit-eating oilbird, all Caprimulgiformes are mainly

insectivorous. The majority seem to preferentially eat beetles (Coleoptera). Detailed reviews on the foraging behaviour (Jackson, 2003c) and diet (Jackson, 2000a) of Afrotropical nightjars show that the principle prey are Coleoptera (85% occurrence), followed by Lepidoptera (35%), Orthoptera (25%) and Hemiptera (16%). Common poorwills were also found to forage preferentially on large Coleoptera (>6.7 mm) and Lepidoptera (Csada et al., 1992; Bayne & Brigham, 1995).

Diet may vary throughout the year and in different habitats. For example, several diet studies on the common nighthawk indicate that variation occurs depending on the location and time of year. In the Okanogan Valley of British Columbia, Canada, the proportions of Hymenoptera, Trichoptera and Coleoptera in the diet of common nighthawks were greater than would be predicted on the basis of prey availability (Brigham, 1990; Brigham & Fenton, 1991). In contrast, in Southern Saskatchewan, Canada, the diet of this species consisted largely of Lepidoptera and Coleoptera, as well as a high proportion of flying Formicidae (Todd et al., 1998). In New Mexico, USA, flying Formicidae were preferred (Caccamise, 1974). This suggests that while common nighthawks and perhaps many species of Caprimulgiformes prefer beetles, they will opportunistically prey on a variety of insects. Caprimulgids appear to select prey based primarily on size rather than type (Todd et al., 1998).

Nightjars rarely forage on vertebrates, although small frogs, toads, mice, bats and small birds have been recorded for tawny (*Podargus strigoides*), Papuan, and marbled frogmouths, chuck-will's-widow (*Caprimulgus carolinensis*), northern potoos (*Nyctibius jamaicensis*), and great potoos (*Nyctibium grandis*; Rose & Eldridge, 1997; Holyoak, 2001). In winter, more than 10% of the ~500 g tawny frogmouth's diet may consist of vertebrates, including frogs, toads, mice and small birds, but it is restricted to <5% during the rest of the year (Rose & Eldridge, 1997). The smaller 120 g chuck-will's-widow consume tree frogs and small birds and the great potoo (500 g) eats small bats (see Holyoak, 2001). Small birds have been found in the stomachs of the marbled and Papuan frogmouths and in the northern potoo (Holyoak, 2001).

### **Aegothelidae Diet and Foraging Behaviour**

All nine species of owlet-nightjars are likely entirely insectivorous (Holyoak, 2001), although only one detailed diet study has been published to date (Schulz, 1988). The diet of the mountain owlet-nightjar at Mt Missim in Papua New Guinea was dominated by Coleoptera,

but also included Lepidoptera, Diptera, Orthoptera, and earthworms (Opisthopora) based on 32 faecal samples and 14 samples from stomach flushing (Schulz, 1988). Unidentified insects, including beetles were recorded in the stomach contents of the feline and Wallace's owlet-nightjar (*A. wallacii*; Holyoak, 2001). There are no data on diet for the other four species of owlet-nightjar in New Guinea or for the critically endangered New Caledonian owlet-nightjar (*A. savesi*).

Limited reports on the contents of stomachs of mostly road-killed Australian owlet-nightjars indicate that the diet is mainly comprised of beetles (Coleoptera) and ants (Hymenoptera; Barnard, 1914; White, 1917; Lea & Gray, 1935; Serventy, 1936; Gray, 1938; Rix, 1943; Webb, 1989; Rose, 1973; Rose, 1997; Jones, 2004). Many stomachs also contained crickets (Orthoptera), moths (Lepidoptera), and spiders (Aranea). Cockroaches (Blattodea), flies (Diptera), millipedes (Diplopoda) and true bugs (Hemiptera) were also present (Serventy, 1936; Webb, 1989; Jones, 2004).

The presence of ground-dwelling invertebrates, such as earthworms, non-flying worker cast ants, and spiders in the diet of both mountain and Australian owlet-nightjars has led to the suggestion that they spend at least part of their time foraging on the ground pecking at food (Schodde & Tideman, 1990; Schulz, 1988). Owlet-nightjar legs are moderately long and strong, making them far more agile on the ground than frogmouths or caprimulgids (Schodde & Mason, 1980). Brigham et al. (1999) light-tagged six Australian owlet-nightjars and reported no instances of birds walking or foraging on the ground, but these observations were made during late summer/ early spring when aerial insects were abundant. Foraging attempts were exclusively sally-type from perches (Brigham et al., 1999). Previously, Schodde & Mason (1980) proposed that when flying insects are most abundant owlet-nightjars hunt by hawking on the wing through open space, and when the insect abundance wanes in winter they employ the 'perch-and-pounce' and sallying methods more. There is no direct evidence to support this theory. In contrast to other species of Caprimulgiformes, Australian owlet-nightjars only forage during true night and not crepuscularly (Brigham et al., 1999) and activity levels decrease on or near full moon nights. Both of these behaviours are likely due to high levels of predation (Brigham et al., 1999).

### **Home Range Size and Territoriality of Caprimulgiformes**

Few home range estimates are available for Caprimulgiformes, and I could only find quantitative data for two species. A study of two unpaired plumed frogmouths (*Podargus*

*ocellatus plumiferus*, 145 g), a subspecies of the marbled frogmouth, estimated that the home range of the male was 10.6 ha and the female 8.1 ha (Smith et al., 1993). A study based on roost locations of the much larger tawny frogmouths (500g) estimated a home range size of 20 ha (Körtner & Geiser, 1999). Based on roosting records, Schodde & Mason (1980) predicted that home range of Australian owlet-nightjars should 'rarely be larger than 80 ha', and Schodde & Tideman (1990) estimated a territory size of 50-100 ha for this species. Blakers et al. (1984) estimated a territory size of 10 ha for Australian owlet-nightjars based on bird density in a eucalypt woodland in Victoria.

It has been suggested that Australian owlet-nightjars are permanently territorial and solitary (Schodde & Mason, 1980); however, no quantitative evidence is available to support this hypothesis (Higgins, 1999). Mountain owlet-nightjars are described as solitary, while Moluccan owlet-nightjars (*A. crinifrons*) have been observed, singly, in pairs and occasionally in groups (Holyoak, 2001). Two to three Moluccan owlet-nightjars were described as often perching near each other and calling loudly (Holyoak, 2001). Territoriality could have significant consequences for energy use by owlet-nightjars, especially if prey is limited. The degree of territoriality may affect prey selection and warrant increased energy conservation during times of adverse conditions.

Amongst the Caprimulgidae, a comparative study of two species with sympatric ranges revealed differences in territoriality (Caccamise, 1974). Lesser nighthawks did not actively patrol a well-defined territory, but roamed over large distances in search of food and water. At local concentrations of food, many individuals congregated with little aggression. When food became especially scarce, lesser nighthawks would congregate near an abundant resource, such as when a swarm of flying-ants was found. In contrast, common nighthawks were strongly territorial, defending territories with flight displays and vocalizations. They spent the major portion of time within territorial boundaries. Since search area could not be increased, common nighthawks compensated for low food resources by using less preferred food resources. This species did not forage in groups when insect swarms occurred. Caccamise (1974) suggested that the disparity in the degree of territoriality between these two species could be accounted for by differences in flight modes and ability of to fly large distances. However, the system seems to largely follow Brown's (1964) principle that species will only defend areas where food distribution is uniform. The patchy food distribution experienced by lesser nighthawks in the lowland deserts evidently precludes territoriality.

## **Aims:**

The Australian owlet-nightjar is an interesting and unusual Australian bird about which little is known, and its biology warrants further investigation. Ecological and physiological adaptations have allowed the Australian owlet-nightjar to exploit a variety of habitats throughout Australia. I will examine the biological qualities that allow this species to survive and thrive in two of these habitats, the hot, arid desert of central Australia and the comparatively cold, mesic, eucalypt woodlands atop the Northern Tablelands of NSW. These habitats should be energetically taxing for a small, nocturnal bird, yet owlet-nightjars are successful and found in abundance at both sites.

**Chapter 2:** The aim of chapter 2 is to assess the importance of cavity roosts for thermoregulation and torpor use by Australian Owlet-nightjars in the semi-arid zone of central Australia. In this region owlet-nightjars use both rock crevices and tree hollows as roosts. If rock crevices and tree cavities differ in thermal buffering capabilities, I expect that thermoregulatory patterns and use of torpor will differ. I predict that rock crevice roosts will be more thermally stable than tree cavities and would remain warmer at night and early in the morning. This would allow individuals returning to rock roosts after foraging to maintain a high  $T_b$  and use torpor less frequently than when in tree roosts.

**Chapter 3:** The purpose of chapter 3 is to examine the ecological factors influencing roost selection by owlet-nightjars in the arid zone of central Australia. Tree and rock roosts used by owlet-nightjars are compared to randomly selected, unoccupied cavities to determine the important ecological parameters of roosts. Roost parameters are divided into those that increase the thermal buffering capability of the roost and those that increase the protective value of the roost from predators. I predict that owlet-nightjars will select roosts based on increased thermal buffering capacity rather than parameters that offer increased protection.

**Chapter 4:** The aim of chapter 4 is to quantify the thermal biology and torpor use by Australian owlet-nightjars in relation to ambient temperature, rainfall, and insect abundance in two different habitats, the arid zone of central Australia and eucalypt woodlands of the Northern Tablelands, NSW. Ecological differences between the two sites should enable me to establish which variables are most relevant in predicting torpor use in free-ranging birds. I predict torpor frequency and duration will be greater in the desert if torpor is strongly influenced by food availability. However,  $T_{as}$  are lower in the eucalypt woodland, thus, if torpor is determined by low  $T_a$ , the frequency and duration should be greater in the eucalypt

woodland. I have also included a third site in the comparison, an irrigated wildlife park 150 km east of the desert site, which is similar in habitat, vegetation, and  $T_a$ . Insect abundance at this site is expected to be high and winter  $T_a$  at this site should be equivalent to the desert site, and therefore higher than the eucalypt woodland. Torpor frequency and depth at this irrigated desert site should be less than at either of the other two sites.

**Chapter 5:** In chapter 5 I will compare the seasonal (summer versus winter) MR of owlet-nightjars exposed to temperature ranging from 0°C to 37°C in the laboratory. I predict that during winter, when owlet-nightjars possess increased plumage insulation, thermal conductance and RMR will be less at low  $T_a$  as the energetic effort required maintaining high  $T_b$  is decreased. Less plumage insulation during summer should result in increased energy expenditure and higher RMR at low  $T_a$ .

**Chapter 6:** The purpose of Chapter 6 is to evaluate the diet of owlet-nightjars by examining faecal samples from birds in two diverse habitats during different seasons and relate it to arthropod availability and foraging tactics. Owlet-nightjars are thought to primarily use sally type aerial foraging; however I predict that when insect abundance is lower during times of drought (arid zone) or cold temperatures (winter), birds will reduce or abandon aerial foraging in favour of ground foraging and will expand their diet to include a wider range of arthropod orders.

**Chapter 7:** The aim of chapter 7 is to compare home range size of owlet-nightjars in the arid zone with individuals in eucalypt woodlands of northern NSW during summer (breeding season) and winter. I predict that home range size will be directly related to insect abundance and season. Home ranges should be larger in the arid zone and during winter on the Northern Tablelands when arthropod abundance is low and the birds require a larger area to obtain adequate prey to meet their energetic needs. Home range size should decrease during summer, as insect abundance is higher and the owlet-nightjars are feeding nestlings, and thus, should be making short frequent foraging runs from the nest hollow. I will use vocalization type and frequency, aggressive behaviours, percentage of home range overlap between neighbouring birds, and the degree of site fidelity between seasons to assess territoriality in owlet-nightjars.

All chapters are presented in the thesis as complete papers, although most will be shortened prior to publication.

**Table 1:** Summary of published data on basal metabolic rates (BMR), torpid metabolic rates (TMR), and body temperatures ( $T_b$ ) of Caprimulgiformes.  $\Delta T_b$  indicates the difference between normothermic  $T_b$  and minimum  $T_b$  during torpor.

Species	Mass (g)	Normothermic $T_b$ ( $^{\circ}\text{C}$ )	Minimum Torpid $T_b$ ( $^{\circ}\text{C}$ )	$\Delta T_b$ ( $^{\circ}\text{C}$ )	BMR ( $\text{ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$ )	TMR ( $\text{ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$ )	References
<b>Camprimulgidae</b>							
Common Poorwill ( <i>Phalaenoptilus nuttallii</i> )	40	39.1	4.3	34.8	0.72-0.80	<0.05	Bartholomew et al, 1957; 1962; Withers, 1977; Brigham, 1992a
Whip-poor-will ( <i>Caprimulgus vociferus</i> )	50		18.5		1.25		Lane 2004a; 2004b
European Nightjar ( <i>Caprimulgus europaeus</i> )	80	37.4	19.3	18.1			Peiponen 1965
Lesser Nighthawk ( <i>Chordeiles acutipennis</i> )	50	39.5	19	23.8			Marshall 1955
Common Nighthawk ( <i>Chordeiles minor</i> )	80	37	25	12	1.1	<0.2	Lasiewski & Dawson 1964
Spotted Nightjar ( <i>Eurostopodus argus</i> )	90	40.5	23.7	16.8	0.83	0.40	Dawson & Fisher 1969
White-throated nightjar ( <i>Eurostopodus mysticalis</i> )	162				0.53		McNab & Bonaccorso 1995
Large-tailed Nightjar ( <i>Caprimulgus macrurus</i> )	70				0.81		McNab & Bonaccorso 1995
Freckled Nightjar ( <i>Caprimulgus tristigma</i> )	80	37	12.8	24.2			McKechnie et al. 2007
Pauraque ( <i>Nyctidromus albicollis</i> )	45				1.5-2.3		Scholander et al. 1950
<b>Podargidae</b>							
Tawny Frogmouth ( <i>Podargus strigoides</i> )	500	36	27.2	8.8	0.38-0.59		Körtner et al, 2001; McNab & Bonaccorso 1995; Bech & Nicol 1999
Marbled Frogmouth ( <i>Podargus ocellatus</i> )	145				0.70		Lasiewski et al. 1970
Papuan Frogmouth ( <i>Podargus papuensis</i> )	315				0.61		McNab & Bonaccorso 1995
<b>Aegothelidae</b>							
Australian Owlet-Nightjar ( <i>Aegotheles cristatus</i> )	50	39	19.6	19.4			Brigham et al. 2000

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## CHAPTER 2

### Roost Type Influences Thermoregulatory Behaviour of Australian Owlet-Nightjars (*Aegotheles cristatus*) in Central Australia

#### Abstract

Owlet-nightjars represent the only family (Aegothelidae) of Caprimulgiformes that roost in cavities, which offer protection and act as thermal buffers against extreme temperature variations, and thus are an interesting group with regard to their thermal energetics. I used radiotelemetry to locate diurnal winter roost sites of Australian owlet-nightjars (*Aegotheles cristatus*) and to measure body ( $T_b$ ) and skin ( $T_{skin}$ ) temperature. I also recorded ambient temperature inside ( $T_{IN}$ ) and outside ( $T_{OUT}$ ) of roosts to determine if roosts differed in thermal qualities. Individual owlet-nightjars used between one and seven different roosts (tracking time: three to ten weeks), selecting either rock crevices (4 birds) or tree hollows (4 birds) as roosts, or switching between the two roost types (7 birds). Rock crevices were warmer and thermally more stable than tree hollows. The range of temperatures inside tree hollows (-4.0 to +37 °C) was generally twice that in rock crevices (+9 to +33 °C). Torpor was influenced by roost selection, with birds roosting in tree hollows using torpor almost twice as often as those in rock crevices. Despite the potential energy savings from torpor use, owlet-nightjars roosted in tree hollows more often (65% bird-days,  $n=398$ ) than rock crevices (35% bird-days,  $n=211$ ). Decreased risk of predation and lower costs of arousal from torpor via passive rewarming are two possible explanations for this preference to roost in tree hollows. Owlet-nightjars reduced  $T_{skin}$  from around 38 °C during activity to as low as 18.6 °C during bouts of torpor, which typically began near dawn and lasted two to three hours.  $T_b$  was reduced from 40.0 °C during activity to 24.8 °C during torpor. Selection of appropriate roost sites may be vital in offering protection from predators while in torpor and in determining the energy expenditure of these small cavity roosting birds.

#### Introduction

Cavity roosts are typically buffered against extremes in ambient temperature ( $T_a$ ) and offer birds and mammals that inhabit them substantial energy savings (Kendeigh, 1961; Walsberg, 1985; 1986; Chruszcz & Barclay, 2002; Lausen & Barclay, 2006). During cold conditions, birds may experience significant thermoregulatory stress during their resting phase when the daily fast occurs. Thus, cavity roosts may be vital for some species in reducing the energy

expended to maintain high body temperatures ( $T_b$ ) during adverse weather or food shortages. For diurnal birds roosting in cavities or domed nests, nocturnal energy consumption may be reduced by up to 43% compared to that expected for birds roosting in exposed sites (Walsberg, 1985). One source of potential energy savings is the retention of metabolically produced heat by a bird within the roost (White et al., 1975; 1978; but see Walsberg, 1986). However, this benefit is greatest for colonial roosting species, such as swifts (Bartholomew et al., 1957) and nuthatches (Knorr, 1957), that use clustering for warmth. For a solitary roosting bird, the relative importance of roost thermal microclimate is enhanced as they must rely solely on roost insulation for a thermal advantage and reduced energetic costs. Cavities that are deeper, with thicker walls, generally have better thermal insulation (Gibbons & Lindenmayer, 2002).

Cavity roosts also offer increased protection from predators, especially for torpid birds as they do not readily respond to disturbance (Carpenter & Hixon, 1988) and thus have no means for active defence against predators if discovered (Bartholomew et al., 1957). Caprimulgiformes are an order of birds known to use torpor regularly (McKechnie & Lovegrove, 2002; Brigham et al., 2006), but of the Caprimulgiformes owlet-nightjars (Aegothelidae) are the only family that roost in cavities (Holyoak, 2001). Their small body size (40-50 g) makes them more susceptible to predation than most other species (Brigham et al., 1999), and appropriate cavity roosts may be crucial for protection.

The use of well-insulated roost cavities has important implications for the use of torpor by birds, and roosts that remain warmer than outside  $T_a$  may aid owlet-nightjars in energy conservation and reduce the requirement for frequent use of deep torpor. Many studies on the ecologically-similar, heterothermic, insectivorous bats that live in cold climates have identified roost thermal microclimate as important in roost selection (Kerth et al., 2001; Sedgeley, 2001; Chruszcz & Barclay, 2002; Turbill et al., 2003; Smith & Racey, 2005; Solick & Barclay, 2006; Lausen & Barclay, 2006). Bats tend to select roosts that are warmer at night and thermally stable, such as deep rock crevices (Lausen & Barclay, 2003), warm buildings (Lausen & Barclay, 2006) or tree cavities with stable microclimates (Sedgeley, 2001; Willis & Brigham, 2007). By roosting in warmer locations, bats lowered their thermoregulatory costs and did not need to enter torpor as often (Lausen & Barclay, 2006). However, Turbill et al. (2003) found that Australian long-eared bats (*Nyctophilus geoffroyi*) preferred poorly insulated roosts that allowed for passive rewarming during summer. Passive rewarming can

reduce arousal costs by up to 85% in small mammals (Geiser et al., 2004). Lovegrove et al. (1999) suggested that nocturnal animals should be specific in their choice of refugia as the thermal buffering capacity of refugia would have a significant impact on ability to passively rewarm.

Australian owlet-nightjars (*Aegotheles cristatus*) are one of Australia's most widespread birds and are common across a variety of habitats (Schodde & Mason, 1980). Despite this, relatively little is known about their behaviour, physiology and ecology. Australian owlet-nightjars are small, insectivorous birds that would be greatly affected by decreased insect abundance and activity during cold periods, and likely experience significant energetic challenges during adverse conditions (Racey & Swift, 1985; Brigham et al., 2000; Woods, 2002; Lane et al., 2004). Brigham et al. (2000) studied a population of owlet-nightjars on the temperate Northern Tablelands of NSW and found they frequently employed daily torpor during winter, and that they are obligate cavity roosters, typically occupying large trees with multiple hollows (Brigham et al., 1998). However, essentially nothing is known of the behaviour and ecophysiology of Australian owlet-nightjars in the arid zone of central Australia.

The desert region of central Australia is a harsh environment characterised by unpredictable rainfall, variable arthropod availability and large daily fluctuations in  $T_a$  during winter ( $-5^{\circ}\text{C}$  to  $+30^{\circ}\text{C}$ ). I found that owlet-nightjars in central Australia regularly roosted in both rock crevices and tree hollows. No field studies have been conducted on the thermoregulatory behaviour of arid zone birds that use rock crevices as thermal refugia from cold, or on birds that actively switch between using rock crevices and tree hollows as roosts. If rock crevices and tree cavities differ in thermal buffering capabilities, it is expected that thermoregulatory patterns and use of torpor will differ for birds using the two roost types. I predict that rock crevice roosts are more thermally stable than tree cavities and will remain warmer at night and early in the morning. Thus, individuals returning to rock crevice roosts after nocturnal foraging should be able to maintain a high  $T_b$  and use torpor less frequently than those roosting in tree roosts.

## Methods

### *Study Sites*

This study was conducted between early May and mid-October in 2004 and 2005 at two field sites in the MacDonnell Ranges bioregion arid zone of central Australia, west of Alice Springs, Northern Territory. Ormiston Gorge (23°37'S, 132°43'E) is located in the West MacDonnell Ranges National Park at the junction of the Chewings and Heavitree Ranges, about 150 km west of Alice Springs. Geologically, the Ormiston Gorge area and associated ranges is complex, but mainly consists of metamorphic quartzite rock (van Oosterzee, 1995). Vegetation associations in the vicinity of Ormiston Gorge include eucalypt woodland dominated by river red gums (*Eucalyptus camaldulensis*) growing in and beside sandy river channels, mulga (*Acacia aneura*) tall open shrubland and hummock grassland. Mulga shrubland occurs on the foothills and lower slopes of the ranges, and consists of an upper-storey of mulga and other *Acacia sp.* shrubs with a ground-storey dominated by spinifex grasses (*Triodia brizoides*, *T. longiceps*). The upper slopes of the ranges support hummock grassland (*Triodia spp.*) with emergent trees and shrubs including ghost gum (*Eucalyptus papuana*), desert bloodwood (*Eucalyptus gamophylla*), and corkwood (*Hakea suberea*). River channels (Ormiston Creek, George Creek) in the Ormiston study area were typically dry, with a few permanent waterholes. Ormiston Creek has one semi-permanent waterhole at Ormiston Gorge below quartzite cliffs several hundred metres high, which contained water throughout the duration of the study.

Average yearly rainfall at Ormiston Gorge is 333 mm (1972-2004 data from the Ranger Station at Ormiston Gorge), with high variability between years (lowest=74 mm (1994), highest=897 mm (2000), standard deviation=190.5 mm) and a tendency for summer rainfall (January and February). There are marked seasonal  $T_a$  fluctuations with winter lows and summer highs. Mean minimum and maximum  $T_a$  for July 2004-2005 are -1 °C and 29 °C and for January are 10.5 °C and 45 °C. Daily fluctuations are also high with an average daily  $T_a$  range of 16 °C in both summer and winter.

The second study site was at the Alice Springs Desert Park (23°37'S, 132°43'E), 7 km west of Alice Springs, NT. The area of the park is 1300 ha at the base of Mt Gillen on the Heavitree Range. The core area of the park is open to the public and located within a >50 ha enclosure that is fenced to exclude feral mammalian predators. This public area includes three artificially created habitats designated desert rivers, sand country and woodland. An undeveloped area of the park within the predator proof fencing consists of *Acacia sp.*

woodlands which are kept free of non-native vegetation. All habitats in the park are irrigated once a fortnight for 4 hours on a rotating basis so that at least one area of the park is being irrigated each day. Outside of the park fence the habitat consists of *Acacia sp.* trees and shrubs, occasional desert bloodwoods (*E. gamophylla*) and a dense under-storey of invasive buffel grass (*Cenchrus ciliaris*). Average yearly rainfall in Alice Springs is 277 mm (1941-2006, Bureau of Meteorology, Alice Springs Airport), with high variability between years (lowest=82 mm (1965); highest=783 mm (1974)). Mean minimum and maximum  $T_a$  for July from 1941-2006 are 4.0 °C and 19.9 °C and for January are 21.4 °C and 36.4 °C.

### ***Telemetry***

Owlet-nightjars were captured by broadcasting taped owlet-nightjar calls to lure individuals into mist nets. Following capture I determined each bird's body mass and placed an alloy band (Australian Bird and Bat Banding Scheme Project 1418-8; banded in 2005 only) on the right leg. No external characteristics can reliably distinguish the sex of owlet-nightjars. The sex of birds caught in 2005 was determined through DNA analysis using the shaft of feathers pulled from the chest area (Genetic Science Services, Fitzroy, Victoria, Australia). As birds caught in 2004 were not sampled for DNA, results were not analyzed by sex.

Birds were fitted with either external temperature-sensitive radio transmitters (model PD-2T, Holohil Systems, Carp, Ontario, Canada) to measure skin temperature ( $T_{skin}$ ; 13 birds) or kept overnight for surgical implantation of internal temperature-sensitive transmitters (Sirtrack Ltd, Havelock North, New Zealand; 3 birds) to measure core  $T_b$ . The transmitters had been calibrated based on pulse rate against a mercury thermometer to the nearest 0.1 °C to measure temperature from 0 °C to 40 °C in a water bath. Transmitter mass was between 1.8 g and 2.6 g which represented less than 6.5% of bird body mass (mean =  $47.8 \pm 3.9$  g). External transmitters were attached using a back-pack-style harness made from elastic thread (Figure 5.1e in Kenward, 1987). The transmitters were placed underneath the bird's feathers and affixed so that the harness kept the temperature sensor in contact with the bird's skin in the interscapular region to record  $T_{skin}$  (Brigham, 1992; Brigham et al., 2000; McKechnie et al., 2007). Internal transmitters were implanted intraperitoneally under general Forthane (0.5-4% in oxygen) anaesthesia. Following surgery, birds were held for 24 hours before being released at the site of capture. This methodology was approved by the University of New England Animal Ethics Committee.

Birds were tracked to day roosts using 3-element Yagi antennae and Merlin (Custom Electronics, Nokomis, U.S.A.) or Icom (IC\_R10, Icom, Bellevue, WA, U.S.A.) receivers. Remote receiver/data logging stations were set up on high ground and/or by placing antennae in trees to receive the signal from the bird in its roost. The effective range of the transmitter signal was greater for external (up to 1 km) than internal transmitters (~ 200 m) and was greater when birds roosted in tree hollows than in rock crevices. For one bird, with an internal transmitter and roosting in a rock crevice, it was necessary to place a short 20 cm long antenna inside its hollow to receive a signal. When roosts were far apart more than one data logger was used per bird.  $T_{\text{skin}}$  or  $T_{\text{b}}$  was recorded every 10 minutes 24 hours a day when the bird was in range of the receiver. Data were recorded using custom-made data loggers (Körtner & Geiser, 1998) or a Lotek SRX\_400 receiver/logger (Lotek Engineering, Aurora, Ontario) attached to a 3-or 5-element Yagi antennae. Data were downloaded to a laptop computer every 4-5 days. The custom-made data loggers measured the interval between two transmitter pulses and the Lotek recorded an event when it detected four consecutive pulses and provided  $T_{\text{b}}$  or  $T_{\text{skin}}$  based on the calibration curve entered into the system. The data recorded by both types of loggers were equivalent in terms of precision. Pulse rates recorded on loggers were confirmed by collecting data manually several times daily by using a receiver and timing 10 pulse intervals using a stopwatch.  $T_{\text{skin}}$  or  $T_{\text{b}}$  was estimated from pulse intervals using the calibration curve previously determined for each transmitter.

### ***Roost Parameters and Temperature***

Roosts were found by tracking radio-tagged birds to their respective roosts each morning and recording the position using a GPS. Small temperature data loggers (Thermochron iButtons®, Model DS1921,  $\pm 0.5$  °C, Dallas Semiconductor Corp., Dallas, TX, U.S.A, 13 mm diameter) were placed in the roosts to record the internal roost temperature ( $T_{\text{IN}}$ ) each hour. For rock crevice roosts, the iButtons were either placed near the entrance (2004) or tied to a stick and put as far into the roosts as possible (2005). However, these iButtons were probably not placed into the crevice as deeply as the birds could access due to installation constraints such as sharp bends in the orientation of the crevice. Placement of iButtons was always conducted when the birds was either roosting in a different cavity or out foraging at night. To preclude the possibility of the bird's body heat increasing the  $T_{\text{IN}}$ , only days when the bird was in an alternate roost were used in analysis. To further examine  $T_{\text{IN}}$  variation in rock crevices iButtons were placed inside a cave (entrance approximately 1.5 x 1.5 m) at depths of 8.2, 8.9 and 9.2 m.

'Substitute' tree roosts were used to measure the  $T_{IN}$  of tree roosts rather than putting iButtons directly in the bird's roost. Substitute roosts were of the same diameter, with the same opening aspect, and were within 20 m of the actual roost, but were generally lower in the tree (2.8 to 5 m). Specifically designed holders with iButtons attached were tied to a piece of cord and dropped as far into the roost as possible (40 to 180 cm). Again, these depths likely did not always resemble the points within the tree that the birds could travel but were the best possible approximation. The actual tree roosts were not used for  $T_{IN}$  measurements as they were typically too high to reach safely (i.e. >10 m), and the risk of the bird becoming entangled in the iButton cord was too great. To determine how the height difference between real and substitute roosts affected  $T_{IN}$ , a device was created to measure  $T_{IN}$  of hollows of uniform diameter at different heights. A hollow fence post was cut into six segments of uniform length (25 cm) and diameter (inner diam. = 7.0 cm, outer diam. = 11.7 cm). The bottom of each segment was blocked with thick cardboard and an iButton was secured about 3 cm from the bottom. A rope was secured high in a red river gum in a dry creekbed and each segment was secured to the rope at a different height above ground level (0.0, 1.6, 3.1, 5.0, 7.0, and 8.8 m). The device was left in place for 76 days.

Each iButton placed inside a roost cavity to measure  $T_{IN}$  was paired with one placed outside the roost (outside temperature ( $T_{OUT}$ )). For rock crevices this iButton was tied to a bush or tree within several meters of the opening and for tree roosts it was tied to the outside of the roost branch. A 'general' iButton was placed in the shade 1 m above the ground at a central location in each of the two study sites to measure  $T_a$ .

Several ecological parameters were recorded for each roost. For rock roosts I recorded opening diameter, opening aspect, slope of cliff, cliff aspect, and depth of iButton placement. For tree roosts I recorded opening diameter, opening aspect, cavity height, and depth of iButton placement. Details on methods used for these measurements are given in Chapter 3.

### ***Data Analysis***

Mean  $\pm$  SE active  $T_{skin}$  for owlet-nightjars tagged with external transmitters was  $37.9 \pm 0.1$  °C. I followed Brigham et al. (2000) and defined owlet-nightjars as having entered torpor when  $T_{skin}$  fell below 30 °C for birds with external transmitters for 20 minutes or more (also see Reinertsen, 1996). Mean active  $T_b$  of owlet-nightjars with internal transmitters implanted was  $40.0 \pm 0.2$  °C and birds were defined as having entered torpor when  $T_b$  fell below 33 °C for 20 minutes or more. These thresholds exceed the recommended  $T_b$  reduction of >5 °C from

normothermia to define torpor use in birds (Schleucher, 2004). Brigham et al. (2000) compared  $T_{\text{skin}}$  and  $T_{\text{b}}$  of an owlet-nightjar in captivity with both an external and internal transmitter attached and found the difference to be  $3.0 \pm 0.8$  °C. For comparison of minimum  $T_{\text{skin}}$  (MIN  $T_{\text{skin}}$ ) amongst birds by analysis of covariance (ANCOVA), 3 °C was subtracted from the minimum  $T_{\text{b}}$  (MIN  $T_{\text{b}}$ ) of birds with internal transmitters to achieve MIN  $T_{\text{skin}}$ . Days in which  $T_{\text{skin}}$  or  $T_{\text{b}}$  data were missing for more than a 2 hour period during daylight hours (sunrise to sunset) were excluded from analysis. Torpor-days are defined as days in which at least one bout of torpor occurred. ANCOVAs were used to compare MIN  $T_{\text{skin}}$  and duration of torpor bouts using  $T_{\text{a}}$  as a covariant. Differences in torpor frequency of birds for each roost type were determined using two-way contingency tables (Quinn & Keough, 2002). For two birds, which entered torpor in both roost types, the mean MIN  $T_{\text{skin}}$  and bout duration was calculated separately for torpor use in rock crevices and tree hollows.

Microclimate was compared between rock and tree roosts using several measures of temperature: minimum daily (24 h) temperature (MIN  $T_{\text{IN}}$ ), maximum daily (24 h) temperature (MAX  $T_{\text{IN}}$ ), minimum daytime (sunrise to sunset) temperature (DMIN  $T_{\text{IN}}$ ), maximum daytime temperature (DMAX  $T_{\text{IN}}$ ), minimum nighttime (sunset to sunrise) temperature (NMIN  $T_{\text{IN}}$ ), maximum nighttime temperature (NMAX  $T_{\text{IN}}$ ), range of roost temperature (the maximum minus the minimum temperature for a particular day; RANGE  $T_{\text{IN}}$ ), and number of minutes to reach the maximum temperature from sunrise (TIMEMAX). For microclimate analysis of rock crevices only data from 2005 were used as iButtons placed near the entrance to roosts in 2004 tended to reflect outside  $T_{\text{a}}$ . Kruskal-Wallis analyses of variance (ANOVAs) on ranks with a Dunn's post-hoc pair-wise comparison were used to compare particular cavities on the same days. Roost types were compared for each temperature measure using an ANCOVA with the relevant  $T_{\text{a}}$  measure as a covariant. RANGE  $T_{\text{IN}}$  was  $\log_{10}$  transformed to achieve equality of variance between the two roost types. The effects of roost parameters on the  $T_{\text{IN}}$  of roosts were analyzed using multiple linear regressions with forward stepwise elimination for rock and tree roosts separately. The appropriate  $T_{\text{a}}$  was used as a covariate in each model (Lausen & Barclay, 2003). Aspect was converted to sine and cosine radians to allow for analysis as continuous variables for multiple linear regressions (Neubaum et al., 2006). For example, a positive value for hill cosine indicates a northerly direction and a negative hill sine indicates a westerly direction (Figure 1). The percentage contribution of each parameter is based on additive  $R^2$  values. Mean cavity aspects were determined as described by Lehner (1996) for analysis of circular statistics.

Rates of passive re-warming from torpor bouts were calculated from the 25 morning torpor bouts in rock crevices with the lowest MIN  $T_{\text{skin}}/T_{\text{b}}$  and a random selection of 25 morning torpor bouts in tree roosts from the comparable MIN  $T_{\text{skin}}/T_{\text{b}}$  range (21.5 to 28.5 °C). The overall slope of the arousal stage of the torpor bout was calculated from the first point after the MIN  $T_{\text{skin}}/T_{\text{b}}$  to the MAX  $T_{\text{skin}}/T_{\text{b}}$  at the end of the bout.

ANCOVAs and forward stepwise multiple regressions were performed using Minitab Statistical Software (version 13.1). Kruskal-Wallis ANOVAs were performed using SigmaStat (version 2.0). StatistiXL (version 1.6) was used to perform two-way contingency tables. Yates correction factor was used for all  $\chi^2$  tests with 1 degree of freedom (Zar, 1998). Numerical values are presented as means  $\pm$  SE for  $n$  = number of individuals and  $N$  = number of days observations recorded. An alpha value of 0.05 was used for all tests.

## **Results**

### ***Owlet-nightjar Captures***

Sixteen owlet-nightjars were captured and data were collected for 14 individuals. One bird was caught twice in 2004. This bird originally had an internal transmitter and was re-released with an external transmitter and as a result of the difference in transmitter type was analyzed as two separate birds (thus  $n=15$ ). Both sexes of owlet-nightjars are equally likely to be caught using playback (45% female, 55% male,  $n=22$ ,  $\chi^2_{0.05,1}=0.18$ ,  $P=1.00$ ) and both males and females were caught in 2005 (6 birds sexed=3 males, 1 female, 2 undetermined). It is unknown whether some of the birds studied in 2004 were recaptured in 2005, as birds were not banded in 2004. Owlet-nightjars were generally captured in the riverine woodland or mulga shrubland habitats.

### ***Roost Selection***

Telemetry data were recorded for a total of 609 bird-days with a mean of 40 days per bird (range 12 to 72 days). Individual birds used between one and seven different roosts (tracking time: two to ten weeks), with the number of roosts used independent of the time tracked (Chapter 3). Half of the birds used either rock crevices ( $n=4$ ) or tree hollows ( $n=4$ ) exclusively, and the rest used both rock crevice and tree roosts ( $n=7$ ), switching at apparently random intervals (see Chapter 3). With the exception of two birds that used rock and trees roosts equally, the other five birds that used both rock and tree roosts generally preferred one type and spent only a few days in the other.

Tree hollows were used as roosts on 398 days (65%) and rock crevices were used on 211 days (35%). A total of 23 rock crevice roosts and 22 tree hollow roosts were located (see Chapter 3). Tree hollow and rock crevice roosts were available in excess at both sites. Birds at the Desert Park roosted in rock crevices more often (57%) than at the Ormiston (20%). However, as the frequency of torpor use was the same for both sites (Chapter 4), the data for the two sites were combined for these analyses. Details of torpor use comparing sites are discussed elsewhere (Chapter 4). Birds roosted in rock crevices less in 2004 (32%) than in 2005 (42%), however, torpor use in each roost type followed the same pattern each year.

### *Torpor Use*

Owlet-nightjars entered torpor twice as often when roosting in tree hollows than when roosting in rock crevices (Figure 2). Birds entered torpor significantly more often when roosting in tree hollows in 2004 ( $\chi^2_{0.05,1}=12.87$ ,  $n=10$ ,  $N=418$ ,  $P<0.0001$ ) and 2005 ( $\chi^2_{0.05,1}=5.75$ ,  $n=5$ ,  $N=136$ ,  $P<0.05$ ) and in both years combined ( $\chi^2_{0.05,1}=15.47$ ,  $n=15$ ,  $N=554$ ,  $P<0.0001$ ). Data on torpor use for the two years were combined for further analysis of the effects of roost type. Detailed analysis of differences in torpor use between years is discussed elsewhere (Chapter 4). Birds consistently used torpor more when roosting in tree hollows throughout the winter, irrespective of month (Figure 3).

Thirteen of the 15 radio-tagged birds entered torpor at least once for a total of 231 torpor bouts (199 torpor-days), comprising 36% of the 554 bird-days that  $T_{\text{skin}}$  or  $T_{\text{b}}$  was successfully recorded. Birds were radio-tagged from 10 May to 6 October 2004 and 1 June to 5 September 2005. Torpor bouts were recorded between 18 May and 13 September 2004 and 3 June to 16 August 2005. The lowest MIN  $T_{\text{skin}}$  during a torpor bout was 18.6 °C, which occurred at 7:31 h on 11 July 2005 when the MIN  $T_{\text{a}}$  was a relatively warm 7 °C (Figure 4a). The lowest  $T_{\text{b}}$  measured for a bird with an internal transmitter was 24.8 °C. The duration of the longest bout of torpor was 640 min (10.7 h), which occurred at night (started at 19:36 h) on 7 July 2005. This bout occurred only 90 min after sunset by a bird roosting in a tree hollow.

Roost type and MIN  $T_{\text{a}}$  did not significantly affect duration of torpor bouts (ANCOVA: roost type:  $F_{1,228}=0.09$ ,  $P=0.76$ ; MIN  $T_{\text{a}}$ :  $F_{1,228}=1.35$ ,  $P=0.25$ ; Figure 5). MIN  $T_{\text{skin}}$  reached during torpor bouts was related to MIN  $T_{\text{a}}$  (ANCOVA:  $F_{1,230}=4.84$ ,  $P<0.05$ ), but was not influenced by roost type ( $F_{1,230}=0.67$ ,  $P=0.41$ ; Figure 5). However, it is noteworthy that the 12 lowest MIN  $T_{\text{skin}}$  readings during torpor bouts ( $20.1 \pm 0.3$  °C) were all for birds roosting in tree hollows. The lowest MIN  $T_{\text{skin}}$  for a bird roosting in a rock crevice was 21.5 °C. The mean

MIN  $T_{\text{skin}}$  during torpor for each individual was negatively related to the mean duration of torpor bouts ( $F_{1,14}=31.47$ ,  $P<0.001$ ,  $R^2=0.71$ ,  $\text{MIN } T_{\text{skin}}=30.51- 0.02$  (Duration)).

One of the two owlet-nightjars with an internal transmitter roosted in a tree hollow and the other in a rock crevice (Figure 6). The individual roosting in the tree hollow entered torpor more than three times as often (46% of bird-days,  $N=23$ ) as the bird in the rock crevice (14% of bird-days,  $N=9$ ;  $X^2_{0.05,1}=6.98$ ,  $P<0.01$ ). The mean duration of torpor bouts for the bird in the tree hollow ( $173 \pm 15$  min,  $N=24$ ) was greater than the rock crevice roosting bird ( $113 \pm 19$  min,  $N=14$ ;  $t_{36}=2.49$ ,  $P<0.05$ ). The mean minimum  $T_b$  reached during torpor did not differ between the two birds (tree:  $31.2 \pm 0.3$  °C, rock:  $30.2 \pm 0.7$  °C;  $t_{36}=1.47$ ,  $P=0.15$ ).

Typically birds entered torpor once on any given day (single bout = 87%, Figure 4b) for several hours. Occasionally birds entered torpor twice daily (double bout = 12%,  $n=9$ ,  $N=28$ ), entering torpor either at dawn and again in the afternoon, or at night (i.e. 1:00-2:00 h) and at dawn (Figure 4a). One bird executed three torpor bouts in a 24 hour period on two occasions, entering torpor at night, dawn and again in the afternoon, but always arousing and sometimes changing roosts between bouts (Figure 4a, 11 July 05). When based on the number of bird-days that owlet-nightjars used respective cavities, there was no difference in the use of double bouts between the two roost types (tree hollows:  $n=6$ ,  $N=18$ , 4.9% bird-days; rock crevices:  $n=4$ ,  $N=9$ , 4.8% bird-days). However, double torpor bouts in tree hollows usually consisted of a night and a morning bout (59%), whereas in rock crevices they consisted of a morning and afternoon bout (80%). One bird entered torpor in the morning in a tree hollow and again at 23:00 h that night in a rock crevice. The two triple bouts were observed for a bird roosting in a tree hollow.

Torpor was most frequently entered in the morning between 6:00-12:00 h ( $N=182$ , 78.8%,  $7:39 \pm 5$  minutes). Arousals from morning torpor bouts coincided with the time of increasing  $T_a$  ( $10:21 \pm 8$  minutes). Afternoon (12:00-18:00 h; mean start time =  $13:36 \pm 14$  minutes) torpor bouts occurred on 15 occasions and almost always followed a morning torpor bout ( $n=8$ ,  $N=14$ ). Birds entered torpor more often in the afternoon when they were roosting in rock crevices ( $n=3$ ,  $N=8$ , 4.3% of bird-days) than in tree hollows ( $n=5$ ,  $N=7$ ; 2.0% of bird-days). Afternoon (double) torpor bouts occurred on days with lower MIN  $T_a$  ( $2.1 \pm 0.8$  °C,  $N=15$ ), than on days when only morning torpor bouts occurred (MIN  $T_a = 4.8 \pm 0.3$  °C,  $N=151$ ). Five different individuals entered torpor at night (18:00-6:00 h) on a total of 32 occasions (13.9%). Night torpor bouts occurred on days with a mean MIN  $T_a$  of  $3.1 \pm 0.6$  °C.

As four of the five birds that used night torpor typically used only one type of roost (either rock or tree) as a day roost, I assumed they were using that roost type for night torpor. Based on this assumption, birds that roosted in trees entered torpor at night more often ( $n=3$ ,  $N=25$ , 6.8% of bird days) than those that roosted in rock crevices ( $n=2$ ,  $N=7$ , 3.7% of bird-days).

The daily  $\text{MIN } T_{\text{skin}}$  of owlet-nightjars was significantly greater for birds roosting in rock crevices versus tree hollows (ANCOVA:  $F_{1, 543}=17.86$ ,  $P<0.0001$ ) when the daily  $\text{MIN } T_a$  was less than 14 °C ( $F_{1,543}=94.44$ ,  $P<0.0001$ ; Figure 7). At higher daily  $\text{MIN } T_a$  (>14 °C), indicative of high mid-day  $\text{MAX } T_a$  in excess of 35 °C, the  $\text{MIN } T_{\text{skin}}$  was higher for birds roosting in tree hollows ( $\text{MIN } T_{\text{skin}}$  up to 37.9 °C). This illustrates the thermal buffering capabilities of rock crevice roosts, allowing birds to maintain higher  $T_{\text{skin}}$  on cold days and remain cool on hot days (roost type\*  $\text{MIN } T_a$ ,  $F_{1,543}=5.96$ ,  $P<0.05$ ).

Eighty percent of all torpor bouts occurred on days when the  $\text{MIN } T_a$  was below 6.8 °C. However, torpor occurred occasionally even when  $\text{MIN } T_a$  was as high as 14.5 °C. Seven birds used both tree hollows and rock crevices as roosts and the  $\text{MIN } T_a$  on a given day had no effect on their selection of roost type. Birds used tree hollows nearly 3 times as often as rock crevices when  $\text{MIN } T_a$  was <6.8 °C (tree=77.3%; rock=22.7%) or >6.8 °C (tree=78.8%; rock=21.2%;  $\chi^2_{0.05,1}=0.03$ ,  $P=0.87$ ). However, when  $T_a$  was <6.8°C birds roosting in rock crevices were less likely to enter torpor ( $\chi^2_{0.05,1}=9.04$ ,  $P<0.01$ ; Figure 8). When  $\text{MIN } T_a$  was >6.8 °C birds entered torpor less frequently, but there was no statistical difference in torpor use between the two roost types ( $\chi^2_{0.05,1}=0.40$ ,  $P=0.53$ ; Figure 8).

The rewarming rates of owlet-nightjars from torpor bouts varied considerably and showed no relationship to  $\text{MIN } T_{\text{skin}}/T_b$  during torpor or  $\text{MIN } T_a$ . One individual roosting in a rock crevice rewarmed faster than all other owlet-nightjars roosting in rock crevices ( $n=9$ ,  $N=25$ ). This individual was caught in late August and only used torpor twice, rewarming very quickly each time at 0.12 and 0.19 °C  $\text{min}^{-1}$ . ANCOVA models (using either  $\text{MIN } T_a$  or  $\text{MIN } T_{\text{skin}}/T_b$  as covariate) which included data for this individual indicated no significant difference between rewarming rates between birds in rock crevices and tree hollows ( $n=7$ ,  $N=25$ ). However, given that the rewarming rate of this individual was an extreme outlier, ANCOVA models were recalculated with these values excluded. This analysis showed that owlet-nightjars roosting in tree hollows rewarmed faster ( $0.08 \pm 0.009$  °C  $\text{min}^{-1}$ ) than those roosting in rock crevices ( $0.04 \pm 0.005$  °C  $\text{min}^{-1}$ ). There was no relationship between re-warming rates and  $\text{MIN } T_a$  (roost type:  $F_{1,47}=8.34$ ,  $P<0.01$ ;  $\text{MIN } T_a$ :  $F_{1,47}=0.62$ ,  $P=0.43$ ;  $R^2=0.18$ ; Figure 9a)

or MIN  $T_{\text{skin}}/T_b$  (roost type:  $F_{1,47}=8.86$ ,  $P<0.01$ ; MIN  $T_{\text{skin}}/T_b$ :  $F_{1,47}=0.00$ ,  $P=0.95$ ; model  $R^2=0.17$ , Figure 9b).

### ***Cavity Characteristics and Thermal Buffering Capacity***

Rock crevice roosts appeared to have excellent thermal insulation capabilities and consistently maintained higher MIN  $T_{\text{IN}}$  and lower MAX  $T_{\text{IN}}$  than tree roosts (Figure 10a-d; Table 1).  $T_{\text{IN}}$  of 13 rock crevice roosts (2004:  $n=5$ ,  $N=235$ ; 2005:  $n=8$ ,  $N=257$ ), indicated that they were never colder than +9 °C or warmer than +33 °C. In contrast, tree roosts had MIN  $T_{\text{IN}}$  as low as -4 °C and MAX  $T_{\text{IN}}$  up to +37 °C (11 roosts; 2004:  $n=2$ ,  $N=27$ ; 2005:  $n=9$ ,  $N=347$ ). The overall RANGE  $T_{\text{IN}}$  was 24 °C in rock crevices and 41 °C in tree hollows (Figure 11a). Due to the insulating capacity of rock crevices there was a strong interaction between roost type and  $T_a$  for most measures (Table 2; Figures 10 and 11). For MAX  $T_{\text{IN}}$ , rock crevices were consistently warmer than tree roosts below MAX  $T_a$  of 28° C (day) and 25 °C (night), but remained cooler than tree roosts above this threshold (Figure 10b & 10d).

Results comparing  $T_{\text{IN}}$  to  $T_{\text{OUT}}$  indicate that the cliff faces in which the rock crevice roosts were located radiated considerable amounts of heat (Figure 12). MAX  $T_{\text{OUT}}$  reached 51.5 °C with a mean 24 hour MAX  $T_{\text{OUT}}$  of 32.5 °C (Figure 12b). MIN  $T_{\text{OUT}}$ , which occurred in the early morning hours, never went below 0 °C and rarely receded 10 °C (Figure 12a). The warmer conditions outside of the rock roosts are due to solar heat that is absorbed by the dark red rocks and radiated throughout the day and night, and also because of the higher altitude on the ranges where most of these rock roosts were located. During the night, cool air flows into the gullies and dry river channels that run between the ranges and warmer air remains at the higher locations where the birds select roosts in the rock crevices (nocturnal thermal inversion; Arbuthnott & Brigham, 2007). Below MAX  $T_{\text{OUT}}$  of 31 °C the rock crevices were warmer than tree roosts, but above this threshold they remained cooler (Figure 12b, Table 2). As a result of extensive variation between individual rock and tree roosts, I found no clear explanation for the effect of roost type on TIMEMAX (ANCOVA:  $R^2 = 0.02$ , Table 2, Figure 11b).

Thermal characteristics of individual tree roosts differed substantially (e.g. Figure 13a). Kruskal-Wallis ANOVA comparisons between the four tree roosts used by an individual owl-nightjar (ONJ 16), showed that these roosts differed significantly for MIN  $T_{\text{IN}}$  ( $H_3=46.37$ ,  $P<0.001$ ), MAX  $T_{\text{IN}}$  ( $H_3=69.44$ ,  $P<0.001$ ), RANGE  $T_{\text{IN}}$  ( $H_3=89.49$ ,  $P<0.001$ ) and MAXTIME  $T_{\text{IN}}$  ( $H_3=161.56$ ,  $P<0.001$ ). All four roosts were located within 250 m of each

other in the same dry creekbed. ONJ 16 seemed to prefer the thermally moderate roost, spending 46.5% of its days in roost 1. The low MAX  $T_{IN}$  and lag in time to MAX  $T_{IN}$  of roost 1 (Dunn's test:  $P < 0.05$ ), was likely a result of morning shading.

$T_{IN}$  variation between individual rock crevices was less than tree roosts. There was little difference in temperature amplitude between four roosts located within 300 m of each other on the same range (Figure 13b). However, Kruskal-Wallis ANOVA comparisons did show significant differences between roosts for MIN  $T_{IN}$  ( $H_3 = 28.11$ ,  $P < 0.001$ ), MAX  $T_{IN}$  ( $H_3 = 10.98$ ,  $P < 0.05$ ), RANGE  $T_{IN}$  ( $H_3 = 72.60$ ,  $P < 0.001$ ) and MAXTIME  $T_{IN}$  ( $H_3 = 35.57$ ,  $P < 0.001$ ). These roosts were used by two individual owlet-nightjars. ONJ 18 used roost 3 on 60% of bird-days, which was the warmest and most thermally stable as it was located at the top of the Heavitree Range, 209 m above the base of this range. This roost only had an 8.5 °C RANGE  $T_{IN}$  over the 26 days it was measured and the MIN  $T_{IN}$  was never below 20 °C, illustrating the higher temperatures found at the top of the range. ONJ 19 used only one roost during the 22 days it carried a transmitter.

Results of multiple linear regression analysis of  $T_{IN}$  of rock crevices indicated that most of the variation in MIN  $T_{IN}$  (51%) and MAX  $T_{IN}$  (72%) was explained by MIN  $T_a$  and MAX  $T_a$  respectively (Table 3). Deeper crevices on cliffs facing north had higher MIN  $T_{IN}$ . RANGE  $T_a$  (10%), depth (33%), and cliff slope (30%) combined to explain the variation in RANGE  $T_{IN}$ . Deeper rock crevices (> 80 cm) positioned on steep cliffs (> 70°) were more thermally stable (RANGE  $T_{IN}$  = 1.9 to 6.7 °C; Table 3). Roosts on slopes facing west took longer to warm to MAX  $T_{IN}$  than roosts on eastern slopes (TIMEMAX = 591 to 663 minutes).

The MIN  $T_{IN}$  inside crevices was higher at greater depths (ANCOVA using MIN  $T_a$  as a covariant: depth:  $F_{1,484} = 143.14$ ,  $P < 0.0001$ ; MIN  $T_a$ :  $F_{1,484} = 344.96$ ,  $P < 0.0001$ ; depth\*MIN  $T_a$ :  $F_{1,484} = 18.09$ ,  $P < 0.0001$ ; model  $R^2 = 0.60$ ; Figure 14), presumably due to lack of cooling at greater depths during night and times of cold  $T_a$ . Despite the large opening area, the  $T_{IN}$  recorded inside the test cave at 8.2 m differed significantly from  $T_a$  for MIN  $T_{IN}$  (M-W  $U$ -test:  $U = 914.0$ ,  $N_1 = N_2 = 40$ ,  $P < 0.001$ ), MAX  $T_{IN}$  ( $U = 1933.5$ ,  $N_1 = N_2 = 40$ ,  $P < 0.001$ ), RANGE  $T_{IN}$  ( $U = 2340.0$ ,  $N_1 = N_2 = 40$ ,  $P < 0.001$ ), and TIMEMAX  $T_{IN}$  ( $U = 1258.0$ ,  $N_1 = N_2 = 40$ ,  $P < 0.01$ ). The  $T_{IN}$  at 8.2 m depth ranged from +13.0 to 23.5 °C over 42 days during August and early September 2005 with a mean  $T_{IN}$  of 19.9 °C. During this same time period the  $T_a$  ranged from -1.5 to 34.0 °C with a mean of 17.5 °C.

Almost all parameters entered into the multiple linear regression models explained some of the considerable variation seen in  $T_{IN}$  of tree hollows (Figure 13a; Table 4). Most of the variation in MIN  $T_{IN}$  (79%) and MAX  $T_{IN}$  (77%) was explained by  $T_a$  alone. MIN  $T_{IN}$  (3.4 to 19.3 °C) increased with depth ( $89.8 \pm 14.7$  cm), eastern aspect, small cavity openings ( $18.4 \pm 2.8$  cm diameter), and greater height ( $4.2 \pm 0.9$  m). MAX  $T_{IN}$  (14.8 to 30.2 °C) decreased with depth and height, but increased with north-western aspect and larger opening diameters.  $T_a$  had less effect on RANGE  $T_{IN}$  (6.4 to 23.4 °C), which decreased with depth and height, and increased with north-western aspect and increasing opening diameter (Table 4). TIMEMAX  $T_{IN}$  (426 to 832 minutes) increased with cavity depth, height and easterly aspects, but decreased with increasing diameter.

Cavity height explained very little (1% to 7%) of the variation in  $T_{IN}$ . To better assess the affect of height on tree hollow  $T_{IN}$ , I analyzed the  $T_{IN}$  of iButtons in the fence post segment hollows suspended at different heights. A one-way ANOVA analysis using square root transformed values indicated a significant difference of MIN  $T_{IN}$  ( $F_{5,467}=3.0$ ,  $P<0.05$ ) and MAX  $T_{IN}$  ( $F_{5,467}=6.8$ ,  $P<0.001$ ). It was hollows at 0 and 1.56 m that caused this difference (Tukey Test  $P<0.05$ ). The hollow on the creekbed at 0 m had a significantly higher MIN  $T_{IN}$  than the other hollows. This hollow segment was in direct contact with the sand which likely retained some radiant heat at night and had some insulative value. The hollow at 1.56 m had a higher MAX  $T_{IN}$  than other hollows, perhaps due to radiant or reflective heat from the sand during the day. IButtons placed in hollows higher than 1.56 m showed little difference in  $T_{IN}$ . TIMEMAX also differed between hollows (K-W:  $H_5=188.5$ ,  $P<0.001$ ) as hollows less than 1.56 m warmed faster than those higher (Dunn's Test:  $P<0.05$ ). This may explain some of the considerable variation in TIMEMAX between roosts.

**Table 1:** Mean  $\pm$  SE and range of values for each of the thermal measures for rock crevice and tree hollow roosts.  $T_{IN}$  = temperature in cavity,  $T_{OUT}$  = temperature outside cavity,  $T_a$  = general ambient temperature at the site.

Variable	$T_{IN}$ ( $^{\circ}C$ )		$T_{OUT}$ ( $^{\circ}C$ )		$T_a$ ( $^{\circ}C$ )	
	Mean $\pm$ SE	RANGE	Mean $\pm$ SE	RANGE	Mean $\pm$ SE	RANGE
<b>ROCK</b>						
MIN	20.0 $\pm$ 0.9	9.0-26.5	13.0 $\pm$ 0.6	0.0-24.0	8.1 $\pm$ 1.1	-3.4-20.0
MAX	24.0 $\pm$ 0.6	16.0-33.0	33.3 $\pm$ 2.3	18.0-51.5	25.3 $\pm$ 0.8	15.0-35.0
TIMEMAX (minutes)	600.8 $\pm$ 13.4	147-981			518.6 $\pm$ 4.3	356-616
RANGE (amplitude)	4.0 $\pm$ 0.7	0.5-10.5	20.4 $\pm$ 1.9	3.5-35.0	17.2 $\pm$ 0.4	7.0-24.5
<b>TREE</b>						
MIN	13.2 $\pm$ 1.8	-4.0-26.0	10.4 $\pm$ 1.7	-5.0-21.5	10.9 $\pm$ 1.5	-1.5-21.5
MAX	24.9 $\pm$ 1.9	10.5-37.0	31.1 $\pm$ 2.1	13.0-44.5	26.2 $\pm$ 1.7	13.0-39.0
TIMEMAX (minutes)	622.4 $\pm$ 35.7	382-1000			502.1 $\pm$ 8.5	295-621
RANGE (amplitude)	12.6 $\pm$ 1.5	1.5-33.0	20.7 $\pm$ 1.0	2.5-39.0	15.4 $\pm$ 0.2	3.0-23.0

**Table 2:** Results of ANCOVA models describing temperature inside ( $T_{IN}$ ) owl-nightjar roosts. Roost type (rock or tree) was a categorical variable and ambient temperature ( $T_a$ ) was included as a covariant in all ANCOVA models. Model  $R^2$  is given for each model.

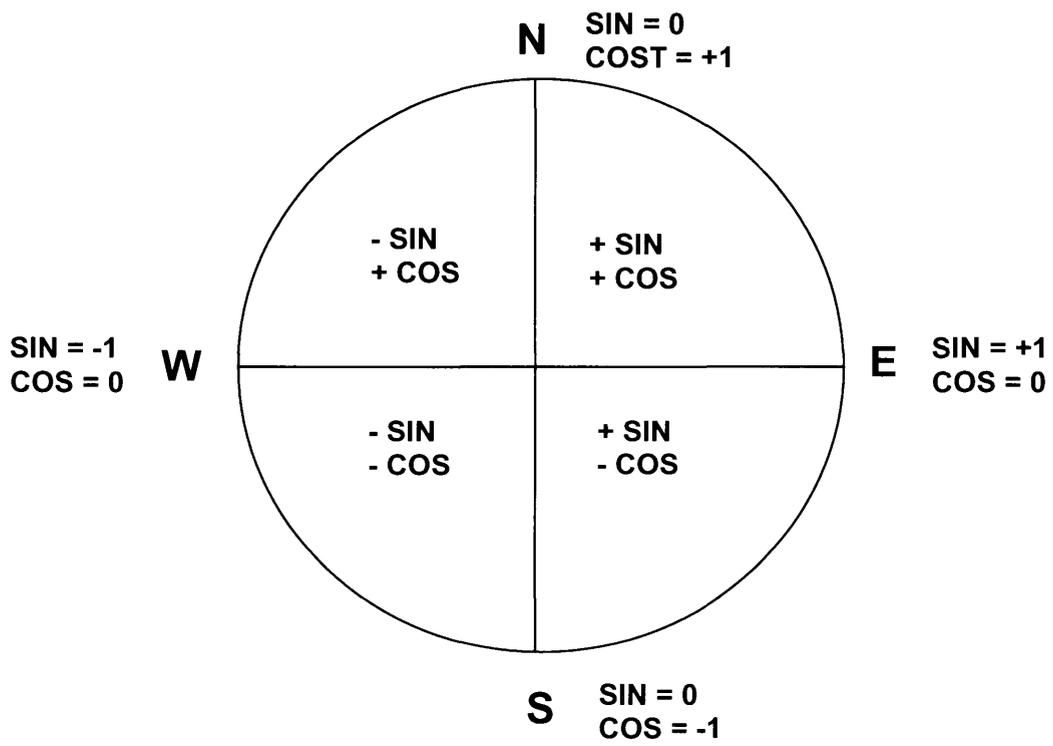
	<b>Source</b>	<b>F</b>	<b>P</b>	<b>R<sup>2</sup></b>
MIN $T_{IN}:T_{OUT}$	Roost Type	$F_{1,625}=357.61$	<0.0001	0.90
	$T_{OUT}$	$F_{1,625}=2107.69$	<0.0001	
	Roost Type* $T_{OUT}$	$F_{1,625}=85.10$	<0.0001	
MAX $T_{IN}:T_{OUT}$	Roost Type	$F_{1,626}=41.58$	<0.0001	0.45
	$T_{OUT}$	$F_{1,626}=263.89$	<0.0001	
	Roost Type* $T_{OUT}$	$F_{1,626}=40.16$	<0.0001	
DMIN $T_{IN}:T_a$	Roost Type	$F_{1,621}=768.42$	<0.0001	0.82
	$T_a$	$F_{1,621}=1045.15$	<0.0001	
	Roost Type* $T_a$	$F_{1,621}=153.17$	<0.0001	
DMAX $T_{IN}:T_a$	Roost Type	$F_{1,621}=144.55$	<0.0001	0.76
	$T_a$	$F_{1,621}=1243.85$	<0.0001	
	Roost Type* $T_a$	$F_{1,621}=121.36$	<0.0001	
NMIN $T_{IN}:T_a$	Roost Type	$F_{1,621}=1167.03$	<0.0001	0.84
	$T_a$	$F_{1,621}=1311.22$	<0.0001	
	Roost Type* $T_a$	$F_{1,621}=235.87$	<0.0001	
NMAX $T_{IN}:T_a$	Roost Type	$F_{1,621}=224.06$	<0.0001	0.83
	$T_a$	$F_{1,621}=1729.78$	<0.0001	
	Roost Type* $T_a$	$F_{1,621}=142.88$	<0.0001	
Log RANGE: $T_{IN}$	Roost Type	$F_{1,597}=5.83$	<0.05	0.53
	$T_a$	$F_{1,597}=100.16$	<0.0001	
	Roost Type* $T_a$	$F_{1,597}=19.42$	<0.0001	
MAXTIME: $T_{IN}$	Roost Type	$F_{1,563}=5.32$	<0.05	0.02
	$T_a$	$F_{1,563}=5.97$	<0.05	

**Table 3:** Results of multiple forward stepwise linear regression analysis on temperatures recorded inside rock roosts. MIN  $T_{IN}$ , MAX  $T_{IN}$ , RANGE  $T_{IN}$  and TIMEMAX  $T_{IN}$  were independent variables. The relevant ambient temperature ( $T_a$ ) and roost parameters (depth of iButton placement (cm), cavity opening aspect (sine and cosine), opening diameter (cm), the slope of the cliff face (degrees) and the aspect of the cliff face (sin and cos)) were included in each regression model. The final regression model and results of the forward stepwise regression are presented.

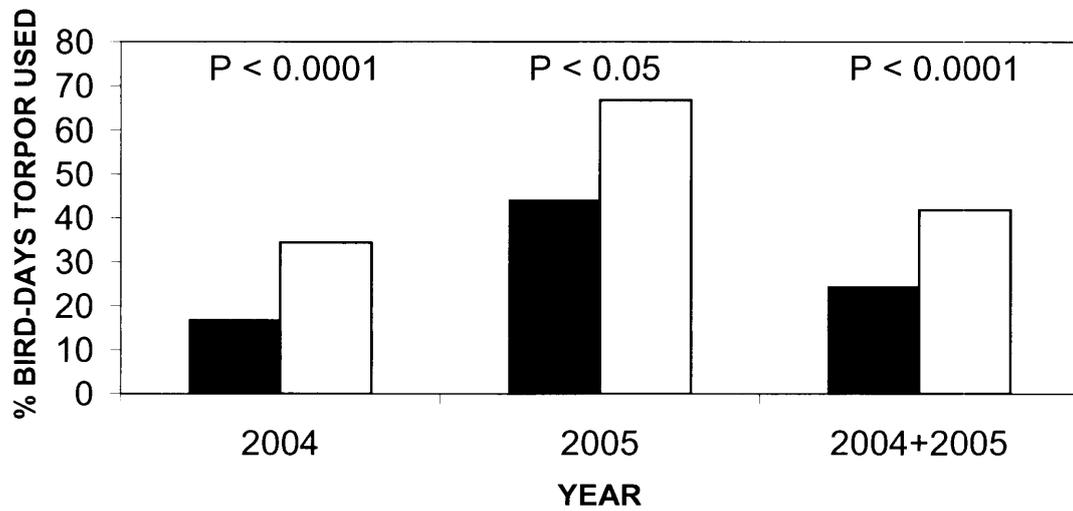
<b>Rock Crevices</b>	<b>Test Statistic</b>	<b>P</b>	<b>Adjusted <math>R^2</math></b>
<b>MIN <math>T_{IN} = 7.24 + 0.49(\text{MIN } T_a) + 0.04(\text{depth}) + 7.38(\text{cliff cos})</math></b>			
Regression	$F_{4,151} = 161.84$	<0.001	0.76
MIN $T_a$	$t = 15.98$	<0.0001	
Depth	$t = 4.28$	<0.0001	
Cliff Cos	$t = 10.38$	<0.0001	
<b>MAX <math>T_{IN} = 9.60 + 0.54(\text{MAX } T_a)</math></b>			
Regression	$F_{1,154} = 399.58$	<0.001	0.72
MAX $T_a$	$t = 19.99$	<0.0001	
<b>RANGE <math>T_{IN} = 13.52 + 0.18(\text{RANGE } T_a) - 0.06(\text{depth}) - 0.12(\text{cliff slope})</math></b>			
Regression	$F_{3,152} = 137.11$	<0.0001	0.72
RANGE $T_a$	$t = 7.67$	<0.0001	
Depth	$t = 13.46$	<0.0001	
Cliff Slope	$t = 14.28$	<0.0001	
<b>TIMEMAX <math>T_{IN} = 544.68 - 86.06(\text{cliff sin})</math></b>			
Regression	$F_{1,143} = 32.52$	<0.0001	0.18
Cliff Sin	$t = 5.70$	<0.0001	

**Table 4:** Results of multiple forward stepwise linear regression analysis on temperatures recorded inside tree hollows. MIN T<sub>IN</sub>, MAX T<sub>IN</sub>, RANGE T<sub>IN</sub> and TIMEMAX T<sub>IN</sub> were dependent variables. The relevant T<sub>a</sub> and roost parameters (depth of iButton placement (cm), cavity opening aspect (sin and cosine), opening diameter (cm), and cavity height (m)) were included in each regression model. The final regression model and results of the stepwise regression are presented.

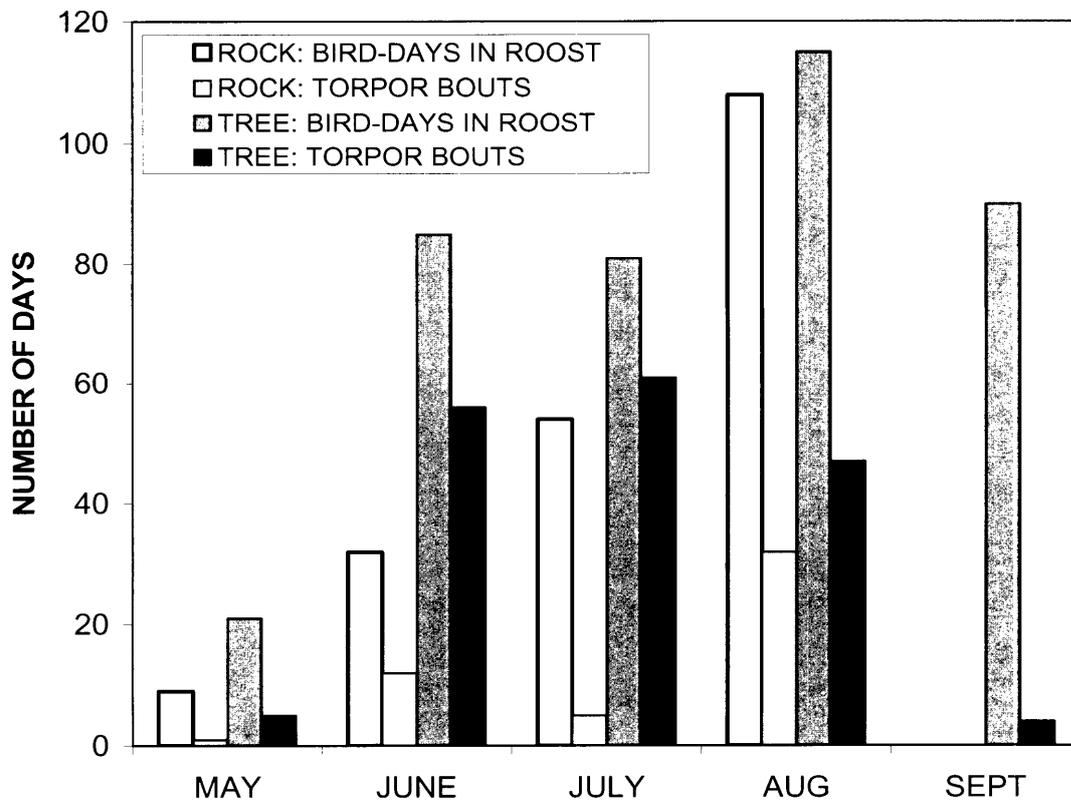
Tree Hollows	Test Statistic	P	Adjusted R <sup>2</sup>
<b>MIN T<sub>IN</sub> = 0.08 + 0.97(MIN T<sub>a</sub>) + 0.04(depth) + 2.12(aspect sin) – 0.13(diameter) + 0.32(height)</b>			
Regression	$F_{5,341} = 406.96$	<0.001	0.85
MIN T <sub>a</sub>	$t = 37.00$	<0.0001	
Depth	$t = 7.93$	<0.0001	
Aspect Sin	$t = 8.58$	<0.0001	
Diameter	$t = 6.13$	<0.0001	
Height	$t = 5.11$	<0.0001	
<b>MAX T<sub>IN</sub> = 7.21 + 0.81(MAX T<sub>a</sub>) – 0.02(depth) – 2.07(aspect sin) + 1.11(aspect cos) + 0.15(diameter) – 0.99(height)</b>			
Regression	$F_{6,340} = 454.00$	<0.001	0.89
MAX T <sub>a</sub>	$t = 32.88$	<0.0001	
Depth	$t = 5.05$	<0.0001	
Aspect Sin	$t = 9.30$	<0.0001	
Aspect Cos	$t = 2.46$	<0.05	
Diameter	$t = 6.74$	<0.0001	
Height	$t = 17.77$	<0.0001	
<b>RANGE T<sub>IN</sub> = 11.67 + 0.69(RANGE T<sub>a</sub>) – 0.08(depth) -1.8(aspect sin) + 7.80(aspect cos) + 0.47(diameter) – 1.41(height)</b>			
Regression	$F_{6,340} = 72.99$	<0.001	0.56
RANGE T <sub>a</sub>	$t = 13.61$	<0.0001	
Depth	$t = 8.66$	<0.0001	
Aspect Sin	$t = 3.71$	<0.0001	
Aspect Cos	$t = 8.57$	<0.0001	
Diameter	$t = 10.02$	<0.0001	
Height	$t = 12.68$	<0.0001	
<b>TIMEMAX T<sub>IN</sub> = 253.15 + 0.46(TIMEMAX T<sub>a</sub>) + 1.99(depth) + 134.29(aspect sin) – 11.09(diameter) + 37.82(height)</b>			
Regression	$F_{5,312} = 63.50$	<0.001	0.50
TIMEMAX T <sub>a</sub>	$t = 4.60$	<0.0001	
Depth	$t = 8.53$	<0.0001	
Aspect Sin	$t = 11.60$	<0.0001	
Diameter	$t = 10.71$	<0.0001	
Height	$t = 13.21$	<0.0001	



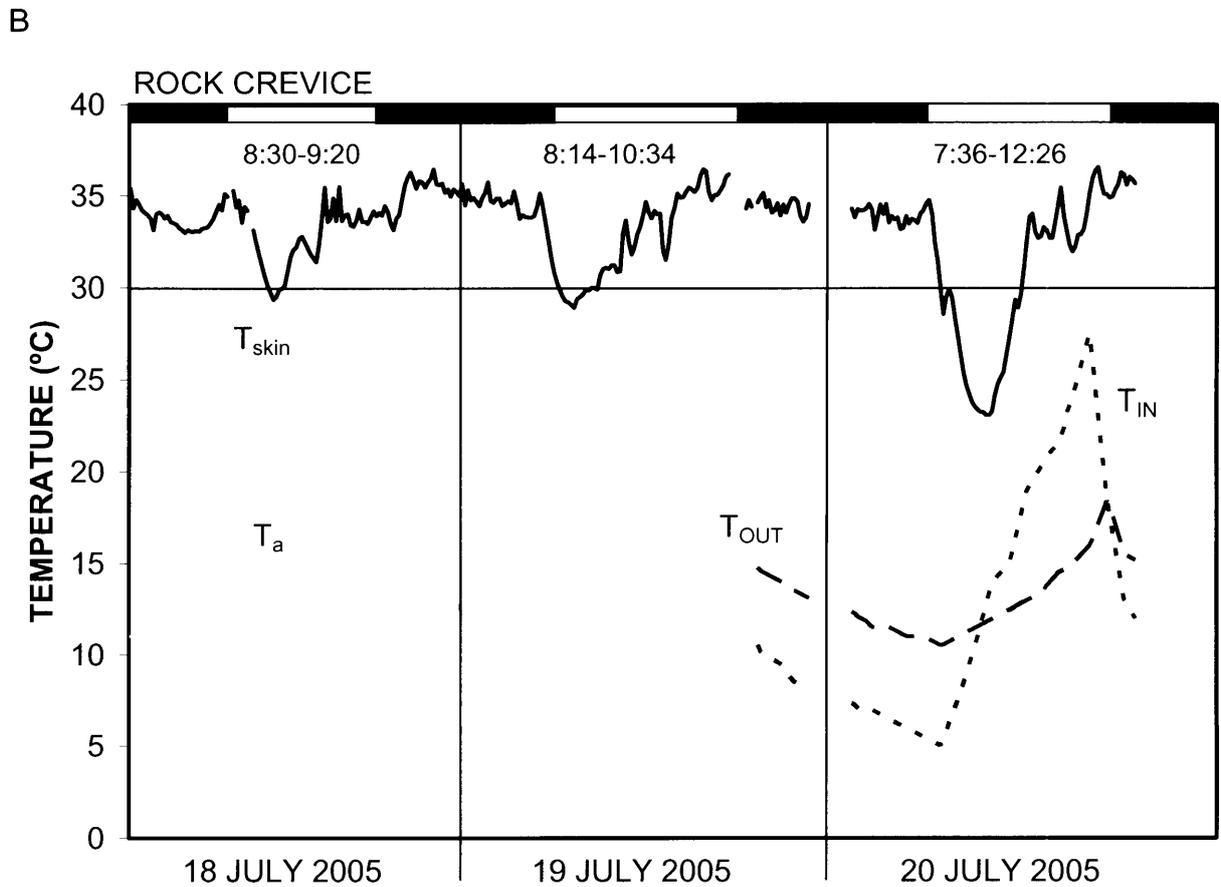
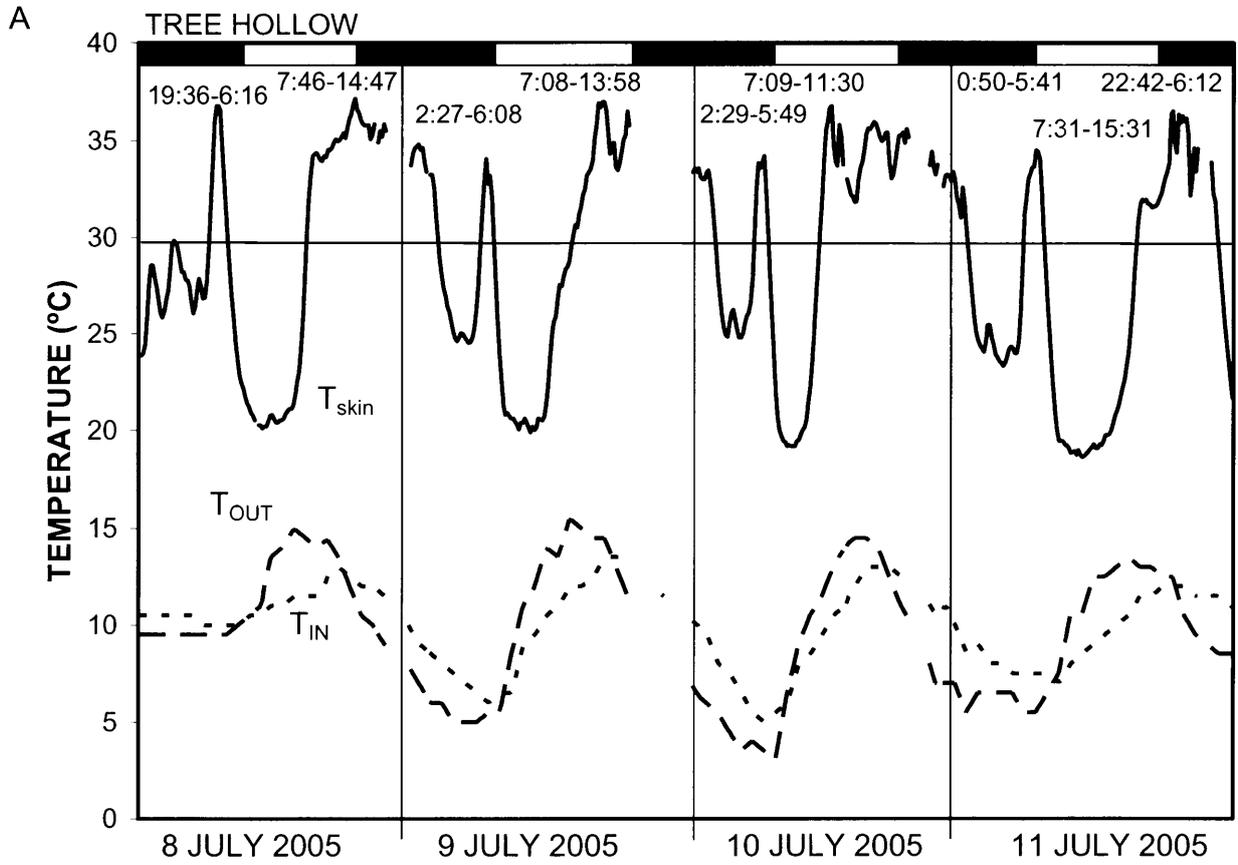
**Figure 1:** Diagram of a unit circle showing positions of sine and cosine values in relation to compass directions. Based on information in Zar (1998).



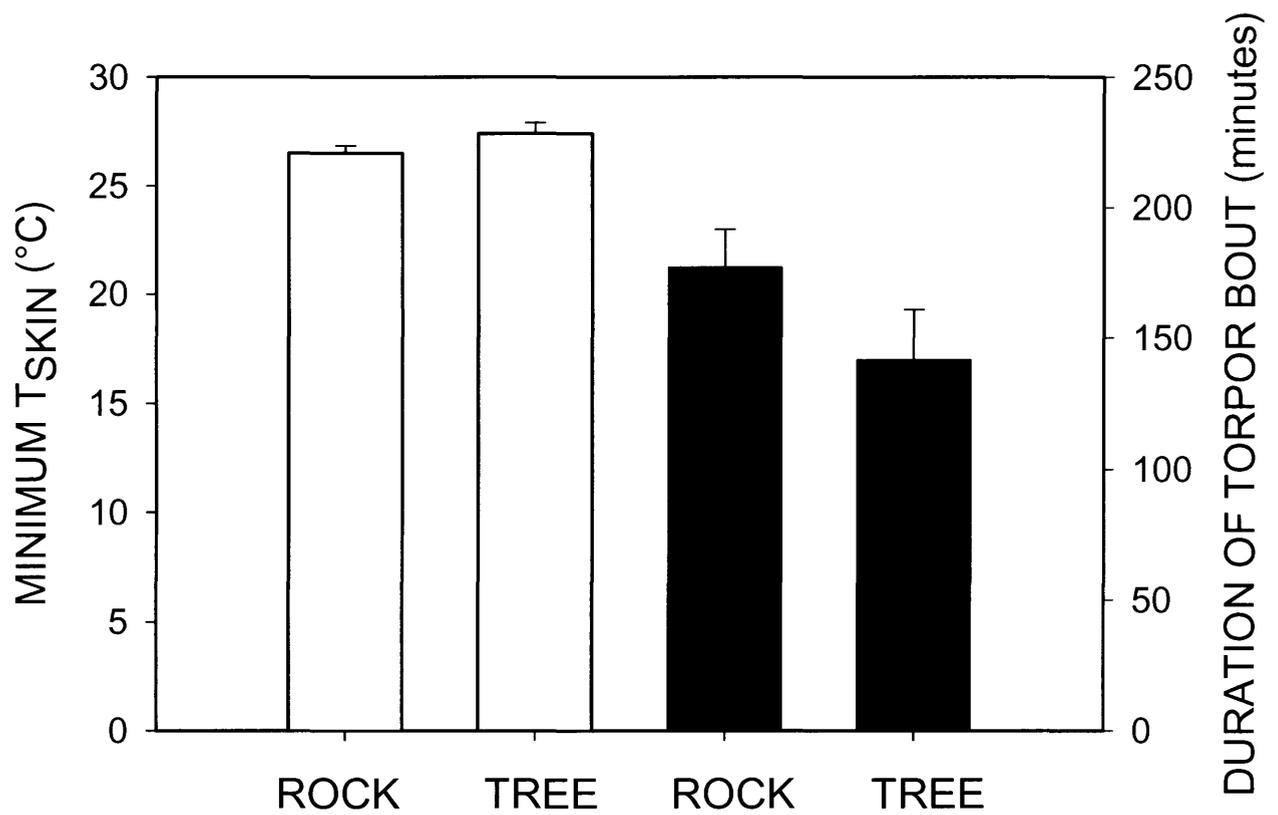
**Figure 2:** Owlet-nightjars entered torpor nearly twice as often when roosting in tree hollows (white bars; 2004+2005:  $n=11$ ,  $N=366$ ) than when in rock crevices (black bars; 2004+2005:  $n=10$ ,  $N=188$ ).  $P$  values are based on chi-square analysis.



**Figure 3:** Owlet-nightjars roosted in both rock crevices and tree hollows throughout the winter months. Torpor use was consistently more frequent in tree hollows compared to rock crevice roosts for each month. Data for 2004 and 2005 combined.

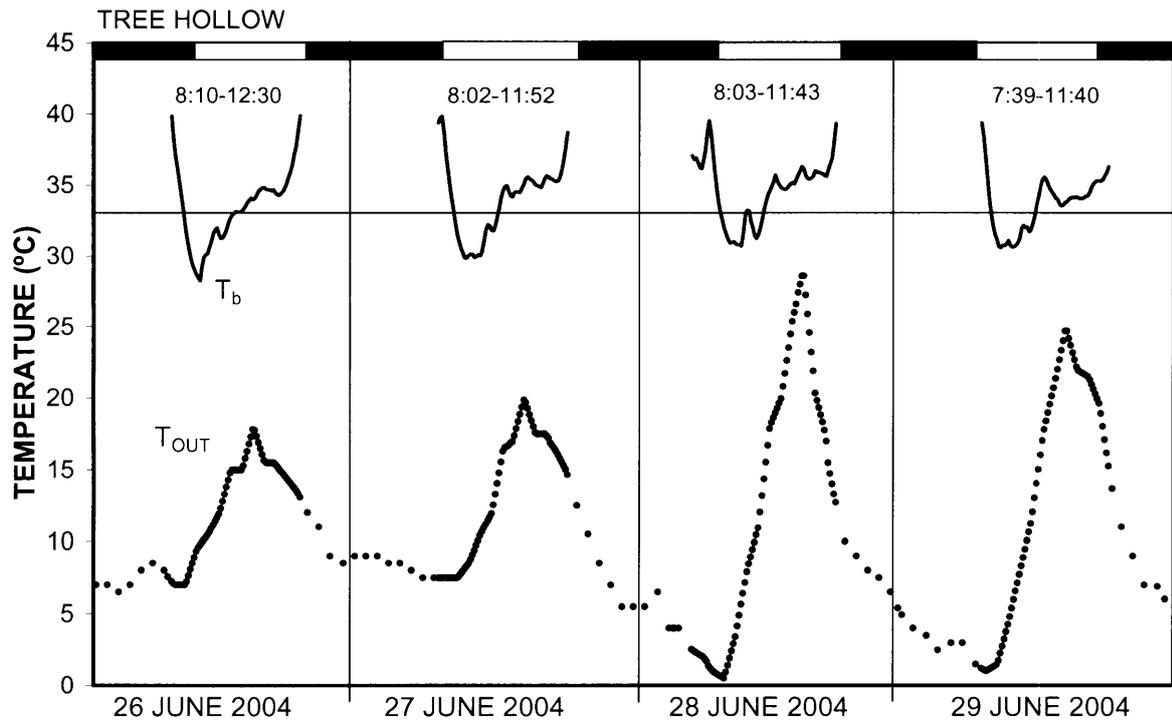


**Figure 4:** Examples of torpor bout patterns of owlet-nightjars using rock crevice and tree hollow roosts. A) Plot of an owlet-nightjar (ONJ 16)  $T_{\text{skin}}$  (solid line) in a tree hollow ( $T_{\text{IN}}$ , dotted line) during 4 days in July 2005. The first three days of the plot illustrate double torpor bouts, with a bout occurring at night followed by another bout at dawn. On 11 July 2005 this bird entered three torpor bouts and the lowest  $T_{\text{skin}}$  (18.6 °C) for an owlet-nightjar was recorded. Temperature inside the roost ( $T_{\text{IN}}$ , dotted line) showed a lag in warming behind ambient temperature outside the roost ( $T_{\text{OUT}}$ , dashed line) and the range in daily  $T_{\text{INS}}$  are less than the daily  $T_{\text{OUT}}$ , illustrating that tree roosts do have some thermal buffering capacity. B) Plot of ONJ 17  $T_{\text{skin}}$  (black solid line) in a rock crevice ( $T_{\text{IN}}$ , dotted line) during 3 days in July 2005. Each day shows a single torpor bout, with  $T_{\text{skin}}$  reaching minimum  $T_{\text{skin}}$  of 23.1 °C on 20 July 2005. Roost temperature data was unavailable for 18-19 July so the general  $T_{\text{a}}$  at the site is given (grey solid line). The high peak in  $T_{\text{OUT}}$  (dashed line) on 20 July 2005 illustrates how the cliff face outside the roost was warmed by the sun in the late afternoon and the inside of the roost heated later in the day. The minimum  $T_{\text{IN}}$  was well above  $T_{\text{a}}$  on the previous night. The cliff face and roost opening faced 279°W. Dark and light bars at the top of each figure represent photophase (day) and scotophase (night).

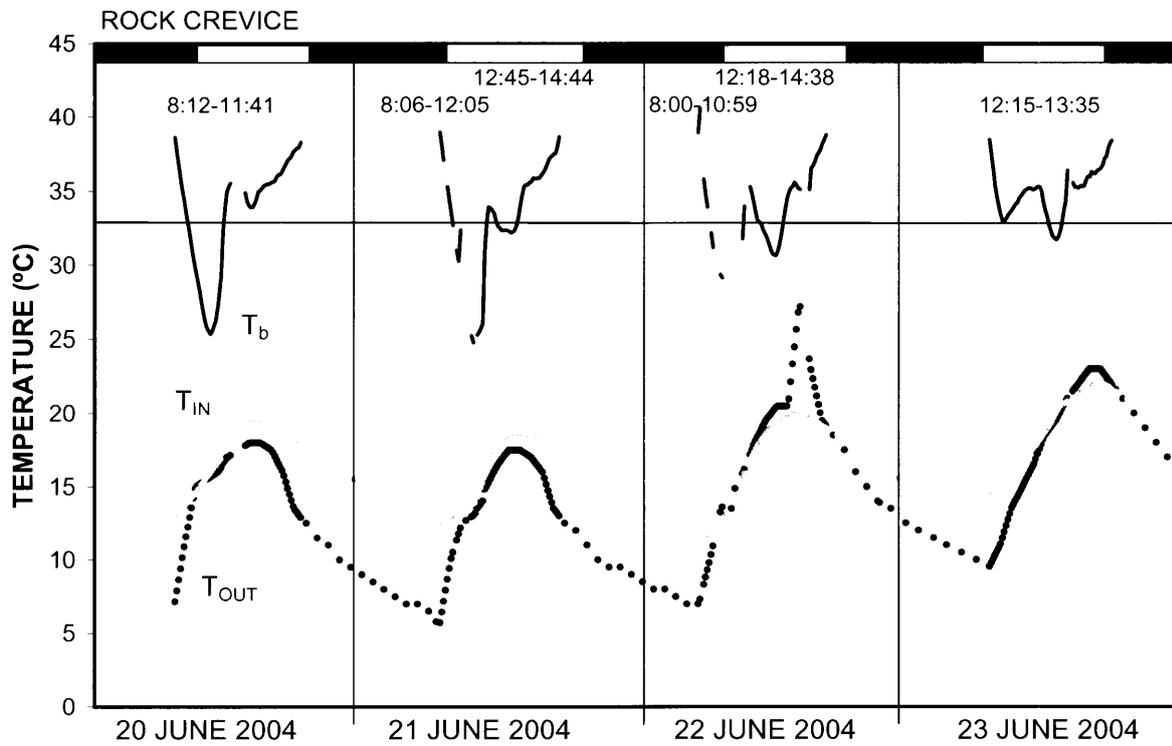


**Figure 5:** The mean  $\pm$  SE torpid MIN T<sub>skin</sub> (°C, white bars) ( $t$ -test;  $t_{13}=-1.26$ ,  $P=0.23$ ) and duration of torpor bouts (minutes, black bars) ( $t$ -test:  $t_{13}=1.34$ ,  $P=0.20$ ) did not differ significantly between birds roosting in rock crevices and tree hollows.

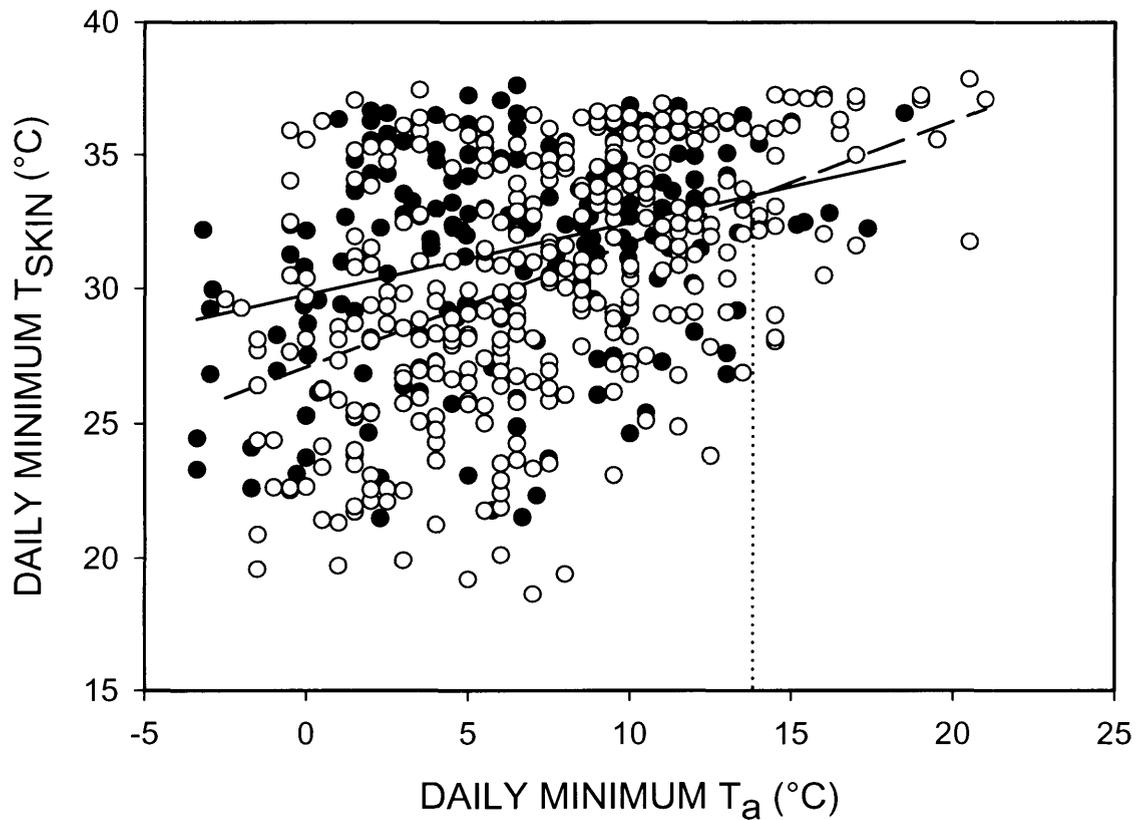
A



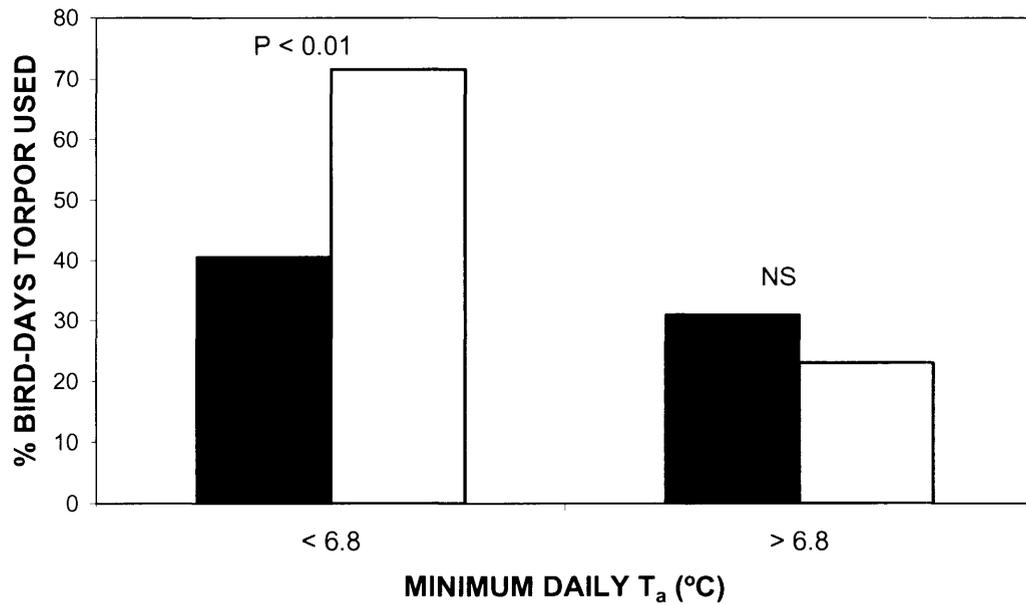
B



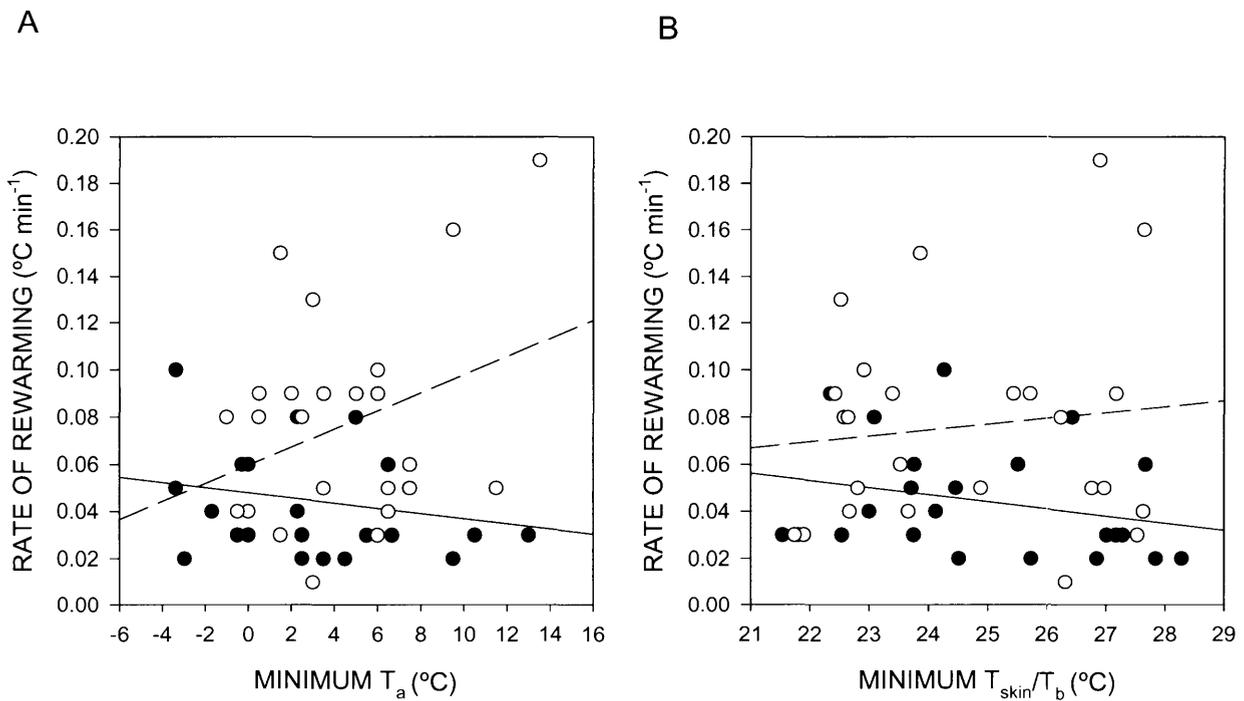
**Figure 6:** Examples of torpor bout patterns of owlet-nightjars with internal transmitters using tree hollow and rock crevice roosts. Both birds entered torpor daily for the periods shown. For birds with internal transmitters, torpor was said to occur when  $T_b$  was below 33°C. A) Plot of an owlet-nightjar (ONJ 4)  $T_b$  (solid line) in a tree hollow compared to the temperature outside the roost ( $T_{OUT}$ , dotted line) during 4 days in June 2004. A single torpor bout occurred each day, with  $T_b$  reaching a minimum of 28.2 on 26 June 2004. The temperature inside this roost was not recorded. B) Plot of ONJ 6  $T_b$  (solid line) in a rock crevice ( $T_{IN}$ , grey dotted line) during 4 days in June 2004. Three days show a single torpor bout, with  $T_b$  reaching minimum  $T_b$  of 24.8 °C on 21 June 2004. A double torpor bout occurred on 22 June 2004. The temperature data logger for  $T_{IN}$  was placed just inside the entrance to the roost, thus the difference between  $T_{IN}$  and  $T_{OUT}$  (black dotted line) is less than for other roosts where the temperature logger was placed deeper. The high peak in  $T_{OUT}$  on 22 June 2004 illustrates how the cliff face outside the roost was warmed by the sun in the late afternoon. Dark and light bars at the top of each figure represent photophase (day) and scotophase (night).



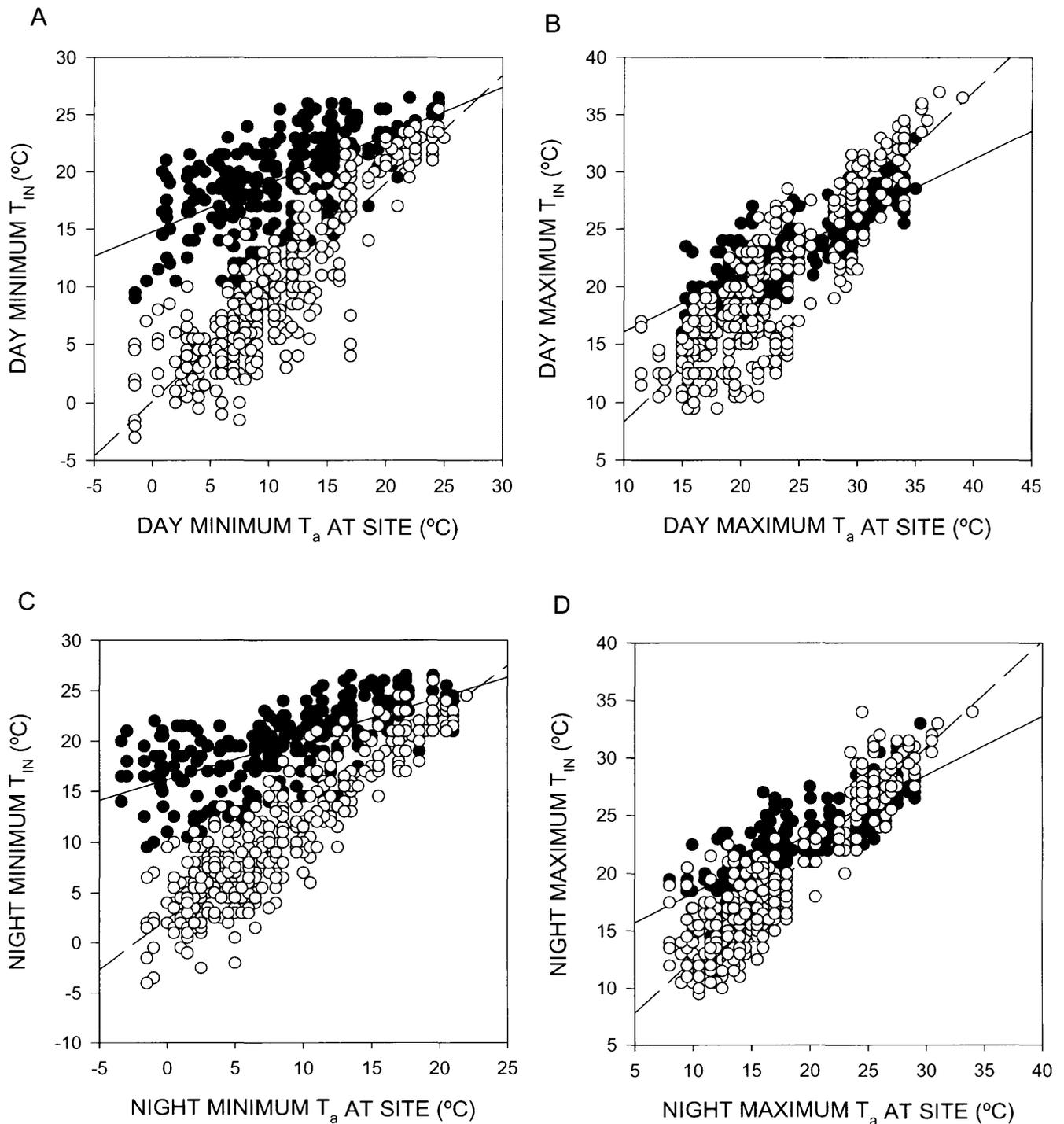
**Figure 7:** Plot of daily minimum ambient temperature (MIN  $T_a$ ) and daily minimum skin temperature (MIN  $T_{skin}$ ) of owlet-nightjars ( $n=15$ ,  $N= 544$ ) roosting in rock crevices (● solid line) and tree hollows (○ dashed line). Linear regression for rock crevice:  $MIN T_{skin}=29.76 + 0.27 (MIN T_a)$ ,  $P<0.001$ , tree hollows:  $MIN T_{skin}=27.09 + 0.46 (MIN T_a)$ ,  $P< 0.001$ . ANCOVA: roost type,  $F_{1, 543}=17.86$ ,  $P<0.0001$ ; MIN  $T_a$ ,  $F_{1,543}=94.44$ ,  $P<0.0001$ ; roost type\* MIN  $T_a$ ,  $F_{1,543}=5.96$ ,  $P<0.05$ , model  $R^2=0.20$ . At  $T_a<14$  °C (dotted line) owlet-nightjars roosting in rock crevices had higher  $T_{skin}$  than birds in tree hollows, but at  $T_a> 14$  °C  $T_{skin}$  was lower for individuals in rock crevices.



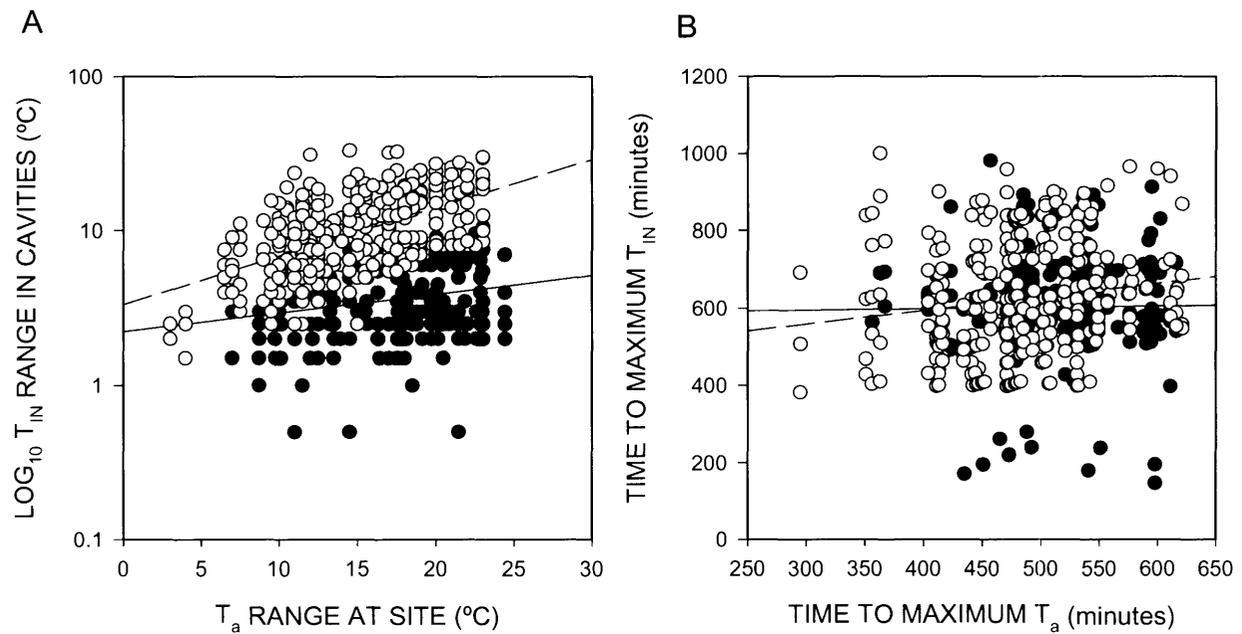
**Figure 8:** On bird-days when minimum ambient temperature (MIN T<sub>a</sub>) was <6.8 °C, owlet-nightjars roosting in tree hollows (white bars, n=6, N=109) entered torpor more often than birds roosting in rock crevices (black bars, n=6, N=32;  $\chi^2_{0.05,1}=9.04$ ,  $P<0.01$ ). When MIN T<sub>a</sub> was >6.8 °C birds were equally likely to enter torpor in either roost type (tree: n=7, N=108; rock: n=5, N=29;  $\chi^2_{0.05,1}=0.40$ ,  $P=0.53$ ).



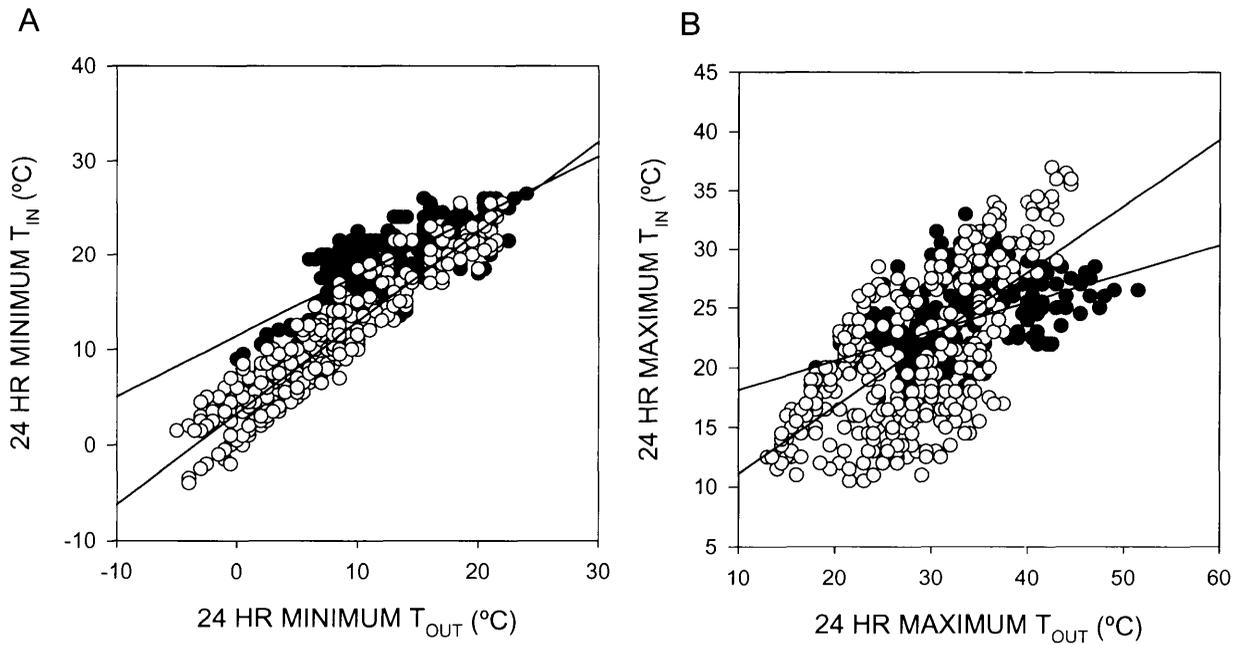
**Figure 9:** Plots of rate of rewarming ( $^{\circ}\text{C min}^{-1}$ ) for birds roosting in rock crevices ( $\bullet$  solid line) and tree hollows ( $\circ$  dashed line). Owllet-nightjars warmed faster in tree hollows versus rock crevices irrespective of A) MIN  $T_a$  ( $^{\circ}\text{C}$ ) or B) MIN  $T_{\text{skin}}/T_b$  ( $^{\circ}\text{C}$ ). A) ANCOVA: roost type:  $F_{1,47}=8.34$ ,  $P<0.01$ ; MIN  $T_a$ :  $F_{1,47}=0.62$ ,  $P=0.43$ ; model  $R^2=0.18$ ; Linear regression for rock crevices: Rewarming rate= $0.05 - 0.001$  (MIN  $T_a$ ),  $F_{1,22}=0.92$ ,  $P=0.35$ ; tree hollows: Rewarming rate= $0.06 + 0.004$  (MIN  $T_a$ ),  $F_{1,24}=2.69$ ,  $P=0.12$ . B) ANCOVA: roost type:  $F_{1,47}=8.86$ ,  $P<0.01$ ; MIN  $T_{\text{skin}}/T_b$ :  $F_{1,47}=0.00$ ,  $P=0.95$ ; model  $R^2=0.17$ ; Linear regression for rock crevices: Rewarming rate= $0.12 - 0.003$  (MIN  $T_{\text{skin}}/T_b$ ),  $F_{1,22}=1.54$ ,  $P=0.23$ ; tree hollows: Rewarming rate= $0.01 + 0.002$  (MIN  $T_{\text{skin}}/T_b$ ),  $F_{1,24}=0.31$ ,  $P=0.58$ .



**Figure 10:** Plots of MIN  $T_{IN}$  and MAX  $T_{IN}$  in rock crevices (● solid line) and tree hollows (○ dashed line) during day (sunrise to sunset) and night (sunset to sunrise). Results and  $R^2$  for each ANCOVA model are given in Table 2. Linear regressions for each figure are: A) Rock:  $DMIN T_{IN} = 14.75 + 0.42 (DMIN T_a)$ ; Tree:  $DMIN T_{IN} = 0.11 + 0.94 (DMIN T_a)$ ; B) Rock:  $DMAXT_{IN} = 11.05 + 0.50 (DMAX T_a)$ ; Tree:  $DMAXT_{IN} = -1.23 + 0.96 (DMAX T_a)$ ; C) Rock:  $NMIN T_{IN} = 16.16 + 0.41 (NMIN T_a)$ ; Tree:  $NMINT_{IN} = 2.36 + 1.00 (NMIN T_a)$ ; D) Rock:  $NMAXT_{IN} = 13.18 + 0.51 (NMAX T_a)$ ; Tree:  $NMAX T_{IN} = 3.21 + 0.92 (NMAX T_a)$ . All linear regressions are significant to  $P < 0.0001$ .

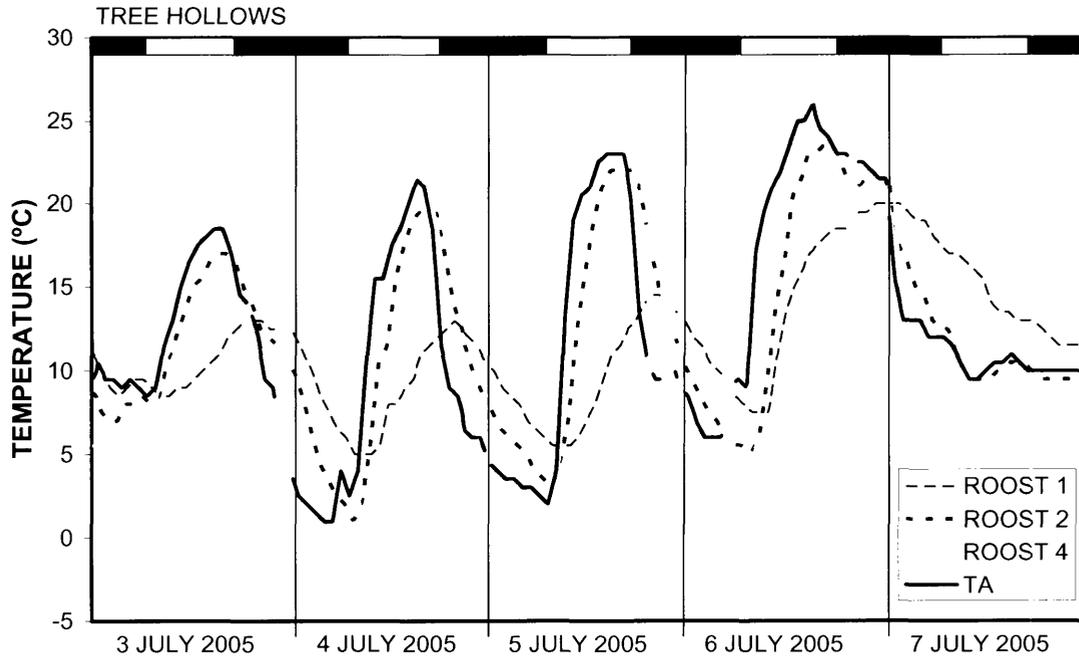


**Figure 11:** Plots of  $\log_{10}$  RANGE  $T_{IN}$  (A) and MAXTIME  $T_{IN}$  (B) in rock crevices (● solid line) and tree hollows (○ dashed line). Results and  $R^2$  for each ANCOVA model are given in Table 2. RANGE  $T_{IN}$  was  $\log_{10}$  transformed to achieve equality of variances. Linear regressions for each figure are: A) Rock: RANGE  $T_{IN} = 0.35 + 0.01$  (RANGE  $T_a$ ),  $P < 0.001$ ; Tree: RANGE  $T_{IN} = 0.52 + 0.03$  (RANGE  $T_a$ ),  $P < 0.0001$ ; B) Rock: MAXTIME  $T_{IN} = 582.92 + 0.04$  (MAXTIME  $T_a$ ),  $P = 0.80$ ; Tree: MAXTIME  $T_{IN} = 452.41 + 0.35$  (MAXTIME  $T_a$ ),  $P < 0.01$ .

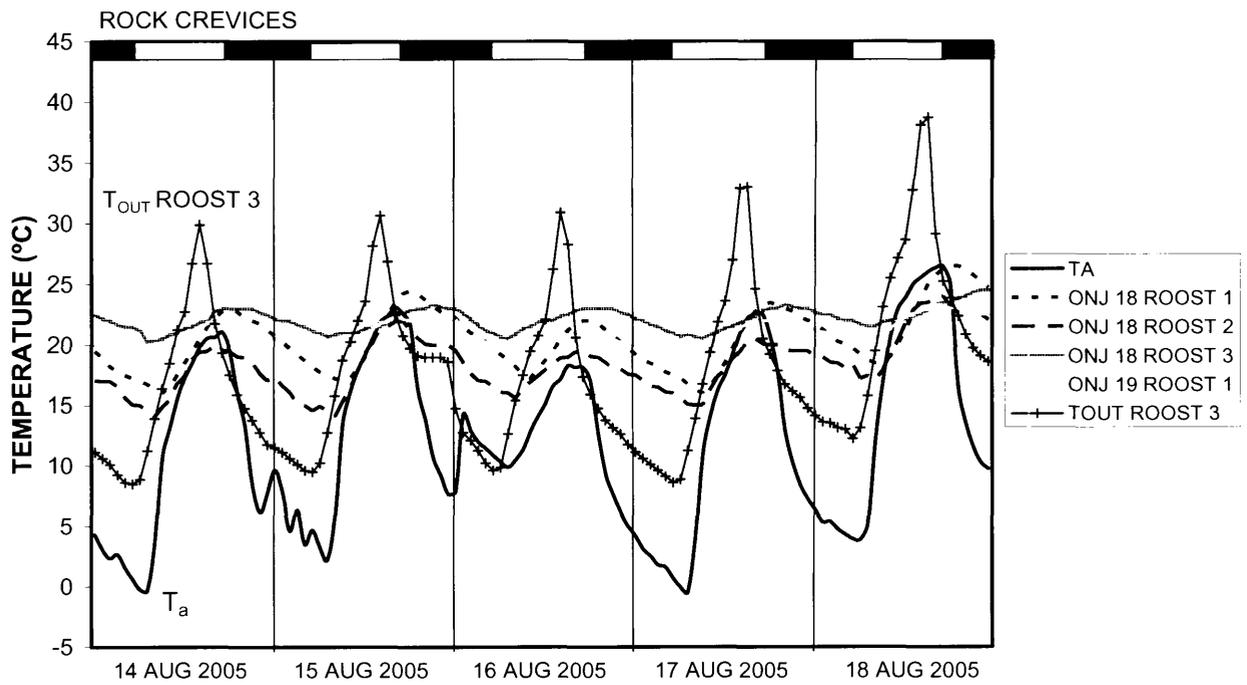


**Figure 12:** Plots of daily (24 hr) MIN  $T_{IN}$  and daily MAX  $T_{IN}$  in rock crevices (● solid line) and tree hollows (○ dashed line) dependant on temperature directly outside the roost ( $T_{OUT}$ ). Results and  $R^2$  for each ANCOVA model are given in Table 2. Linear regressions for each figure are: A) Rock: MIN  $T_{IN} = 11.41 + 0.64$  (MIN  $T_{OUT}$ ); Tree: MINT $T_{IN} = 3.29 + 0.96$  (MIN  $T_{OUT}$ ); B) Rock: MAX  $T_{IN} = 15.70 + 0.24$  (MAX  $T_{OUT}$ ); Tree: MAX  $T_{IN} = 5.45 + 0.56$  (MAX  $T_{OUT}$ ). All linear regressions are significant ( $P < 0.0001$ ).

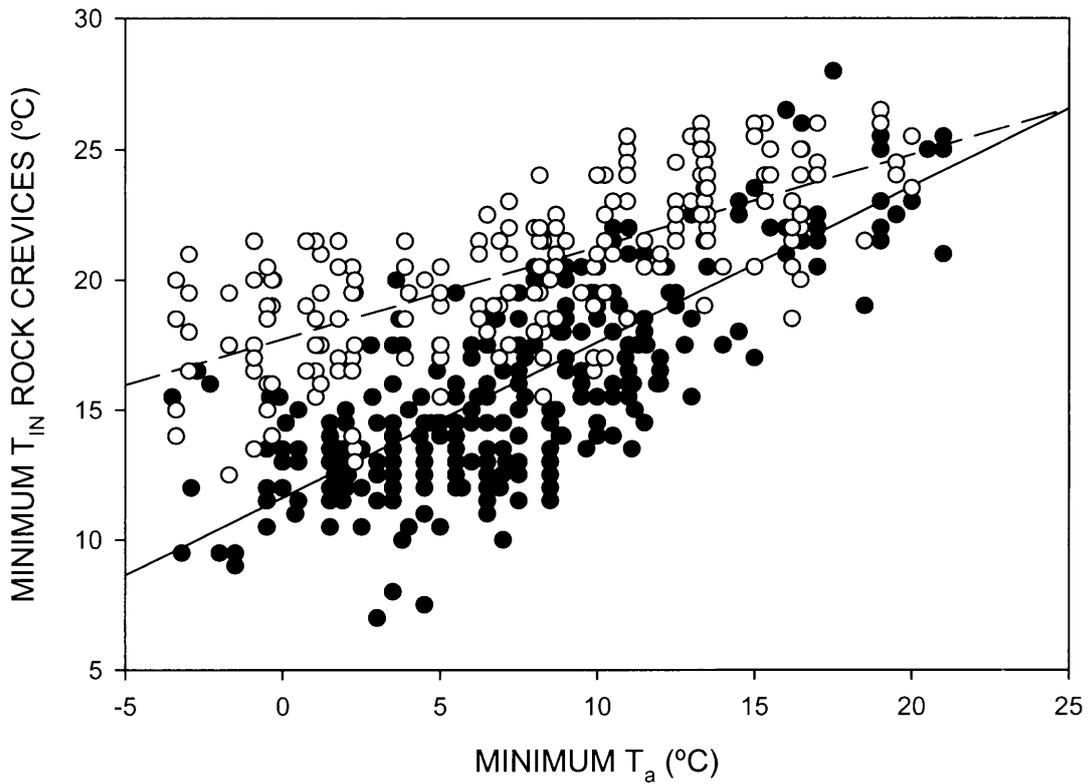
A



B



**Figure 13:** A) Plot of temperature in cavities ( $T_{IN}$ ) for three tree roosts of one individual (ONJ 16) and general  $T_a$  at the site. The plot demonstrates the variation in temperature range shown in tree roosts and illustrates how closely the temperature inside the tree roosts traces the  $T_a$ . Roost 3 was excluded for visual clarity as the  $T_{IN}$  for this roost closely matched roost 2. B) Plot of  $T_{IN}$  for four rock crevices roosts used by two birds at the Alice Springs Desert Park site in 2005. There is little difference in temperature amplitude between the four roosts. However, all four roosts greatly differed from the general  $T_a$  and roost 3  $T_{OUT}$ . The  $T_a$  iButton at the site was at the bottom of the range and showed a RANGE  $T_a$  that was shifted lower than that of any of the roosts.  $T_{OUT}$  for roost 3, located at the top of the range (209 m above iButton  $T_a$ ) illustrates how the cliffs remain warmer at higher altitudes compared to the  $T_a$  at the bottom of the range. ONJ 18 Roost 1 and 2 and ONJ 19 Roost 1 were all located halfway down the slope of the range (85 to 115 m) and still remained warm and stable. Dark and light bars at the top of each figure represent photophase (day) and scotophase (night).



**Figure 14:** MIN  $T_{IN}$  in rock crevices was lower at depths <50 cm (● solid line) and greater at depths >50 cm (○ dashed line). Linear regressions: <50 cm:  $MIN T_{IN}=11.62 + 0.60 (MIN T_a)$ ,  $P<0.0001$ ; >50 cm:  $MIN T_{IN}=17.72 + 0.35 MIN T_a$ ,  $P<0.0001$ . ANCOVA: depth:  $F_{1,484}=143.14$ ,  $P<0.0001$ ;  $MIN T_a$ :  $F_{1,484}=344.96$ ,  $P<0.0001$ ; depth\* $MIN T_a$ :  $F_{1,484}=18.09$ ,  $P<0.0001$ ; model  $R^2=0.60$ .



**Plate 1:** A radio-tagged owlet-nightjar laying flat in a rock crevice roost. Owlet-nightjars will often use this position in rock crevices and horizontal tree branches. This rock crevice roost is unusually large for an owlet-nightjar. Roost openings are usually only big enough for an owlet-nightjar to fit through (5 to 10 cm), and the passages deep and convoluted so the bird cannot be seen. Photo by L. Doucette.

## Discussion

This study is the first to describe torpor use by owlet-nightjars in a semi-arid habitat and the first to describe thermoregulation in a population of birds that regularly roosts in both trees and rock crevices. Owlet-nightjars entered torpor less frequently when roosting in rock crevices, which maintain stable, moderate  $T_{IN}$ . Rock crevices were consistently warmer than tree roosts and  $MAX T_{IN}$  was higher than  $MAX T_a$  during day and night, except when  $MAX T_a$  exceeded 25 °C. The warmer  $T_{IN}$  of rock crevices likely reduced the amount of energy required for owlet-nightjars to maintain high  $MIN T_{skin}$ , and decreased the need to use torpor to conserve energy on cold days. Despite these energy savings, owlet-nightjars roosted in tree hollows more often (65% bird-days) than rock crevices (35% bird-days). Decreased risk of predation and lower costs of rewarming are two possible explanations for the preference of using tree hollow roosts.

### *Cavity Characteristics and Thermal Buffering Capabilities*

Since most animals spend the majority of their time at rest, an energy saving strategy, such as selecting a thermally insulated roost, can significantly affect an organism's total energy budget (Kurta, 1985). Although  $T_a$  primarily determined the thermal characteristics of roosts in this study, rock crevices have much greater thermal buffering than tree hollows. Rock crevices were on average 6.7 °C warmer than tree roosts, which would lead to substantial energy savings for a normothermic small bird. Rock crevices selected by owlet-nightjars were primarily on steep, northern facing slopes which benefit from maximum sun exposure throughout the day (see Chapter 3). These crevices had the warmest  $MIN T_{IN}$ . The depth of the crevice and the thickness of the rock increased thermal stability and kept roosts warm overnight. As expected, roosts that faced west were the slowest to warm during the day.

Studies on the effect of burrow depth on temperature regimes have found that although thermal stability increased,  $T_{IN}$  decreased with increasing burrow depth (e.g. Lopez et al., 1998; Huey et al., 1989). In contrast, the rock crevices used in winter by owlet-nightjars showed an increase in both thermal stability and temperature with depth. The difference lies in the fact that these authors examined the temperature of crevices and burrows underground, whereas this study examines  $T_{IN}$  of horizontal crevices, high on steep cliff faces, with dark surfaces and direct sunlight throughout the day. Chruszcz & Barclay (2002) found that horizontal rock crevices had higher daytime  $T_{IN}$  than vertical crevices. The thermal suitability of rocks depends on their thickness and their exposure to the sun (Huey et al., 1989).  $MIN T_{IN}$  under rocks increase and  $MAX T_{IN}$  decrease with increasing rock thickness (Huey et al., 1989). Huey et al.

(1989) found that at night, warmer temperatures exist under rocks than anywhere else. Deeper rock crevices have the added advantage in that they can provide a gradient of thermal conditions that potentially allow for behavioural thermoregulation (Lausen & Barclay, 2003; Chruszcz & Barclay, 2002). This would allow birds to select a thermal microclimate within the roost based on ambient  $T_a$ . Deep rock crevices in this study had the added thermal benefit of lower MAX  $T_{IN}$  on hot days ( $>25$  °C).

Nocturnal thermal inversion means that rock crevice roosts higher on slopes generally stayed warmer overnight and were more thermally stable (Figure 13b; Arbuthnott & Brigham, 2007). Steeper slopes allowed cold air to descend at night, leaving warmer  $T_{IN}$  at high levels, and reducing the overall  $T_{IN}$  fluctuation (RANGE  $T_{IN}$ ) during a 24 hour period. Steep northerly facing slopes would also receive more direct sunlight during the winter months. Roosts at the top of a cliff or range were warmer than those at the bottom irrespective of the height of the cliff itself. The mean roost altitude from the base of the cliff or slope was  $81.5 \pm 4.4$  m (range = 7 to 209 m). Roosts higher than 33 m on a slope had warmer MIN  $T_{IN}$  with increasing height having little effect. Most roosts were at or near the top of their respective cliffs. Roost placement on a cliff will influence the amount of sunlight reaching the roost and the degree to which the roost will be heated, and for what duration during the day. Neubaum et al. (2006) found that 'height to ground above' was the most important variable in determining autumn rock cavity roost selection by big brown bats (*Eptesicus fuscus*).

Daily  $T_{IN}$  of tree hollows may fluctuate widely depending on the thermal buffering qualities of the tree (Körtner & Geiser, 2000). Several studies have shown that bats prefer to roost in tree cavities that are buffered from outside  $T_a$  (Kerth et al., 2001; Sedgeley, 2001; Smith & Racey, 2005; Willis & Brigham, 2007). Tree roosts in my study varied considerably in thermal microclimate because of differences in thermal buffering qualities, exposure to thermal radiation and nocturnal thermal inversion. Diurnal tree hollows can be heated above external  $T_a$  by solar radiation, depending upon aspect and exposure (Kerth et al., 2001). However, roost  $T_{IN}$  in my study rarely exceeded  $T_a$  (Figure 10b). Roosts opening to the northwest had higher MAX  $T_{IN}$ , resulting in a greater temperature fluctuation (high RANGE  $T_{IN}$ ). Tree roosts facing east had higher MIN  $T_{IN}$ , but warmed slower. Roosts facing directly east may have less surface area exposed to the sun in the morning and take longer to warm. Roosts facing south would have increased surface area facing the rising sun and warmed faster.

Deeper hollows had higher MIN  $T_{IN}$ , lower MAX  $T_{IN}$ , lower RANGE  $T_{IN}$  and higher TIMEMAX  $T_{IN}$ . Thus, thermal buffering capacity increases with depth in the hollow. The climbing ability of owl-nightjars may allow them to move freely inside hollow trees and select locations with suitable  $T_{IN}$  throughout the day and night. It is likely that birds move deeper in a hollow to stay warm at night and move nearer the entrance in the morning. This is relevant in terms of energy expenditure during normothermia, as well as for rewarming from torpor bouts.

Linear regression analyses indicated that lower cavity height in trees resulted in higher MIN  $T_{IN}$ , lower MAX  $T_{IN}$ , and reduced RANGE  $T_{IN}$ . However, cavity height explained only 1% to 7% of the variation in roost  $T_{IN}$ . Thus, using lower hollows for iButton placement had only minimal effect on the  $T_{IN}$ . The fence post derived iButton holder used to test for height differences showed that there was no difference in  $T_{IN}$  for tree cavity roosts above 1.56 m. Substitute roosts in this study were never below 2.8 m. Ruczynski (2006) only noted a 1.2 °C increase in mean  $T_a$  on the outside of tree trunks between 0 and 10 m, which she attributed to decreased shading at greater heights in a forest. Calder (1973) found no temperature difference between 2 m and 12 m heights on the outside of an aspen tree and Rosenberg et al. (1983) found little difference in thermal characteristics between tree hollows 4 m and 16 m above the ground. The difference between actual cavity height and substitute cavity height in my study was between 0 and 6 m.  $T_{IN}$  was measured inside the cavity and shading was minimal due to sparsely distributed trees in the arid zone. Thus, any effect on  $T_{IN}$  caused by using lower cavity roosts would likely be <1 °C. This small effect is inconsequential compared to the 6.7 °C difference in  $T_{IN}$  between rock crevices and tree hollows.

Smaller entrances to roosts should minimize air exchange between the cavity and the environment (Soderquist, 1993), and contain heat radiated into the cavity by the tree trunk. In this study, tree roosts with larger opening diameters had decreased MIN  $T_{IN}$ , increased MAX  $T_{IN}$ , and thus increased RANGE  $T_{IN}$ . Lausen & Barclay (2003) found that rock crevices with larger openings cooled faster after sunset, and suggested that this was likely to be a consequence of increased airflow. Increased air flow in a tree hollow would cause the hollow to be quickly affected by external heating, resulting in cooler night MIN  $T_{IN}$  but higher MAX  $T_{IN}$  during the day. Larger diameter openings resulted in shorter TIMEMAX  $T_{IN}$  in the morning, emphasizing the decreased thermal stability in these roosts.

Thermal conductivity of rock (0.6 to 0.8 W/m K) is 5 to 15 times greater than wood (0.04-0.12 W/m K), which is still greater than air (0.024 W/m K; Young, 1992). Postures that allow birds to decrease contact with the roost surface when they are cooler than  $T_a$ , especially during periods of rewarming, could be an advantage in reducing conductive heat loss. Owlet-nightjars will often lay flat in their roosts putting them in direct physical contact with a substrate that conducts heat (rock or wood; Plate 1). There is great variation in heat conductance of various substrates and rock types (Lausen & Barclay, 2002). The rock crevices used by owlet-nightjars were heated extensively throughout the day and maintained high MIN  $T_{IN}$  at night, as a consequence of radiant heat and higher altitude. Owlet-nightjars may have received added warmth by lying in contact with the warm rocks, and thus reduced their energy expenditure to maintain a high  $T_b$ .

One advantage of tree hollows is that the options for variation in body position are greater. I have observed owlet-nightjars hanging suspended, even when in torpor, in the entrance to a near vertical tree hollow supported by splayed legs and toes hooked onto the sides of the hollow. This position would allow the bird to experience maximum ambient heating and sun exposure while preventing heat loss due to conductance. As entrances to rock crevice were all horizontal, and the rock substrate was smooth quartzite, this position would not be possible in a rock crevice, where the ventral surface of the bird would always be close to or in direct contact with the rock. This would be advantageous if the  $T_{IN}$  of rock crevices was high, but could result in increased cooling due to conductance if the  $T_{IN}$  was colder.

Few studies have examined the thermoregulatory behaviour of animals that use such varied roost sites. Baker & Lacki (2006) found that long-legged myotis bats (*Myotis volans*) roosted in rock crevices (6.9%) or decayed trees (82.8%) or switched between the two roost types (10.3%), but offered no explanation for the occasional selection of rock crevice roosts within this population. However, Lausen & Barclay (2006) found that the bat *Eptesicus fuscus* gained a thermal advantage from living in warm buildings as opposed to rock crevices and used torpor less often in the warmer roosts. Female *Scotophilus mhlangani*, a subtropical bat in St. Lucia, entered longer but shallower bouts when roosting in cavities as opposed to foliage (Jacobs et al., 2007).

### ***Thermoregulation and Torpor Use***

Patterns of torpor use suggest that birds roosting in the warmer microclimate of rock crevices use less energy to maintain high  $T_b$  than those roosting in tree hollows and need to enter torpor

less frequently. By using warmer roosts within their thermoneutral zone, bats can lower their thermoregulatory costs and do not need to enter torpor as often (Lausen & Barclay, 2006), and can passively maintain warm, stable  $T_b$  (Speakman & Thomas, 2003). Sedgeley (2001) found that tree hollows used by the bat *Chalinolobus tuberculatus* which were 0.5 °C warmer than unused cavities led to a 1.1 to 7.3% reduction in energy expenditure depending on time of day and cavity structure. The mean 6.7 °C warmer  $T_{IN}$  found in rock crevices should enable substantial energy savings by owl-nightjars. Warmer roosts minimize the cost of resting while remaining normothermic, and animals can avoid the energetically expensive process of arousal from torpor. An earlier study of thermoregulation by owl-nightjars in a habitat where only tree roosts were used found that torpor use and the use of two torpor bouts per day was much more frequent than in this study (double bouts on 36% of bird-days in Brigham et al., 2000 compared to 6% of bird-days in my study).

Normothermy is most energetically expensive when the  $T_a$  is lowest and morning torpor bouts appear to be the most common type in nocturnal heterotherms (Audet & Fenton, 1988; Brigham et al., 2000; Geiser et al., 2000; Turbill et al., 2003).  $T_{IN}$  of both roost types was lowest near dawn and morning torpor bouts were the most common for nocturnal owl-nightjars. Thermally stable rock crevices remained relatively warm in the morning, however,  $T_{IN}$  of tree roosts was generally >10 °C lower than in the afternoon. This largely explains the more frequent use of torpor in tree roosts. Birds also entered torpor at night more often in trees than in rocks crevices. Although owl-nightjars are generally active throughout the night (Brigham et al., 1999; Chapter 7), if conditions are not favourable for foraging (too cold or too wet) they may return to their roosts. Night torpor bouts occurred on cold nights (mean = 3.1 °C) when foraging may not have been energetically feasible due to low insect abundance (see Chapter 4). Once birds have returned to their roosts, the warmer conditions in rock crevices may reduce the need to enter torpor when energy reserves are low.

The MIN  $T_b$  threshold during torpor is controlled by the animal and torpid endotherms are able to increase their heat production to prevent  $T_b$  from falling below this threshold (Bartholomew, 1982). Although the  $T_b$  threshold varies widely among species, the average minimum  $T_b$  during daily torpor for birds and mammals is 17 °C (Geiser & Ruf, 1995). While owl-nightjars were capable of reducing their MIN  $T_{skin}$  during torpor to below 20 °C, they usually kept MIN  $T_{skin}$  at around 25 °C in both roost types. This  $T_{skin}$  may represent the preferred threshold for owl-nightjars that conserves energy but from which rewarming is facilitated. The MIN  $T_{skin}$  of owl-nightjars was inversely related to the duration of torpor bouts, and bout duration for the

two roost types did not differ significantly (Figure 5). Thus, MIN  $T_{\text{skin}}$  and bout duration appear to be unrelated to roost type and may be relatively fixed or directed by other factors, such as prey abundance (Chapter 4). Torpor bout duration has been shown to be inversely related to food availability (Körtner & Geiser, 2000). The slightly longer duration of torpor bouts by birds in rock crevices may be the result of slower rewarming rates. Inability to passively rewarm would also explain the greater frequency of afternoon torpor bouts by birds in rock crevices. Although  $T_{\text{skin}}$  rose above 30 °C, owlet-nightjars did not always warm to active  $T_{\text{skin}}$  between morning and afternoon torpor bouts. In well-insulated, thermally stable rock crevices, where  $T_a$  has less influence, passive rewarming would be more difficult and the birds would be required to use more energetically expensive metabolic heat production to arouse from torpor. Passive rewarming with  $T_a$  and maintenance of high  $T_{\text{skin}}$  throughout the afternoon when  $T_a$  is high may be easier for birds in poorly insulated tree roosts. Thus, the thermal benefits offered by consistently warmer rock roosts and the need to enter torpor less frequently may be outweighed by lower costs of rewarming in tree roosts.

Radiant heating of tree roosts could help birds to arouse passively at much lower energetic costs than active arousal. A number of heterothermic endotherms use passive rewarming to arouse from torpor (Lovegrove et al., 1999; Geiser & Drury, 2003; Geiser et al., 2004). Lovegrove et al. (1999) found that exogenous heating reduced the cost of arousal from 52% to 27% of the total energy expenditure during a torpor bout in a small carnivorous marsupial (*Sminthopsis macroura*). Geiser & Drury (2003) determined that the average arousal cost of passive rewarming of *S. macroura* from torpor was only about 70% of its basal metabolic rate (BMR). At these low metabolic rates any level of torpor would result in a reduction in energy expenditure provided there was access to sufficient external heat. In contrast, the average energy expenditure of active arousal from torpor was 340% of BMR (Geiser & Drury, 2003).

### ***Roost Thermal Stability and Passive Rewarming***

Several studies have found that roost stability is important for facilitating torpor use in bats (Lausen & Barclay, 2006; Solick & Barclay, 2006). When using cooler roosts with more stable microclimates bats entered deeper torpor bouts and stayed in torpor longer. However, thermally stable roosts may increase the cost of rewarming during arousal, as there would be less influence by  $T_a$ . Minimum thermal buffering of a roost has the advantage that animals can benefit from maximum heating by the  $T_a$  cycle (Lovegrove et al., 1999). Some studies have found that bats select poorly insulated roosts in summer to achieve passive heating during the day (Kerth et al., 2001; Turbill et al., 2003). Others have suggested that bats choose unstable

roosts, such as leaf litter, during winter hibernation as they provide thermal buffering from  $T_a$  extremes, but also allowed individuals to monitor  $T_a$  to identify potential foraging opportunities on warmer nights (Dunbar & Tomasi, 2006). By selecting poorly insulated tree roosts on days when torpor is used, owlet-nightjars can use passive rewarming to arouse from torpor bouts with minimal metabolic effort and decreased energy expenditure. In my study, rewarming rates during arousal were twice as fast for owlet-nightjars roosting in tree roosts than in rock crevices irrespective of MIN  $T_{skin}$  or MIN  $T_a$ .

Timing of arousals has also been found to reflect the insulative properties of shelters or roosts selected for torpor (Körtner et al., 2001), as animals synchronize arousal with  $T_a$ , and eliminate the need for metabolic heat production (Körtner & Geiser, 2000). In this study,  $T_{skin}$  often increased with external  $T_a$ . However, there was extensive variation in TIMEMAX and it is difficult to separate arousal times by roost type. As in mammals (Geiser & Drury, 2003; Geiser et al., 2002), there is likely an element of basking involved in rewarming by owlet-nightjars. I have not observed owlet-nightjars basking outside rock roosts (however this could be the result of the difficulty in approaching the roost without disturbing the bird), but I have observed them basking in the entrance to tree hollows on several occasions (also see Higgins, 1999). I have also observed active movement from a torpor roost site to a sunnier basking site (Chapter 4).

### ***Predation Risk***

Risk of predation would be a major consideration in determining roost choice for small birds, especially ones that regularly use torpor. Thus, another possible explanation for owlet-nightjars selecting tree roosts on 65% of bird-days may be that they offer better protection from predators. Although owlet-nightjars typically experience predation while foraging outside the roost (Brigham & Geiser, 1997), monitor lizards, large snakes, foxes (*Vulpes vulpes*) and feral cats (*Felis catus*) represent potential terrestrial predators that could access birds in stumps or shallow rock crevices. Feral cats depredated three birds during this study; however, all of these events occurred when birds were out foraging. Brigham & Geiser (1997) noted high rates of predation on owlet-nightjar eggs in stump cavities by unknown predators. There is one report of an owlet-nightjar being consumed by a lace monitor during the day (Broadbent, 1910), presumably from a cavity roost. Large monitor lizards are known to depredate tawny frogmouth (*Podargus strigoides*) nestlings from tree nests (Kingston, 1980). Owlet-nightjars that are observed at the entrance to tree hollows can quickly drop out of sight inside the tree trunk where they are usually inaccessible. In contrast, birds in rock crevices with only one roost exit or opening may be cornered (see Chapter 3). Terrestrial predators may be able to

access birds in rock crevices easier than in tree hollows, which were often located at great heights (up to 12 m). Rates of nest predation on cavity-roosting birds are greater for nests closer to the ground (Nilsson, 1984; Rendell & Robertson, 1989).

The ability of birds to avoid predation by terrestrial predators is further compromised by using torpor. Lausen & Barclay (2006) proposed that big brown bats (*Eptesicus fuscus*) use shallower torpor bouts when roosting in more exposed rock crevices than when roosting in buildings in order to remain vigilant and more mobile. Although the duration of torpor bouts between roost types did not differ significantly in this study, entering torpor while in a rock crevice would presumably put an owlet-nightjar at increased predation risk. Details of roost characteristics that would likely influence predation risk are discussed further in Chapter 3.

The most common predators of owlet-nightjars are large owls (Beste, 1970; Debus, 1997). Although it would be difficult for owls to access owlet-nightjars in their roosts, they may be vulnerable as they exit. Owlet-nightjars wait until near total darkness before exiting their roosts (Chapter 6). As backlighting against the sky is required, I have only been able to observe them leaving tree roosts, which they leave quickly by diving, with wings folded against their bodies, into lower vegetation. Fenton et al. (1994) found that the faster bats left roosts the lower their risk of attack by raptors. Rock roosts were always in exposed locations, with little to no vegetation and the bird would be vulnerable when leaving the roost and may have no immediate refugia to offer protection. Thus, roosting in rock crevices may expose owlet-nightjars to greater risk of predation risk than those in tree hollows both during the rest phase and as they depart their roosts.

### ***Summary***

Rock crevices are more thermally stable and consistently warmer than tree roosts. The selection of rock crevices as roosts means that owlet-nightjars may avoid using torpor during cold weather, resulting in significant energy savings for a small bird. However, under certain circumstances, such as when food availability is low, it may be advantageous to conserve energy by using torpor, provided passive rewarming can be used during the arousal phase. Cool, poorly insulated tree hollows would facilitate the use of torpor during cold mornings and would warm quickly with  $T_a$  to allow for passive rewarming. Tree hollows are also more likely to allow for behavioural thermoregulation as the bird can select from a variety of thermal microclimates within a single tree. Increased protection from predators may offer a further explanation for the preference of roosts in tree hollows despite cooler temperatures.

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## CHAPTER 3

### **Thermal Characteristics Determine Selection of Winter Cavity Roosts by Australian Owlet-Nightjars (*Aegotheles cristatus*) in Central Australia**

#### **Abstract**

The use of cavities as roosts provide animals with significant advantages, including decreased risk of predation and better insulation from adverse temperature extremes. Australian owlet-nightjars (*Aegotheles cristatus*) are one of the few species of Australian birds that are obligate cavity users and that roost in cavities year round. Owlet-nightjars use a variety of roost types, including tree hollows, and in some habitats, rock crevices, for which roost selection criteria have not been assessed. Examining the roost characteristics for which this adaptable species selects will provide important information on roost structures that are essential for obligate cavity users. I compared characteristics of rock and tree roosts with randomly selected cavities and used an information theoretic approach to determine variables important for roost selection. Owlet-nightjars selected roosts based on variables that increased the thermal buffering capacity of the roost and the exposure of the roost to sunlight. Tree hollows were selected based on reduced canopy cover, greater cavity height and a north-facing cavity entrance. Deep rock crevices, with narrow entrances, located on northern-facing steep slopes were preferred. Individual owlet-nightjars used 1-7 different cavities during 12 to 102 days of tracking. Birds moved between roosts every 17 days on average, often switching between rock and tree roosts. This low roost fidelity may reflect attempts to find better roost microclimate or to avoid predation.

#### **Introduction**

In Australia, 15% of all terrestrial animals use cavities for shelter or nesting (Gibbons & Lindenmayer, 2002). The use of hollows by birds for nesting is relatively common (94 species in Australia), however, the use of cavities as roosts throughout the year is much rarer and is restricted to only a few species. Species that use cavity roosts gain significant advantages, including better thermal buffering from temperature extremes, increased protection from predators, and for birds, reduced energy requirements for nest construction (Gibbons & Lindenmayer, 2002).

Deep cavities with thick walls offer thermal buffering against external ambient temperatures ( $T_a$ ), remaining warmer on cold days and cooler on hot days (White et al., 1978; Gibbons & Lindenmayer, 2002; Chapter 2). At low  $T_a$ , small birds will experience thermoregulatory challenges and may rely on warmer roost microclimates to reduce energy expenditure. The need for a warmer microclimate is especially pronounced in diurnal birds as the resting phase when the daily fast occurs is at night when  $T_a$  is lowest. Nocturnal energy consumption may be reduced by up to 43% for birds using cavity roosts compared to individuals roosting in exposed sites (Walsberg, 1985). For some species, especially those which roost in clusters (Bartholomew et al., 1957; Knorr, 1957), a major source of energy savings is an increase in  $T_a$  in the cavity due to the retention of metabolically produced heat (White et al., 1975; 1978). However, for species which roost solitarily, the characteristics of the roost that increase insulative capacity becomes more important. Studies on cavity roosting birds and the ecologically-similar microbats have identified aspects of cavity roosts that are relevant in terms of thermal microclimate (Ricklefs & Hainsworth, 1969; Finch, 1983; Grubb et al., 1997; Sedgely, 2001; Chruszcz & Barclay, 2002; Lausen & Barclay, 2003; Smith & Racey, 2005; Lausen & Barclay, 2006).

Predation is likely reduced for animals concealed in cavities as they are more difficult to detect; however, few studies have examined the characteristics of cavity roosts that may minimize predation risk. It is known that predation on birds is less for those that nest in cavities higher in trees (Nilsson, 1984; Rendell & Robertson, 1989). Deep hollows with narrow entrances are also known to deter predators (Gibbons et al., 2000). However, most of the research on cavity use and predation has focused on roost fidelity (Sonerud, 1985; Lewis, 1995; Lewis, 1996; Gibbons & Lindenmayer, 2002; Sherwin et al., 2003). Frequent roost switching is relatively common in most species of bats (reviewed in Lewis, 1995) and in several species of birds (Sonerud, 1985; Krebs, 1998) and it has been proposed as one reason animals may exhibit roost lability is to avoid predators (Lewis, 1995; Gibbons & Lindenmayer, 2002). Other reasons that animals may demonstrate low roost fidelity are due to frequent disturbance, to minimize distance to foraging sites, to reduce infestation of ectoparasites, and to choose a more favorable thermal microclimate (Lewis, 1995; Gibbons & Lindenmayer, 2002).

Most Australian bird species only use hollows for nesting and raising young, and only 11% of all species are obligate hollow-nesters (Gibbons & Lindenmayer, 2002). Australian owl-nightjars (*Aegotheles cristatus*) are one of the few species of Australian birds that are obligate

cavity users year-round (Tideman & Flavel, 1987; Gibbons & Lindenmayer, 2002). As one of the smallest species (40-50 g) of nocturnal birds, owlet-nightjars would likely be subjected to high predation risk if they roosted in exposed locations when at rest during the day. Cavity roosts offer them protection from predators during their rest period, especially when they employ torpor and can not readily respond to disturbances (Carpenter & Hixon, 1988; Chapter 2). The thermal buffering capacity of cavity roosts also reduces the energy costs during extremes in  $T_a$ . Thus, cavity use is likely a critical feature for survival of this small nocturnal bird.

Australian owlet-nightjars are found throughout Australia in a wide variety of habitats. In most wooded or forested areas of Australia, owlet-nightjars only roost in tree hollows (Brigham et al., 1998). Due to forestry operations in Tasmania causing a shortage of hollow bearing trees, Australian owlet-nightjars are listed as vulnerable in that state. Owlet-nightjars have also been listed as in decline in Western Australia (Birds Australia, 2005; Davis, 2005). However, less than 6% of Australia is naturally forested (Lunney, 2004). Owlet-nightjars elsewhere have occasionally been found roosting in deep crevices in cliffs or banks, pipes, the roof of buildings, termite mounds, fence posts, nest boxes, and abandoned babbler (Pomatostomidae) domed stick nests (Menkhorst, 1984; Debus, 1994; Higgins, 1999; Holyoak, 2001). Clearly this species is flexible in that it can make use of available resources. However, it is apparent that individuals must find a sheltered roost site during the day. A detailed assessment of the roost requirements of the Australian owlet-nightjar should help to determine the characteristics that are essential for obligate hollow using endotherms.

My study was conducted in a semi-arid region of central Australia, which has the characteristic vegetation expected of such a habitat. Large trees, such as river red gums (*Eucalyptus camaldulensis*), are largely restricted to river channels. Owlet-nightjars in central Australia regularly roosted in rock crevices in addition to tree hollows. Although mention of owlet-nightjars roosting in rock crevices has been made previously (Holyoak, 2001), mine is the first study to quantitatively describe the characteristics of rock crevices used by owlet-nightjars and the frequency of use. Individual tree roosts and rock crevices likely differ in ecological characteristics, which affect both their thermal buffering capabilities and their appeal as protective roost sites. My goal was to determine characteristics that owlet-nightjars select for by comparing both rock and tree roost cavities with randomly selected unoccupied cavities of both types. I also present data on the roost fidelity and roosting behaviour by owlet-nightjars in central Australia.

## Methods

This study was conducted between early May and mid-October of 2004 and 2005 at two field sites in the arid zone of central Australia west of Alice Springs, Northern Territory. Ormiston Gorge (23°37'S, 132°43'E) is located in the West MacDonnell Ranges National Park at the junction of the Chewings and Heavitree Ranges, about 150 km west of Alice Springs. The second site was at the Alice Springs Desert Park (23°37'S, 132°43'E), 7 km west of Alice Springs. A detailed description of both study sites is given in Chapter 2.

Owlet-nightjars were caught by broadcasting taped calls to lure individuals into mist nets. Following capture I determined each bird's body mass and placed an alloy band (Australian Bird and Bat Banding Scheme Project 1418-8; banded in 2005 only) on the right leg. Birds were generally fitted with external radio transmitters (model PD-2T, Holohil Systems, Carp, Ontario, Canada). Two birds had internal transmitters (Sirtrack Ltd, Havelock North, New Zealand) implanted to measure body temperature for purposes of another study (Chapter 2). Transmitters mass ranged from 1.8 to 2.6 g representing less than 6.5% of body mass (mean =  $47.8 \pm 3.9$  g). External transmitters were attached using a back-pack-style harness made from elastic thread (Figure 5.1E in Kenward, 1987). Roosts were found by tracking radio-tagged birds to their respective diurnal roosts each morning using a 3-element Yagi antennae and Merlin (Custom Electronics, Nokomis, U.S.A.) or Icom (IC\_R10, Icom, Bellevue, WA, U.S.A.) receivers. The position of the roost was recorded using a GPS (Garmin GPS 12, Garmin International, Olathe, Kansas, U.S.A.). Birds roosting in trees were observed leaving the roost against a backlit sky at dusk to determine the position of the hollow.

At the end of the study period each year, I measured variables of the tree hollows and rock crevices used as roosts. Variables measured for tree hollows were selected based on those used in other studies on cavity roosting animals (Vonhof & Barclay, 1996; Brigham et al., 1997b; Brigham et al., 1998; Gibbons & Lindenmayer, 2002; Psyllakis & Brigham, 2005; Table 1). Tree species was determined and assigned a category number (1-7) for inclusion in logistic regressions. Tree height, cavity height, height to start of leaves in the canopy, and the slope of the ground were measured using a clinometer. Cavity and slope aspect were measured with a compass and corrected for magnetic declination. Percentage canopy cover was estimated from a position directly below the roost site, looking straight up, facing away from the tree in the direction of the roost branch. The value was defined as the percentage of an observer's circular field of view, centered on the roost, which contained limbs and foliage

that would block overhead sunlight from reaching the roost (Willis & Brigham, 2005). Branches and leaves below the height of the roost were excluded from the estimate. The percentage of canopy cover was estimated by two observers independently and the mean calculated. Most measures of length and circumference were made using a 50 m tape measure accurate to  $\pm 1$  mm. When tree hollows were too high to measure cavity entrance diameter directly, it was estimated. The nearest tree with a circumference  $>30$  cm was used for measures of distance and height. For measures of the nearest tree with a cavity, a tree with a suitable cavity was designated as one with a hollow diameter  $>5$  cm, the approximate diameter of an owlet-nightjar. When the distance to the nearest tree with a cavity was greater than 50 m, GPS positions were used to calculate distance. Each tree was classified into one of seven decay stages (Table 2; (Berman & Todd, 1991), based on characteristics such as foliage density and number of dead, leafless branches (dieback). Termite damage was classified in four categories: none, minimal, moderate and heavy (1-4).

Several studies have examined the variables affecting roost selection by rock cavity roosting bats (Chruszcz & Barclay, 2002; Lausen & Barclay, 2002; Lausen & Barclay, 2003; Solick & Barclay, 2006). I used the information from these studies and examination of the rock crevices used by owlet-nightjars in this study to select relevant variables for measurement (Table 3). Rock type was determined and placed in a category (1-4). Cavity, cliff, and hill aspect were measured with a compass and corrected for magnetic declination. Cliff slope and aspect were small scale measures of the cliff containing the rock crevice, and hill slope and aspect were large scale measures of the range upon which the cliff was situated. Number of cavities in the cliff was determined as the number of available unused cavities  $>5$  cm diameter within a 5 m radius of the roost cavity. Rock crevice depth was measured by pushing a flexible, slender pole as far into the crevice as possible and measuring the distance on the pole. A GPS with a 3D fix was used to determine altitude.

These same variables were measured for a random sample of other potentially available tree hollows and rock crevices. For each roost, I selected two random unused cavities for comparison by choosing a random compass bearing and number of paces between 50 and 200. Thus, random cavities were generally 40 to 170 m from the actual roost cavities. The first suitable cavity ( $> 5$  cm diameter) visible was selected and the same variables measured. The possibility exists that these hollows may have been occupied by other fauna, such as parrots or bats. However, as owlet-nightjars are solitary and territorial (Chapter 7), the radio-tagged

individual and potentially its mate would be the only owlet-nightjars within the immediate area of the known roosts.

Binomial logistic regression analysis was used to determine which variables owlet-nightjars were using to select roosts. Variables for rock and tree roosts were compared to random rock crevices and tree hollows separately. In all cases, aspect was converted to sine and cosine radians for analysis (Neubaum et al., 2006). For each roost type, the variables measured were designated as one that would affect either the thermal qualities of the roost (T) or the degree to which the roost offered protection from predators (P). For example, variables such as cavity and slope aspect were only relevant as thermal variables and distance to the nearest tree with a cavity is only relevant as a protection variable. Several variables, such as canopy cover and cavity diameter, were designated as relevant as both thermal and protection variables and were labeled as such (TP). From these lists of variables I created models using binomial multiple logistic regression analysis comparing the variables of roosts used to unoccupied random cavities. Due to the convoluted nature of some rock crevices, depth could not be measured accurately, reducing the sample size for roost measures. As a result, and to create more parsimonious models, the analysis of rock crevices was divided into roost and landscape variables. The hill slope aspect was measured for trees, but not included in the models as most trees were located on flat ground and slope was zero. Data from 2004 and 2005, and from the two sites, were pooled for analysis.

For each roost type a set of a priori models was created and evaluated using Akaike's Information Criteria (AIC) adjusted for small sample size ( $AIC_c$ ; (Burnham & Anderson, 1998). Akaike's Information Criteria is based on the maximized log-likelihood plus a bias correction or penalty term for the number of parameters (number of variables + constant + error term) in the model. The model with the smallest  $AIC_c$  value is estimated to be the best approximation for the information in the data relative to the other models considered. Because of the penalty term, models with a larger number of parameters may have higher  $AIC_c$  values and thus a poorer fit. This follows the principle of parsimony in model selection and prevents over-fitting (Burnham & Anderson, 1998). Models derived from the data were ranked by  $AIC_c$  values with the model with the lowest  $AIC_c$  being the best approximation of the data.  $AIC_c$  differences between the best model and other models were computed and those with an  $AIC_c$  difference ( $\Delta_i$ ) of less than two are considered useful for making inferences (Burnham & Anderson, 1998). Akaike weights ( $w_i$ ) indicate the probability that a model is the best approximating model among the candidate models. Estimates for the relative importance of

each predictor variable were calculated by summing Akaike weights across all models in the set that include that variable. The larger the Akaike weight for a variable the greater its importance relative to the other variables. Importance values range from 0 (low importance) to 1 (high importance).

Multiple logistic regressions were performed using SigmaStat (version 2.0) and StatistiXL (version 1.6) was used for chi-square analysis of roost availability versus use (Lehner, 1996). Rayleigh and Hodges-Ajne tests were used to test for random and uniform circular distributions respectively (Zar, 1998). Hodges-Ajne tests were used to determine if aspects were uniformly distributed about the circle or focused in a northern direction by dividing the circle along the 90° (East) to 270° (West) line (Zar, 1998). Numerical values are presented as means ± SE for n = number of roosts and N = number of observations/days. An alpha value of 0.05 was used for all tests.

## **Results**

Sixteen owlet-nightjars were captured and the roost sites used by 14 individuals were located. One bird could not be relocated after release and another was killed by a feral cat (*Felis catus*).

### ***Roost Characteristics***

I measured the characteristics of a total of 22 tree hollow and 23 rock crevice roosts. Fifty-six random unoccupied tree hollows and 46 unoccupied rock crevices were measured for comparison (Tables 1 and 3).

#### ***Tree Hollow Roosts***

Analysis of the AICc values for tree roost models convincingly pointed to one model, including canopy cover (%), cavity height (m), and cavity aspect as having a 42% likelihood of being the best approximating model of the characteristics owlet-nightjars use to select tree roosts (Table 4):

$$\text{Logit (P)} = -1.381 - (0.0206*CC) + (0.219*CH) + (0.964*CAVCOS),$$

where P = the probability of a cavity being used by an owlet-nightjar. This model suggests that birds were selecting tree cavities with a low percentage of canopy cover (CC), at greater heights (CH), and with entrances that opened to the north (CAVCOS), compared to those

trees with cavities found randomly. This suggests that birds are selecting for thermal properties and choosing winter roosts with maximum sun exposure and lower quantities of shade. The mean canopy cover of tree roosts used by birds was 27.6% and none had more than 75% (Table 1). Mean cavity height of occupied roosts was 5.6 m compared to 4.2 m for random hollows and roost openings were focused north (Figure 1; Hodges –Ajne test:  $P < 0.05$ ). Analysis of variables indicated that cavity opening aspect (0.97), canopy cover (0.89) and cavity height (0.65) are the most important variables for tree roost selection (Table 5).

#### *Rock Crevice Roosts*

Analysis of AICc values for rock roost models indicates that owllet-nightjars are selecting rock crevices based primarily on depth alone and select deeper hollows (Table 6). There was a 30% probability that a model including depth as the only variable is the best fit:

$$\text{Logit (P)} = -2.323 + (0.0188 * \text{DEPTH})$$

There was also some support ( $\Delta_i < 2$ ; 22% probability of best fit) for a model including opening width and height, indicating that birds were selecting deep rock crevice roosts with narrow entrances.

$$\text{Logit (P)} = -1.739 - (0.00348 * \text{WIDTH}) - (0.0680 * \text{HEIGHT}) + (0.0316 * \text{DEPTH})$$

Analysis of rock crevice landscape models indicate that birds were selecting roosts on steeply sloped ranges facing northwest. There was a 39% probability that the best model includes hill slope (HILLSLP) and hill cosine (HILLCOS; north-south indicator) as variables and a 28% probability that a model adding hill sine (HILLSIN; east-west indicator) is the best fit (Table 6).

$$\text{Logit (P)} = -1.1913 + (0.0238 * \text{HILLSLP}) + 0.246 * \text{HILLCOS}$$

$$\text{Logit (P)} = -2.224 + (0.0298 * \text{HILLSLP}) + (0.225 * \text{HILLCOS}) - (0.716 * \text{HILLSIN})$$

A positive value for hill cosine indicates a northerly direction and a negative hill sine indicates a westerly direction (Figure 2). Both of these landscape models suggest that thermal

properties are an important consideration in owl-nightjar rock roost selection, and together there is a 67% probability that one of these two models represents the best model.

Analysis of the variables independently based on the Akaike weights of the models in which they were included strongly suggest that depth (0.96), hill slope (0.84) and hill cosine (0.84) are the most important variables used for roost selection (Table 7). Roost crevices were on average 22 cm deeper than random crevices, were on hills with a mean slope of 52°, and faced north rather than south. Hill aspects for both roosts and random cavities were distributed randomly (Rayleigh test: roosts:  $Z=2.15$ ,  $P=0.12$ ; random:  $Z=2.11$ ,  $P=0.12$ ), but both roosts and random cavities faced north (Hodges-Ajne test:  $P<0.0001$ ; Figure 2).

Owlet-nightjars did not select for rock type, using crevices in different rock types in the same proportion as they were available at random (Figure 3;  $X^2_{0.05,3}=1.93$ ,  $P=0.59$ ). Likewise, owl-nightjars selected tree species in the same proportion as those available ( $X^2_{0.05,3}=6.01$ ,  $P=0.11$ ), although there was a trend for birds to select desert bloodwood trees (*Eucalyptus gamophylla*) over stumps (Figure 4). Trees with hollows other than river red gums (*E. camaldulensis*) and bloodwoods were uncommon and never used as roosts. Trees in all stages of decay were used as roosts, and again the use of trees compared to random hollows did not differ (Figure 5;  $X^2_{0.05,5}=3.28$ ,  $P=0.66$ ). The degree of termite damage of roosts did not differ significantly from random trees ( $X^2_{0.05,3}=2.17$ ,  $P=0.54$ ).

### **Roosting Behaviour**

Individual birds used between one and seven different roosts, and most birds used a combination of rock crevices and tree hollows (Table 8; Figure 6). Data on roost choice were recorded for a total of 609 bird-days with a mean of 40 days per bird (range 12 to 102 days). On average, birds changed roosts every  $16.8 \pm 6.8$  days; however, this was highly variable (range = 1 to 102 days; Table 8). Birds seemed to rotate their use of roosts and frequently returned to cavities that had been used previously (N=22 occasions; n=9 birds). With the exception of two birds that used rock and trees roosts equally, the other five birds that used both rock and tree roosts generally preferred one type and spent only a few days in the other (Figure 6). Tree hollows were used as roosts on 398 days (65%) and rock crevices were used on 211 days (35%). Roosts were clustered close together relative to the overall home range area of individual birds (Chapter 7).

Radio-tagged owlet-nightjars always appeared to roost alone in this study. However, in a study I conducted in a eucalypt woodland in Northern NSW (Chapter 4 & 7), pairs of birds roosted together in the same tree hollow for several days during the breeding season (recorded for 2 separate pairs). In central Australia, two birds did use two of the same tree roosts, but because they were not radio-tagged at the same time it is unknown if they were roosting together or alternating roost occupancy. There was evidence that birds roosting in rock crevices scraped the crevice clean. Dried faeces were occasionally found outside the roost, but the inside floors of roosts were smooth and bare. There was no evidence of nest-building; however, old nest material, including pieces of wool, was found in a hollow stump used by one owlet-nightjar. It is likely that this material was placed there previously by another species of bird, as no other incidences of nest building by owlet-nightjars have ever been observed. Cavities used by owlet-nightjars were never occupied by another species of vertebrate. However, other species occasionally occupied a different hollow in the same tree including insectivorous bats, budgerigars (*Melopsittacus undulatus*), ringneck parrots (*Barnardius zonarius*), boobook owls (*Ninox novaeseelandiae*), and colonies of bees. Owlet-nightjars were observed basking at the entrance to tree hollows on three occasions (2 different individuals).

**Table 1:** Variables of owlet-nightjar tree hollow roosts and randomly selected unused hollows with mean  $\pm$  SE and the range of values for each variable. The abbreviation for each variable term is shown. Mean aspects in degrees are shown with 95% confidence intervals in brackets.

<b>VARIABLES</b>	<b>ABBREV.</b>	<b>ROOSTS Mean<math>\pm</math>SE</b>	<b>ROOSTS Range</b>	<b>RANDOM Mean<math>\pm</math>SE</b>	<b>RANDOM Range</b>
		n=22		n=56	
Tree Species	TS	2.09 $\pm$ 0.29	1-5	2.43 $\pm$ 0.24	1-7
Decay Stage (1-7)	DS	3.41 $\pm$ 0.34	2-7	3.31 $\pm$ 0.22	2-7
Diameter Breast Height (cm)	DBH	79.30 $\pm$ 12.52	10.5-225.1	78.28 $\pm$ 8.24	16.9-270.0
Tree Height (m)	TH	13.23 $\pm$ 0.29	1.9-28.5	15.15 $\pm$ 1.17	0.7-32.4
Cavity to First Leaves (m)	FLEAVES	3.27 $\pm$ 0.49	0-6	3.00 $\pm$ 0.25	0-6
% Canopy Cover	CC	27.64 $\pm$ 5.47	0-75	38.23 $\pm$ 4.00	0-90
Cavity Height (m)	CH	5.55 $\pm$ 0.71	0.5-11.3	4.24 $\pm$ 0.30	0.6-10.4
Cavity Aspect Cosine	CAVCOS	0.31 $\pm$ 0.13	-0.83-+1.00	-0.16 $\pm$ 0.10	-1.00-+0.99
Cavity Aspect Sine	CAVSIN	-0.05 $\pm$ 0.16	-1.00-+1.00	0.11 $\pm$ 0.67	-1.00-+0.98
Cavity Aspect (Deg.)		350 (70)		147 (72)	
Cavity Diameter (cm)	CAVDIA	16.07 $\pm$ 1.21	6-25	17.62 $\pm$ 1.50	5-66
Number Cavities in Tree	CAVNO	5.46 $\pm$ 0.97	1-19	3.91 $\pm$ 0.62	1-21
Distance to Nearest Tree (m)	DNT	7.12 $\pm$ 1.09	0.7-18.8	8.07 $\pm$ 0.0.73	0.9-25.1
Height Nearest Tree (m)	HNT	8.64 $\pm$ 3.73	3.6-18.0	10.10 $\pm$ 0.71	1.7-27.2
DNT with cavity (m)	DNTCAV	36.71 $\pm$ 35.23	2.0-160.0	29.01 $\pm$ 3.91	1.7-160.0
Degree of Hill Slope	HILLSLP	13.05 $\pm$ 3.20	0-45	9.36 $\pm$ 1.79	0-70
Hill Aspect Cosine	HILLCOS	0.02 $\pm$ 0.04	-0.22-+0.40	0.14 $\pm$ 0.08	-1.00-+1.00
Hill Aspect Sine	HILLSIN	0.25 $\pm$ 0.19	-1.00-+0.99	-0.03 $\pm$ 0.07	-1.00-+1.00
Hill Aspect (Deg.)		54 (77)		10 (>90)	
Fire Damage		1.14 $\pm$ 0.07	1-2	1.18 $\pm$ 0.05	1-2
Termites		0.73 $\pm$ 0.22	0-3	0.96 $\pm$ 0.16	0-3

**Table 2:** Decay stage classification of eucalypts applied to roost and random trees.

<b>Stage</b>	<b>Description</b>
1	Dense foliage, no sign of previous dieback. No dead, leafless branches.
2	Dense foliage, slight sign of dieback. Some dead leafless branches.
3	Average foliage density, obvious sign of dieback.
4	Sparse foliage. More leafless branches than those with leaves.
5	Virtually no leaves. Nearly dead.
6	Tree dead. Trunk > 3 m high. No leaves. Branches broken.
7	Tree dead. Trunk/stump < 3 m high. No leaves. Extensive decay. Outer shell soft.

Modified from Berman and Todd (1991).

**Table 3:** Roost and landscape variables of owlet-nightjar rock crevice roosts and randomly selected unused crevices with mean  $\pm$  SE and the range of values for each variable. The abbreviation for each variable term is shown. Mean aspect ( $^{\circ}$ ) shown with 95% confidence intervals in brackets.

	<b>ABBREV.</b>	<b>ROOSTS</b> Mean $\pm$ SE	<b>ROOSTS</b> Range	<b>RANDOM</b> Mean $\pm$ SE	<b>RANDOM</b> Range
<b>ROOST VARIABLES</b>		n=23		n=46	
Rock Type (1-4)	RT	2.04 $\pm$ 0.19	1-3	1.98 $\pm$ 0.15	1-4
Opening Width (cm)	WIDTH	24.63 $\pm$ 6.66	6-117	21.28 $\pm$ 2.72	5-85
Opening Height (cm)	HEIGHT	16.53 $\pm$ 2.97	5-56	18.94 $\pm$ 2.00	5-63
Depth of Crevice (cm)	DEPTH	75.33 $\pm$ 11.24	27-132	53.66 $\pm$ 4.95	12-135
Number of Exits	EXITS	1.32 $\pm$ 0.15	1-3	1.30 $\pm$ 0.08	1-3
Cavity Aspect Cosine	CAVCOS	0.19 $\pm$ 0.13	-0.97-+1.00	0.005 $\pm$ 0.10	-1.00-+1.00
Cavity Aspect Sine	CAVSIN	-0.16 $\pm$ 0.18	-0.99-+1.00	0.03 $\pm$ 0.11	-1.00-+1.00
Cavity Aspect (Degrees)		311 (>90)		85 (>90)	
<b>LANDSCAPE VARIABLES</b>		n=23		n=46	
Altitude	ALT	716 $\pm$ 14	616-858	718 $\pm$ 8	612-858
No. of Crevices in Cliff	CAVNO	4.70 $\pm$ 0.96	0-21	3.65 $\pm$ 0.61	0-20
Degree of Cliff Slope	CLFSLP	70.30 $\pm$ 5.00	20-100	72.07 $\pm$ 3.23	32-110
Cliff Aspect Cosine	CLFCOS	0.42 $\pm$ 0.15	-1.00-+1.00	0.25 $\pm$ 0.77	-0.99-+1.00
Cliff Aspect Sine	CLFSIN	-0.08 $\pm$ 0.12	-1.00-+0.98	-0.02 $\pm$ 0.09	-1.00-+1.00
Cliff Aspect (Degrees)		350 (42)		355 (54)	
Degree of Hill Slope	HILLSLP	52.43 $\pm$ 5.50	5-90	41.48 $\pm$ 2.70	5-90
Hill Aspect Cosine	HILLCOS	0.49 $\pm$ 0.16	-1.00-+1.00	-0.01 $\pm$ 0.08	-1.00-+1.00
Hill Aspect Sine	HILLSIN	-0.09 $\pm$ 0.09	-0.91-+0.99	0.35 $\pm$ 0.11	-1.00-+1.00
Hill Aspect (Degrees)		353 (34)		358 (37)	

**Table 4:** Rankings based on Akaike’s Information Criteria corrected for small sample size ( $AIC_c$ ) for 23 logistic regression models comparing tree roosts of owlet-nightjars to random unused tree hollows. Type indicates whether the model contains only variables that affect thermal properties (T), or protective properties (P) of the cavity, or a combination of the two (TP).  $K$  is the number of parameters in the model including all variables, the constant, and the error term.  $\Delta_i$  is the difference in  $AIC_c$  value between the  $i$ th and top-ranked model and  $w_i$  is the Akaike weight (probability that the  $i$ th model is actually the best approximating model among the candidate models). Twenty-two roosts were compared to 56 randomly selected hollows. See Table 1 for variable definitions.

TYPE	MODEL	$K$	$AIC_c$	$\Delta_i$	$w_i$
T	CH, CC, CAVCOS	5	89.49	0.00	0.421
T	CC, CAVCOS	4	91.56	2.07	0.150
T	DBH, CH, CC, CAVCOS	6	91.84	2.35	0.130
T	CC, CAVCOS, CAVSIN	5	93.27	3.78	0.064
P	CH, CC, DNTCAV	5	93.92	4.43	0.046
T	CAVCOS, CAVSIN, HILLSLP	5	94.63	5.14	0.032
T	CC, CAVCOS, CAVSIN, CAVDIS	6	95.06	5.57	0.026
TP	CAVNO, CH, DNTCAV	5	95.47	5.98	0.021
TP	DBH, CH, CC	5	95.72	6.23	0.019
P	TH, CAVNO	4	95.96	6.47	0.017
P	CH, CC, CAVNO, DNT	6	96.43	6.94	0.013
TP	DS, DBH, TH, CC, CH, CAVNO, DNT	9	96.64	7.14	0.012
TP	DS, DBH, TH, CC, CH, CAVCOS, CAVDIA, CAVNO, DNTCAV	11	96.80	7.31	0.011
TP	CH, CAVDIA	4	97.12	7.63	0.009
T	DBH, CH, CC, CAVCOS, CAVSIN, CAVDIA, HILLSLP	9	97.14	7.65	0.009
TP	CAVNO, CH, DNTCAV, TS	6	97.56	8.07	0.007
P	TH, FLEAVERS, CC	5	98.36	8.87	0.005
P	CH, CC, CAVDIA, CAVNO, DNT, HNT, DNTCAV	9	98.75	9.26	0.004
TP	TS, DS, DBH, TH, FLEAVES, CC, CH, CAVCOS, CAVSIN, CAVDIA, CAVNO, DNT, HNT, DNTCAV, HILLSLP	17	100.75	11.25	0.002
TP	DBH, TH, CAVDIA	5	101.41	11.92	0.001
P	TH, DNT, HNT	5	101.74	12.25	0.001
P	TH, FLEAVES, CC, CH, CAVDIA, CAVNO, DNT, HNT, DNTCAV	10	102.55	13.06	0.001
TP	TS, DS, DBH, CAVCOS, CAVSIN, CAVNO, DNT, DNTCAV	10	103.45	13.96	0.000

**Table 5:** Relative importance of variables for predicting tree hollow use by owllet-nightjars. Variables are defined in Table 1. The larger the Akaike weight ( $w_+$ ) for a variable the more important it is relative to the other variables. Importance values range from 0 (low importance) to 1 (high importance).

<b>TYPE</b>	<b>VARIABLE</b>	<b><math>w_+</math></b>
T	CAVCOS	0.973
TP	CC	0.886
TP	CH	0.645
T	CAVSIN	0.262
P	TH	0.210
P	CAVNO	0.190
TP	DBH	0.184
T	HILLSLP	0.172
P	DNTCAV	0.046
P	DNT	0.036
TP	CAVDIA	0.027
T	DS	0.025
P	HNT	0.013
	TS	0.009
P	FLEAVES	0.007

**Table 6:** Rankings based on Akaike’s Information Criteria corrected for small sample size ( $AIC_c$ ) for 22 logistic regression models comparing rock roosts used by owlet-nightjars to random unused rock crevices. Type,  $K$ ,  $\Delta_i$  and  $w_i$  are as described in Table 4. Twelve roosts were compared to 37 random crevices for analysis of roost variables and 23 roosts were compared to 46 random crevices for landscape variables. See Table 3 for variable definitions.

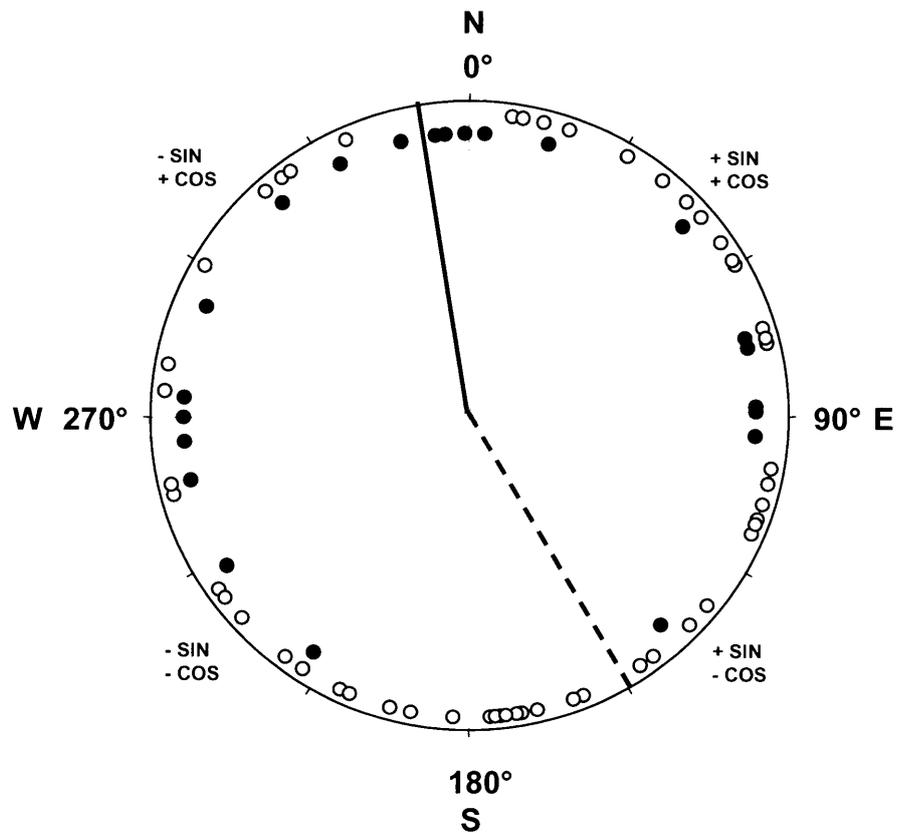
TYPE	MODEL	$K$	$AIC_c$	$\Delta_i$	$w_i$
<b>ROOST VARIABLES</b>					
TP	DEPTH	3	57.38	0.00	0.303
TP	WIDTH, HEIGHT, DEPTH	5	58.04	0.65	0.219
T	DEPTH, CAVCOS	4	59.641	2.26	0.098
P	DEPTH, EXITS	4	59.73	2.35	0.094
T	RT, WIDTH, HEIGHT, DEPTH	6	59.97	2.58	0.083
P	WIDTH, HEIGHT, DEPTH, EXITS	6	60.47	3.09	0.065
T	WIDTH, HEIGHT, DEPTH, CAVCOS	6	60.52	3.14	0.063
TP	WIDTH, HEIGHT	4	62.33	4.95	0.026
T	WIDTH, HEIGHT, DEPTH, CAVCOS, CAVSIN	7	62.46	5.07	0.024
P	WIDTH, HEIGHT, EXITS	5	64.16	6.78	0.010
T	WIDTH, HEIGHT, CAVCOS	5	64.82	7.43	0.007
T	RT, WIDTH, HEIGHT, DEPTH, CAVCOS, CAVSIN	8	64.98	7.60	0.007
TP	RT, WIDTH, HEIGHT, DEPTH, EXITS, CAVCOS, CAVSIN	9	67.87	10.49	0.002
<b>LANDSCAPE VARIABLES</b>					
T	HILLSLP, HILLCOS	4	92.05	0.00	0.386
T	HILLSLP, HILLCOS, HILLSIN	5	92.70	0.66	0.278
TP	CLIFFSLP, HILLSLP, HILLCOS, HILLSIN	6	94.55	2.50	0.110
P	CAVNO, CLFSLP	4	95.42	3.37	0.072
T	CLFSLP, CLFCOS	4	95.66	3.61	0.064
TP	CAVNO, CLFSLP, HILLSLP, HILLCOS, HILLSIN	7	96.24	4.19	0.048
T	CLFSLP, CLFCOS, CLFSIN	5	97.83	5.78	0.021
TP	CLFSLP, CLFCOS, CLFSIN, HILLSLP, HILLCOS, HILLSIN	8	98.76	6.72	0.013
TP	CAVNO, CLFSLP, CLFCOS, CLFSIN, HILLSLP, HILLCOS, HILLSIN	9	99.67	7.64	0.008

**Table 7:** Relative importance of variables in predicting rock crevice use by owlet-nightjars. Variables are defined in Table 3. The larger the Akaike weight ( $w_+$ ) for a variable, the more important it is relative to the other variables. Importance values range from 0 (low importance) to 1 (high importance).

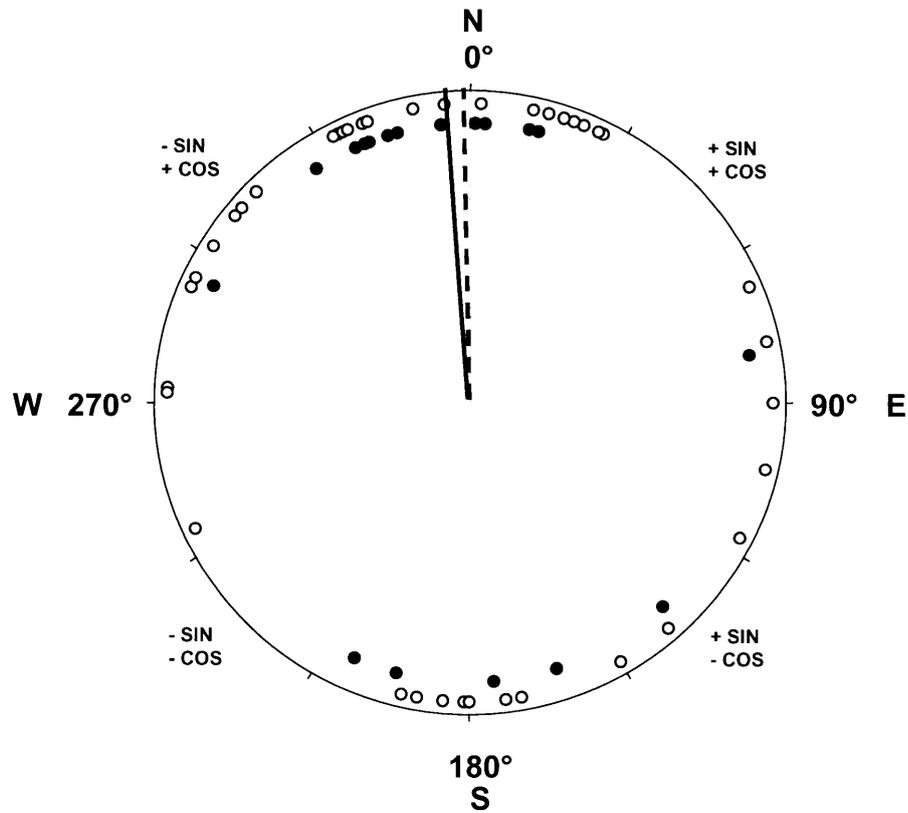
<b>TYPE</b>	<b>VARIABLE</b>	<b><math>w_+</math></b>
<b>ROOST VARIABLES</b>		
TP	DEPTH	0.957
TP	WIDTH	0.505
TP	HEIGHT	0.412
T	CAVCOS	0.201
P	EXITS	0.160
T	CAVSIN	0.032
T	RT	0.008
<b>LANDSCAPE VARIABLES</b>		
T	HILLSLP	0.844
T	HILLCOS	0.844
T	HILLSIN	0.458
TP	CLFSLP	0.366
P	CAVNO	0.128
T	CLFCOS	0.107
T	CLFSIN	0.043

**Table 8:** Roost selection and rate of roost switching (roost fidelity) by Australian owl-nightjars (ONJ) in central Australia.

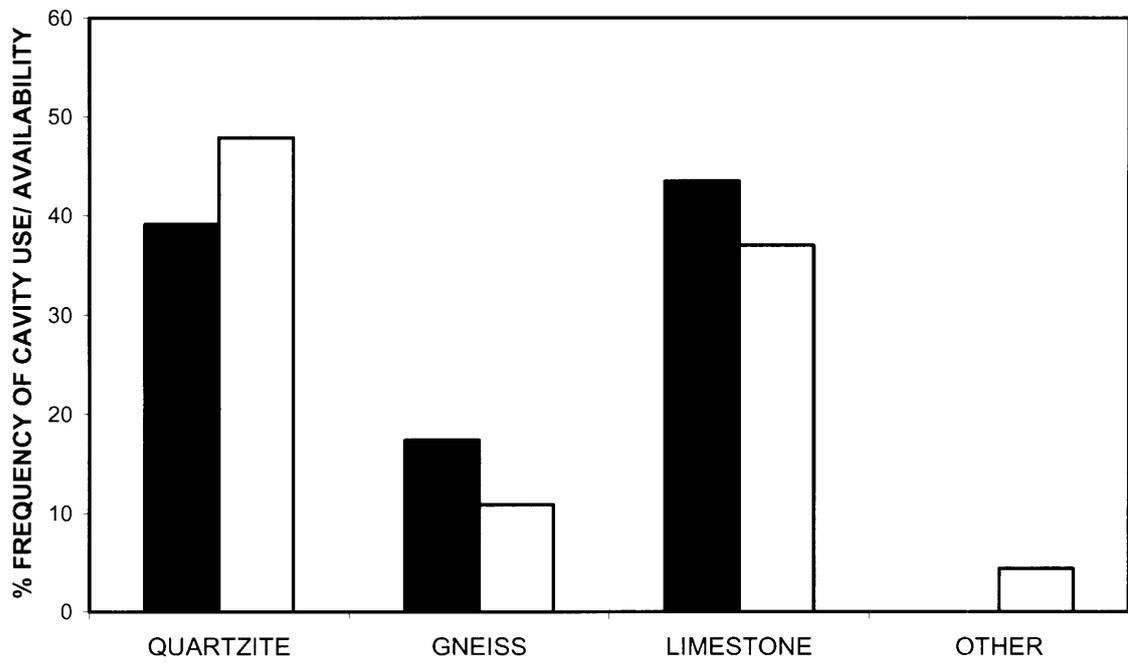
<b>Owlet-Nightjar ID</b>	<b>No. of Roosts</b>		<b>No. of Days in each Roost Type</b>		<b>Mean No. Days Between Roost Switch</b>
	<b>Rock</b>	<b>Tree</b>	<b>Rock</b>	<b>Tree</b>	
ONJ 4	0	1	0	102	102
ONJ 6	3	0	65	0	21
ONJ 7	0	1	0	12	12
ONJ 8	1	3	2	64	12.9
ONJ 9	2	5	30	42	4.2
ONJ 10	2	0	33	0	10.3
ONJ 11	1	2	16	13	9.7
ONJ 13	1	1	4	56	19.7
ONJ 14	1	2	2	29	5.0
ONJ 16	0	5	0	45	4.7
ONJ 17	1	2	4	34	6.5
ONJ 18	3	0	15	0	1.7
ONJ 19	1	0	22	0	22
ONJ 20	2	2	19	4	3.2



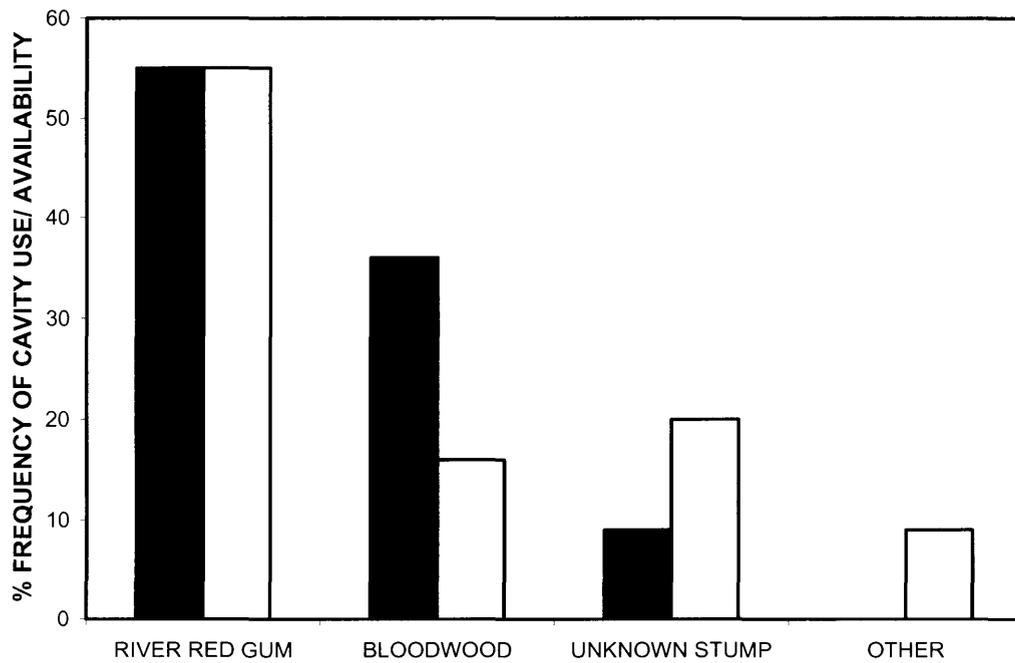
**Figure 1:** Compass orientation of the entrance aspect of occupied tree hollow roosts (•) and unoccupied random tree hollows (o). Entrance aspect were randomly distributed for roosts and random hollows (Rayleigh test: roosts:  $Z=2.15$ ,  $P=0.12$ ; random:  $Z=2.11$ ,  $P=0.12$ ). However, it is evident that owlet-nightjars avoided roosts facing south. Hodges–Ajne tests indicated that roost aspects were focused northerly above the  $90^\circ$  to  $270^\circ$  line ( $P<0.05$ ) and random cavities were uniformly distributed north and south ( $P=0.18$ ). The mean aspect of roosts (solid line) was north while the mean direction of random cavities (dashed line) was south-southeast.



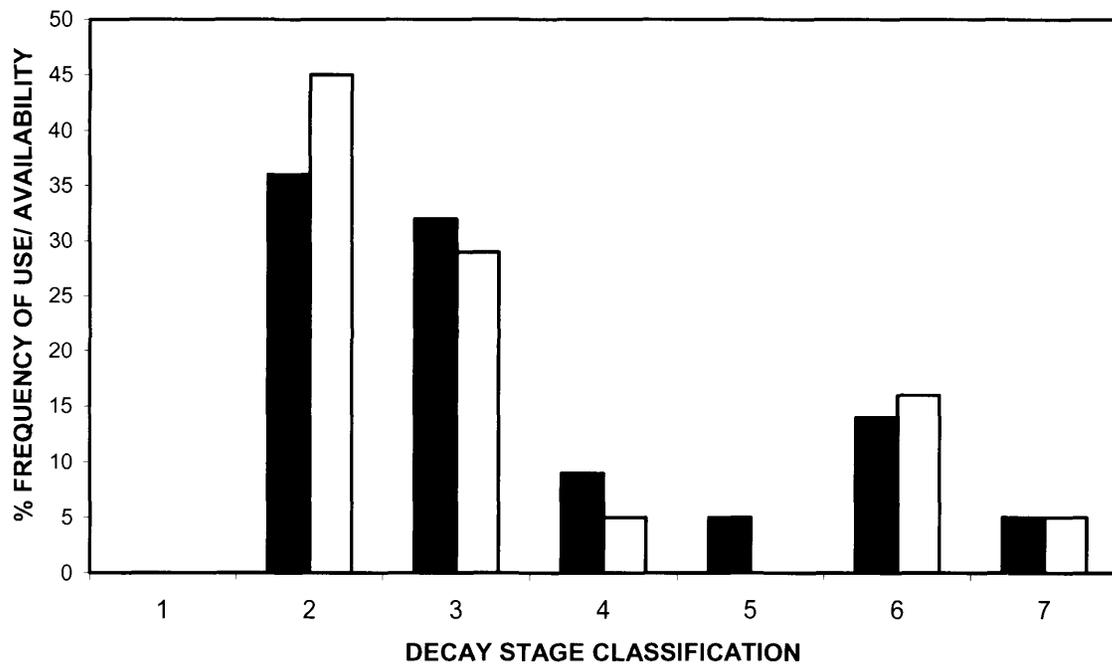
**Figure 2:** Compass orientation of the hill slope where rock crevice roosts (●) and unoccupied random rock crevices (o) were located. Rayleigh tests indicated that both roosts and unoccupied crevices had a non-random distribution (roosts:  $Z=5.66$ ,  $P<0.01$ ; random:  $Z=5.10$ ,  $P<0.01$ ). Sample mean direction is indicated for roosts (solid line) and random cavities (dashed line). Hodges-Ajne tests indicated that the hill aspects of both roosts and random cavities faced north above the  $90^\circ$  to  $270^\circ$  line ( $P<0.0001$ ), which was indicative of the general landscape of the ranges. However, random crevices had a greater dispersion of points than roosts, which were almost exclusively found on hills facing north.



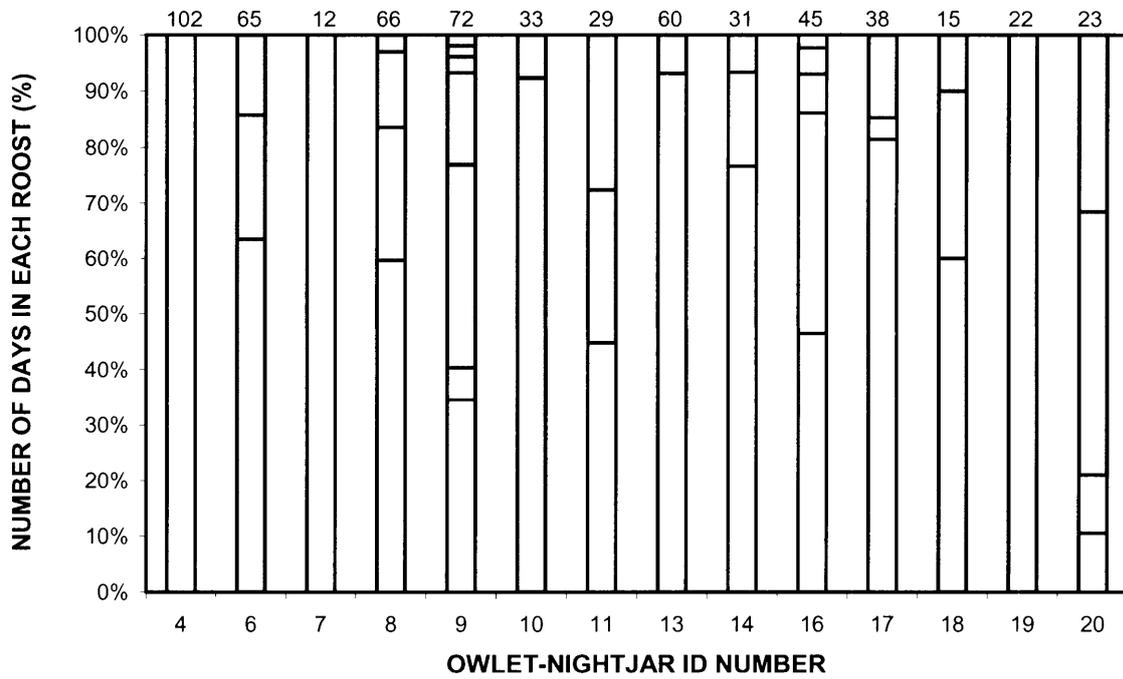
**Figure 3:** Owlet-nightjars roosted in cavities of rock crevices (black bars, n=23) in quartzite, gneiss, limestone or other in the same proportion as random crevices were available (white bars, n=56;  $\chi^2_{0.05,3}=1.93$ ,  $P=0.59$ ).



**Figure 4:** Owlet-nightjars roosted in hollows (black bars, n=22) in river red gums (*Eucalyptus camaldulensis*), desert bloodwoods (*Eucalyptus gamophylla*) or in dead stumps. The use of tree species as roosts did not differ significantly from that expected based on availability of randomly selected hollows (white bars, n=56;  $\chi^2_{0.05,3}=6.01$ ,  $P=0.11$ ). Trees with suitable unoccupied hollows not used by owlet-nightjars included supplejacks (*Ventilago sp.*), ghost gums (*Eucalyptus papuana*), corkwoods (*Hakea suberea*), and mulga (*Acacia aneura*).



**Figure 5:** Owlet-nightjars used roost trees (black bars; n=22) in all decay stages in the same proportion as they were available (white bars; n=56;  $\chi^2_{0.05,5}=3.28$ ,  $P=0.66$ ). Decay stage classifications are given in Table 2.



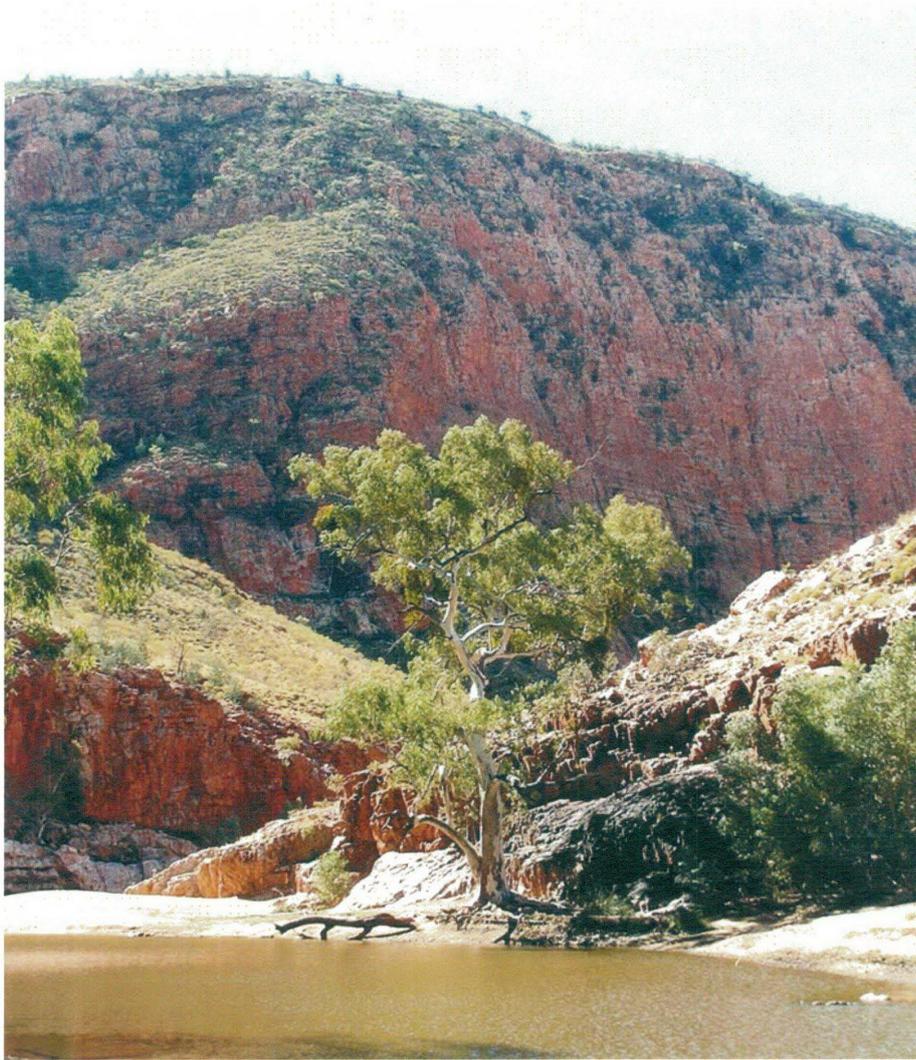
**Figure 6:** The percentage of days in which each of the 14 owlet-nightjars used tree hollow (white) or rock crevice (grey) roosts. The total number of days an individual was tracked is given at the top of each bar.



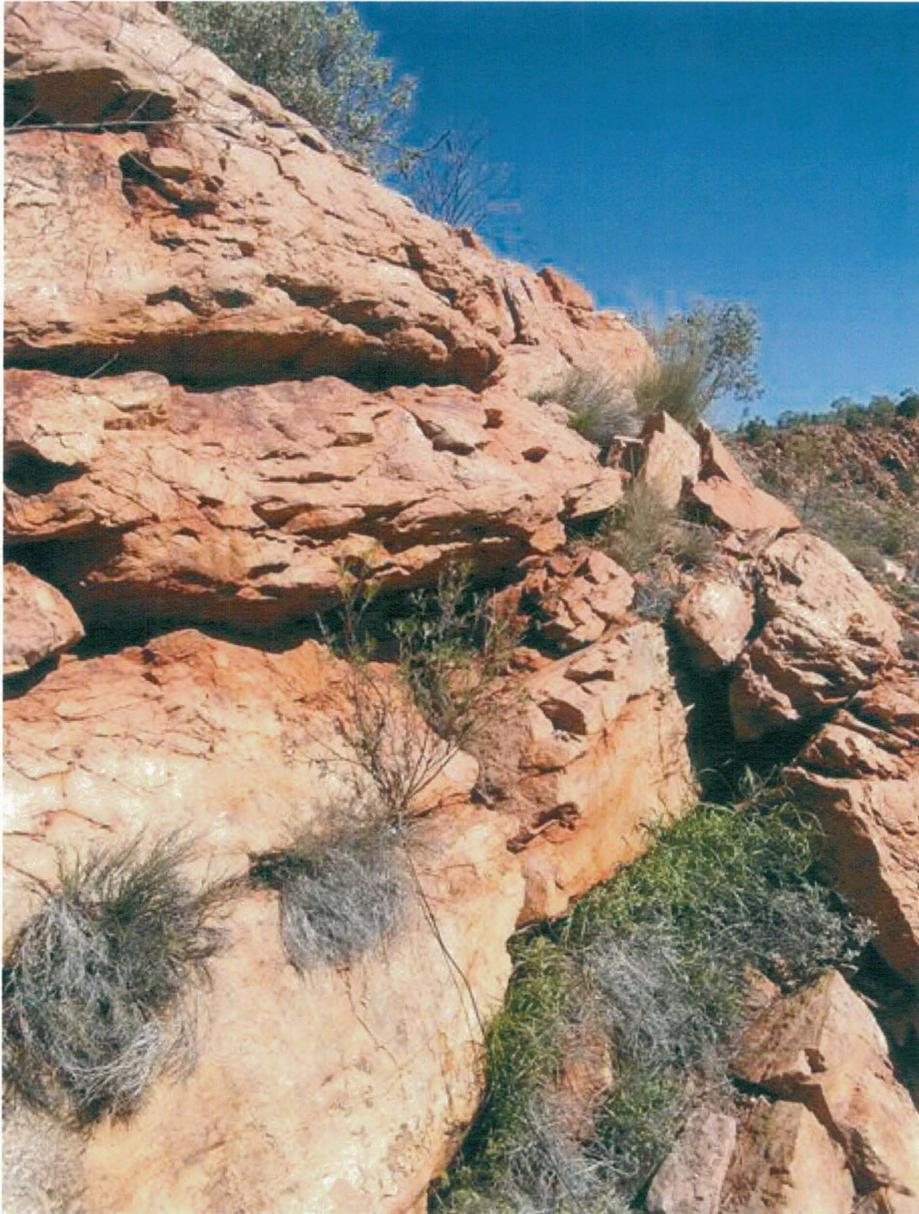
**Plate 1:** Owlet-nightjars often selected tree roosts in the hollow spouts left in river red gums (*E. camaldulensis*) after the branches had decayed and dropped off. Photo by L. I. Doucette.



**Plate 2:** Hollows were abundant in river red gums (*E. camaldulensis*) throughout the dry river channels. Up to 21 hollows were recorded for one tree. Photo by L. I. Doucette.



**Plate 3:** The permanent waterhole at Ormiston Gorge and the surrounding cliffs. Both study sites were set amongst steeply sloping ranges reaching heights up to 400 m with many potential rock crevice roosts available for owlet-nightjars. Photo by L. I Doucette.



**Plate 4:** The quartzite and limestone rock that form these ranges supplied an abundance of rock crevices for potential roosts. In the centre of this image is one of the rock crevice roosts used by an individual owlet-nightjar for 40 days. This steep sloping hill side is north facing. Photo by L. I. Doucette.



**Plate 5:** Although owlet-nightjars usually roosted in crevices, they were occasionally found to roost under rocks. The circle in this image indicates the slab of rock an owlet-nightjar roosted under for 32 days. The large rock beneath this roost, located on a north-facing slope, was heated substantially during the day. Photo by L.I. Doucette.



**Plate 6:** Owlet-nightjars select a variety of roost types. One bird roosted in a hollow between two rocks in this bank on the side of the road for four days. The bank faced west and temperatures inside the roost reached up to 37 °C in late afternoon. Photo by L. I. Doucette.

## **Discussion**

My study suggests that owlet-nightjars are selecting both rock and tree roosts based primarily on their thermal microclimate and that predator avoidance is only a secondary consideration. Since most animals spend the majority of their time at rest, an energy saving strategy such as selecting a thermally insulated roost can significantly affect an organism's total energy budget (Kurta, 1985); Chapter 2). Roosting in a cavity, compared to exposed in the open, would also substantially reduce the predation risk to a small bird. The use of cavities as roosts throughout the year is likely strongly motivated by predator avoidance. However, the actual roost characteristics that an animal selects for may be less motivated by predation risk compared to thermal microclimate. Simply roosting in any cavity may be enough to avoid predation, but roost microclimate is strongly affected by roost characteristics.

### ***Roost Characteristics: Tree Roosts***

Owlet-nightjars typically selected tree roosts in the hollow spouts left in river red gums after the branches have decayed and dropped off (Plate 1). These types of hollows were abundant in river red gums in the dry river channels and did not appear to be a limited resource (Plate 2). Eucalypt trees >120 years old naturally form hollows as the heartwood decays and the tree is hollowed out by fungi and termites. Branches are also shed continually as eucalypts grow and branches may be broken by wind (Gibbons & Lindenmayer, 2002). Up to 21 hollows were identified in some of the river red gums assessed in this study (Table 1). This is likely an underestimate as it is difficult to accurately assess the number of hollows from the ground (Gibbons & Lindenmayer, 2002). At least at my study sites, owlet-nightjars appear to have a variety of tree hollows to choose from when selecting a roost.

My data indicate that owlet-nightjars select winter roosts that provide maximum sun exposure and/or warm, stable microclimates. This supports my prediction that thermal microclimate is the most important determination of hollow use. Australian owlet-nightjars selected tree hollows with a northern entrance aspect, a low percentage of canopy cover, and high cavity height.

Several studies have found cavity entrance aspect to be important for roost selection by birds (Ricklefs & Hainsworth, 1969; Finch, 1983; Tidemann et al., 1992; Zwartjes & Nordell, 1998). Depending on season and reproductive status, individuals may favor (Ricklefs & Hainsworth, 1969; Finch, 1983; Tidemann et al., 1992) or avoid (Zwartjes & Nordell, 1998) cavities that have maximum sun exposure. In my study, northern entrance aspect stood out as

the variable of greatest importance in hollow selection. However, data on  $T_a$  inside tree hollows indicated that northern facing entrances were not warmer than hollows facing other directions (Chapter 2). Poor insulative qualities meant that the temperature inside tree hollows generally reflected outside  $T_a$ . Narrow roost entrances would only allow minimal sun penetration into the hollow and internal  $T_a$  may be more dependent on the surface area of the branch exposed to the sun. However, northern facing entrances would provide the opportunity for owlet-nightjars to bask in the sun to maintain body temperature or passively rewarm from torpor (Geiser et al., 2002; Geiser & Drury, 2003; Geiser et al., 2004). Species that roost in the open on branches frequently choose locations or positions that maximize sun exposure. Tawny frogmouths (*Podargus strigoides*) in Australia select roosts with a northerly orientation during winter to aid them in passive rewarming (Körtner & Geiser, 1999). Likewise, tree roosting bats in the northern hemisphere, a group of mammals that would also substantially benefit from passive rewarming (Turbill et al., 2003), select winter roosts that maximized sun exposure during the day with low canopy cover and southern aspects (Hein et al., 2005; Mormann & Robbins, 2005; Willis & Brigham, 2005).

A low percentage of canopy cover over a roost would also serve to enhance sun exposure, leading to a warmer microclimate inside a cavity. The presence of dense canopy cover and north-facing landscape slopes decreased the  $T_a$  of spotted owl (*Strix occidentalis*) roosts in North America by up to 6 °C (Barrows, 1981). Bats have been found to select roosts in tall trees with a low density of canopy cover that are exposed to sunlight (Vonhof & Barclay, 1996; Brigham et al., 1997b; Campbell et al., 2005; Kalcounis-Rüppell et al., 2005; Ruczynski & Bogdanowicz, 2005; Willis & Brigham, 2005). Common poorwills (*Phalaenoptilus nuttallii*) also chose roost sites with less overhead cover, presumably to take advantage of sunlight to passively rewarm from torpor (Wang & Brigham, 1997). Increased cavity height would further lessen the possibility of shading from the surrounding slopes and landscape (Sedgeley, 2001). Ruczynski (2006) found a 1.2 °C increase in mean  $T_a$  on the outside of tree trunks between 0 and 10 m, which she attributed to decreased shading at greater heights in a forest. Minimum  $T_a$  inside tree cavities was slightly warmer in higher tree cavities and less affected by nocturnal thermal inversion (Chapter 2).

I only observed basking by owlet-nightjars on three occasions during my study in central Australia; however basking was observed more frequently in a colder forested location during winter (4 birds, 5 roosts, 12 occasions during 62 bird-days; Chapter 4). Basking is likely far more common than we detect, but birds may quickly retreat into hollows when approached.

Basking would play an integral part in reducing energetic costs of small birds during winter and would aid in passive rewarming with increasing  $T_a$  and radiant heat (Geiser et al., 2002; Geiser & Drury, 2003; Geiser et al., 2004). All the variables included in the final model for tree hollow selection indicate that owlet-nightjars selected roosts that favor maximum sun exposure and higher internal  $T_a$  during winter.

The characteristics used for selection of tree hollows in my study in central Australia differed from those found during a year-round study of roost selection by forest-dwelling owlet-nightjars in a cool-temperate, montane region (Brigham et al., 1998). Logistic regression modeling by Brigham et al. (1998) comparing roost hollows with unoccupied hollows showed that owlet-nightjars preferentially roosted in tree cavities closer to the ground, in trees with a greater number of cavities, and in cavities significantly closer to another tree with a cavity than expected by chance. As characteristics of cavities used during the breeding season in summer and those in winter were combined by Brigham et al. (1998) it is possible that selection for thermal characteristics may be masked. The finding that birds selected roosts closer to the ground may be a reflection of roost selection during the breeding season, when most of the birds were tracked (see Brigham et al., 2000). Owlet-nightjars typically selected nest sites in stumps low to the ground (Brigham & Geiser, 1997; Brigham et al., 1997a). Selection for trees with multiple hollows and those close to alternate trees with cavities may reflect the higher levels of predation at this site (Brigham & Geiser, 1997; see discussion of Roosting Behaviour below). Trees with many cavities provide more potential escape points and increase the chance of an individual avoiding a predator (Brigham et al., 1998; Britzke et al., 2005). Owlet-nightjars that were flushed from hollows usually flew rapidly into a cavity of a nearby tree, suggesting that predator avoidance was a major function of roost choice.

Roost variables that I characterized as important for minimizing the risk of predation in tree cavities were low on the relative variable importance scale in my study (Table 5). While birds selected trees that had more cavities, were closer to other trees, and closer to trees with cavities than random unused trees (Table 1), these variables were outweighed in importance by thermal characteristics (Table 5). In contrast, bats roosting under bridges in Louisiana selected areas that minimized their visibility and accessibility by predators despite the higher  $T_a$ s (mean  $T_a = 31^\circ\text{C}$ ) in these areas during summer (Ferrara & Leberg, 2005). High tree cavity height has been found to reduce nest predation in birds (Nilsson, 1984; Rendell & Robertson, 1989; Tidemann et al., 1992), and may be one tree roost characteristic selected to reduce predation risk in this study. However, cavity roost height may or may not serve to

deter predators depending on predator type (Tideman & Flavel, 1987; Ruczynski & Bogdanowicz, 2005). Higher cavities reduced the rate of predation by pine martins (*Martes martes*) on tree-roosting bats in Poland (Ruczynski & Bogdanowicz, 2005), but at my study sites there were no potential arboreal predators other than snakes and monitor lizards, which would likely be undeterred by cavity height provided there was clear access to the entrance (Tideman & Flavel, 1987). Higher cavities may be less likely to be discovered by a predator on the ground (Vonhof & Barclay, 1996). Gibbons et al. (2002) proposed that tree hollows with narrow entrances and greater depth may be preferred because they are more difficult to access by predators. I did not measure hollow depth, but cavity entrance diameter appeared in few high ranking models. Animals typically select hollows with entrances only slightly larger than their own body size to deter predators (Saunders et al., 1982; Tideman & Flavel, 1987; Campbell et al., 2005). On average, tree hollow roost entrances were  $16.1 \pm 1.2$  cm in this study, about 10 cm larger than an owlet-nightjar, emphasizing that hollow selection was not focused on predator avoidance.

Similar to Brigham et al. (1998), I found that tree species, decay stage, tree diameter and tree height were not important for roost selection by owlet nightjars. This is in contrast to findings for other cavity roosting species (Brigham et al., 1997b; Gibbons & Lindenmayer, 2002; Gibbons et al., 2002; Broders & Forbes, 2004; Britzke et al., 2005; Campbell et al., 2005; Boyles & Robbins, 2006; Rhodes & Wardell-Johnson, 2006). However, apart from decay stage, these characteristics appear to have relatively little influence on the degree of thermal buffering or predator protection offered by a cavity. Dead timber (greater stage of decay) would heat up more quickly than live trees (Turbill, 2006), but decay stage was not selected for by owlet-nightjars in this study and may be less relevant than other thermal variables.

### ***Roost Characteristics: Rock Roosts***

Both field sites in this study were set amongst steeply sloping ranges reaching heights up to 400 m above the surrounding landscape (Plate 3). The quartzite and limestone rock that formed these ranges supplied an abundance of rock crevices for potential roosts (Plate 4). Owlet-nightjars roosted under rocks (Plate 5) and on the banks by the side of roads (Plate 6), but preferred deep, narrow entranced rock crevices on steep, northern facing slopes that have maximum sun exposure throughout the day.

Greater depth of a rock crevice increases thermal insulation and thermal stability, which keeps roosts warm on cold days and overnight, and cool on hot days (see Chapter 2; (Lausen &

Barclay, 2003; Neubaum et al., 2006). Roosts with stable microclimates are thermally predictable and may enable animals to make decisions regarding energy conservation, such as whether or not to enter torpor (Solick & Barclay, 2006). Deeper rock crevices have the added advantage in that they can provide a gradient of thermal conditions that potentially allow for behavioural thermoregulation (Lausen & Barclay, 2003; Chruszcz & Barclay, 2002). Smaller entrances to roosts should minimize air exchange between the cavity and the environment and increase the thermal buffering capability of the crevice (Ruczynski & Bogdanowicz, 2005). Lausen & Barclay (2003) found that rock crevices with larger openings cooled faster after sunset. Increased air flow would cause the hollow to be thermally unstable and quickly affected by external heating. Deeper crevices with narrow entrances would also aid in decreasing predation risk. However, the large opening size (mean = 24.6 x 16.5 cm) of crevices in this study would not exclude potential predators such as the mulga snake (*Pseudechis australis*). Even if owlet-nightjars would choose crevices with entrances no larger than themselves for maximum predator protection snakes would still be able to gain access (Saunders et al., 1982; Tideman & Flavel, 1987).

Nocturnal thermal inversion means that rock crevice roosts higher on slopes generally stay warmer overnight and are more thermally stable (Chapter 2). Steeper slopes allow cold air to descend at night, leaving warmer air at high levels, and reducing the overall  $T_a$  fluctuation during a 24 h period. Steep, north facing slopes also receive more direct sunlight during the winter months. Rock roosting bats in the northern hemisphere selected roosts in rock fields on steep, south-facing slopes that were unobstructed by vegetation (Solick & Barclay, 2006). In such roosts, daytime roost  $T_a$  often exceeded external  $T_a$ . The aspect of the range itself is more relevant in determining thermal microclimate than the entrance aspect of the roost (Lausen & Barclay, 2002). The dark-colored, north facing slope of the West MacDonnell Range is heated extensively by solar radiation throughout the day and heat is conducted throughout the cliff face to the rock crevice (see Chapter 2).

### ***Predator Avoidance***

Potential arboreal predators of owlet-nightjars roosting in tree hollows are the central carpet python (*Morelia spilota bredli*), and the pygmy mulga monitor lizard (*Varanus gilleni*; C.R. Pavey, pers. comm.). Central carpet pythons were recorded as abundant in the West MacDonnell Ranges with a density of 1 per 6.7 ha in 2003 (G. Bedford, unpublished data.), but I observed none in the course of this study. Large snakes, such as the mulga snake and the perentie (*Varanus giganteus*) may prey on owlet-nightjars in rock crevices (Broadbent, 1910).

However, owlet-nightjars likely experience the greatest risk of predation while out of the roost foraging, especially when foraging on the ground (Chapter 6). In this study three birds were depredated by feral cats (*Felis catus*) and one by a southern boobook owl (*Ninox novaeseelandiae*) while foraging. Barn owls (*Tyto alba*) and dingoes (*Canis lupus dingo*) may also be important predators in this area.

In some cases, selecting a roost with characteristics to avoid or reduce predation would reduce the thermal buffering capacity of a roost. For example, owlet-nightjars did not select rock crevice roosts with multiple exits to potentially allow for escape, indicating that increased thermal buffering of a roost with fewer exits was a more important characteristic than reducing predation risk. Likewise, increased canopy cover may obscure the view of an aerial predator as a bird leaves the roost, but roosts with reduced canopy cover overhead have greater sun exposure resulting in warmer roosts and the potential for basking. Thus, in cases where a bird must choose between a roost with a better thermal microclimate and one with a reduced risk of predation, selection seems to have favoured microclimate. When birds did select roost site characteristics that are consistent with reducing predation risk, such as deeper rock crevices with smaller entrances, the difference was not great enough to preclude predators. These features also functioned to improve the microclimate of the roost. Hence, the use of cavities for protection from predators is likely a secondary consideration in roost selection by owlet-nightjars.

### ***Thermal Microclimate***

Many studies of heterothermic bats and birds living in cold climates have identified roost microclimate as important in roost selection (Calder, 1973; Calder & Booser, 1973; Kerth et al., 2001; Sedgely, 2001; Chruszcz & Barclay, 2002; Turbill et al., 2003; Smith & Racey, 2005; Lausen & Barclay, 2006; Neubaum et al., 2006; Solick & Barclay, 2006). Like owlet-nightjars, bats tended to select either warmer, thermally stable roosts (Sedgely, 2001; Lausen & Barclay, 2003; Lausen & Barclay, 2006; Willis & Brigham, 2007), or those which allowed for passive rewarming through solar radiation (Turbill et al., 2003). Passive rewarming can reduce energetic costs of arousal by up to 85% in small mammals (Geiser et al., 2004). Lovegrove et al. (1999) suggested that nocturnal animals should select refugia that allow individuals to passively rewarm as  $T_a$  increases during the day.

Small birds may experience significant thermoregulatory stress during periods of temperature extremes. Cavity roosts are commonly used to avoid both heat and cold and individuals

roosting in hollows would benefit from substantial thermoregulatory advantages year round. Hummingbirds (Trochilidae) experience high energetic costs due to their small size, high rate of activity, and seasonal food supply, and most species regularly use cavities and caves for thermal protection from both heat and cold. Hillstar hummingbirds (*Oreotrochilus estella*) in the high Andes use caves to avoid extreme cold, and the blue-throated (*Lampornis clemenciae*), Hillstar (*Oreotrochilus chimborazo*) and Calliope (*Stellula calliope*) hummingbirds nest in rocks or tree limbs to avoid direct solar radiation (Calder, 1973; Calder & Booser, 1973). Desert birds regularly use the burrows of other species to avoid extreme heat and can reduce water loss by up to 81% during the hottest part of the day (Williams et al., 1999). The use of cavity roosts can reduce energy costs for birds by up to 43% (Walsberg, 1985).

Given this evidence, it is not surprising that owlet-nightjars select cavity roosts based in large part on thermal microclimate. As a small insectivorous bird with a seasonally, and even daily, fluctuating food supply, owlet-nightjars must select roosts that decrease energy expenditure, both to keep warm in winter, and to reduce the energetic cost of cooling and water loss during the heat of summer. The relative importance of roost thermal microclimate is enhanced for owlet-nightjars as they roost alone. Unlike many cavity roosting birds, such as swifts (Bartholomew et al., 1957), nuthatches (Knorr, 1957), bee-eaters (White et al., 1978), sociable weavers (*Philetairus socius*; (Bartholomew et al., 1976), monk parakeets (*Myiopsitta monachus*; (Caccamise & Weathers, 1977) and some species of bats (Kurta, 1985; Wang & Wolowyk, 1988; Lausen & Barclay, 2002; Smith & Racey, 2005; Solick & Barclay, 2006; Willis & Brigham, 2007), owlet-nightjars do not cluster for warmth but rely on roost insulation for thermal buffering and a reduction of energetic costs for thermoregulation. Thus, appropriate cavity roosts may be crucial for offering owlet-nightjars protection from ambient thermal extremes.

### **Roosting Behaviour**

Low roost fidelity or roost switching behaviour has been observed in many species of mammals and birds (Sonerud, 1985; Lewis, 1995; Krebs, 1998; Gibbons & Lindenmayer, 2002; Sherwin et al., 2003). It has been proposed that animals may exhibit roost lability and change roosts often due to disturbance, to avoid predators, minimize distance to foraging sites, reduce infestation of ectoparasites, and to choose a more favorable thermal microclimate (Lewis, 1995; Gibbons & Lindenmayer, 2002).

My data on the number of roosts used per bird and the likelihood of birds returning to a formerly used roost in this study were comparable to data previously collected for owlet-nightjars (Brigham et al., 1998). Forest-dwelling owlet-nightjars used between two and six tree hollows and spent 1-40 days in the same hollow during a 1-4 month tracking period (Brigham et al., 1998). The number of roosts used in this study (1-7) was similar, supporting the proposal that owlet-nightjars are loyal to a cluster of roosts. Brigham et al. (1998) found that individual owlet-nightjars returned to a previously used cavity on 13 occasions during 337 bird-days. I found that birds returned to previously used roosts on 22 occasions during 609 bird-days. Unlike owlet-nightjars, bats rarely return to roosts used previously (Lewis, 1995; Lausen & Barclay, 2002; Mormann & Robbins, 2005; although see Willis et al., 2006).

Roost fidelity in the current study (roost switching mean = 16.8 days) was almost double the 9.4 day average found by Brigham et al. (1998). Whether this is due to the inclusion of rock crevices as potential roosts or differences in habitat types between studies is unknown. Lewis (1995) proposed that roost fidelity may be based on the availability of alternate roosts in a landscape. The forested landscape in the Brigham et al. (1998) study offered more tree hollows, but the inclusion of rock crevices as potential roosts in the current study may have offset this difference. Owlet-nightjars switched rock crevice roosts far less often than tree-cavity roosting bats, which changed roosts every one to four days (Lewis, 1995; Lewis, 1996; Brigham et al., 1997b; Chruszcz & Barclay, 2002; Willis & Brigham, 2004; Baker & Lacki, 2006; Boyles & Robbins, 2006).

It is unlikely that owlet-nightjars changed roosts to minimize distance to foraging sites. Roosts were typically clustered close together, sometimes only tens of meters apart, in one section of the home range (Chapter 7). Predator avoidance, disturbance, reduction of ectoparasites and selecting a more favorable microclimate are all possible explanations for roost lability of owlet-nightjars. Predation rates on adult owlet-nightjars were higher at the forested study site (57% to 86% of birds depredated; (Brigham & Geiser, 1997) than in central Australia (19% of birds depredated). However, all depredation events in both studies occurred when the birds were outside the roosts foraging at night. Owlet-nightjars have no detectable scent (to humans at least) and rarely defecate inside their roosts; therefore, it is unknown what cues predators might use to find roost sites. Bats will desert roosts after an attack by a predator (Lewis, 1995), but this does not explain the frequent return of owlet-nightjars to previously used roosts. The use of multiple cavities may prevent predators from targeting particular cavities at dusk when owlet-nightjars emerge (Fenton et al., 1994; Lewis,

1995). Owlet-nightjars always wait until the end of civil twilight, about 30 minutes after sunset, when it is no longer possible to discern small objects, before exiting the roost (Chapter 6). This indicates that the risk of predation is light-dependent, providing some support for the predator avoidance hypothesis in explaining roost switching by owlet-nightjars.

Rates of disturbance were minor and likely had little influence on the roost switching behaviour I recorded. Owlet-nightjars were usually tracked to roosts on a daily basis (609 bird-days), but I kept at least 10 m away from known roosts, and birds rarely flushed from roosts (6 occasions). When they did flush, they either returned to the same roost within several minutes (2 occasions) or flew quickly to an alternate known roost nearby (4 occasions). Birds were equally likely to flush from a tree roost (3 occasions) as a rock crevice (3 occasions). Unlike many studies on bats, owlet-nightjars were not caught at roost sites and thus did not avoid previously used roosts after transmitter attachment and release.

Nothing is known about the extent of ectoparasites on owlet-nightjars. I recorded none and no birds were found in obvious poor health during the course of this study. It is unlikely that a bird would return to previously used roosts if they were avoiding ectoparasites (Lewis, 1996). Boyles & Robbins (2006) found low numbers of ectoparasites on cavity roosting evening bats (*Nycticeius humeralis*) and concluded that it was an unlikely explanation for roost switching for this species. Olsson & Allander (1995) examined nest reuse and site choice by four species of cavity-nesting birds and found that the presence of parasites did not affect the site choice of any of the species studied. In contrast, Lewis (1996) found that roost switching was positively correlated with ectoparasites load of pallid bats (*Antrozous pallidus*). However, this species roosts in colonies and ectoparasites are likely transferred between individuals in the roost (Lewis, 1996). Solitary roosting owlet-nightjars would not be vulnerable to this type of parasite transmission.

My data indicate that birds using multiple roosts showed a preference for the ones that were warmer and more thermally stable (Chapter 2). Given my findings on differences in thermal microclimate between roosts (Chapter 2), and the current data indicating that birds selected roosts based on thermal buffering characteristics, the search for an appropriate thermal microclimate stands out as the most important explanation for roost lability. Frequent roost switching by owlet-nightjars may represent a search for optimal thermal conditions. Thus, both changes in thermoregulatory requirements or predator avoidance are the most likely

explanations of roost lability in owlet-nightjars, and access to multiple roost cavities appears to be important for this species.

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## CHAPTER 4

### Effects of Prey Availability and Climate on Daily Torpor of Free-Ranging Australian Owlet-nightjars (*Aegotheles cristatus*) in Diverse Habitats

#### Abstract

Food availability, ambient temperatures ( $T_a$ ), and prevailing weather conditions have long been presumed to influence torpor use by mammals and birds. This information is to a large extent based on measurements on use of torpor in the laboratory by birds placed on restricted diets and kept at low  $T_a$ . In contrast, information on the determinants of torpor use in the field is limited. I used radiotelemetry to investigate winter torpor by insectivorous, free-ranging Australian owlet-nightjars (*Aegotheles cristatus*) in three habitats that differed in annual  $T_a$ , rainfall, and arthropod abundance. Data were collected for 22 birds over six winters for a total of 834 bird-days. The lowest torpid skin temperature ( $T_{skin}$ ) recorded during torpor was 18.6 °C and the longest torpor bout was 640 minutes. Owlet-nightjars entered daily torpor regularly at all sites, but torpor frequency, depth and duration was greatest at two sites with lower arthropod abundance, although there was a strong correlation between environmental variables. Torpor patterns and periodicity were similar among sites, and night torpor was more frequent than previously reported. I found no evidence to suggest that torpor use was restricted to energetic emergencies.

#### Introduction

Birds are endothermic and maintain a high body temperature ( $T_b$ ) by means of endogenous metabolic heat production. The energetic costs of maintaining elevated metabolic rates to compensate for increased heat loss at times of low ambient temperature ( $T_a$ ) are substantial (Withers, 1992). One physiological method that some species use to reduce these costs is to enter daily torpor (McKechnie & Lovegrove, 2002). Torpor in heterothermic endotherms is characterized by a controlled reduction of  $T_b$ , metabolic rate (MR) and activity, and is typically employed by endotherms that periodically face energetic constraints due to extreme climatic conditions and ephemeral food supplies (Geiser, 2004a). Torpor is known to be influenced by a multitude of factors including food and water availability,  $T_a$ , photoperiod, reproductive state, prevailing weather conditions, and circannual cycles (Carpenter, 1974; Lyman et al., 1982; Hiebert, 1992; Csada & Brigham, 1994; Song & Geiser, 1997; Körtner & Geiser, 2000a; Körtner & Geiser, 2000b; Willis et al., 2005; Christian, 2007).

Historically, given the relatively few records for it, torpor was hypothesized to be only used by birds to survive ‘energetic emergencies’. Torpor was thought to be induced when low  $T_a$  and seasonal or daily food shortages reduced energy reserves to a level that could not support endothermic heat production (Bartholomew et al., 1957; Calder, 1973; Carpenter, 1974; Hainsworth et al., 1977; Hiebert, 1992). Supporting evidence came from laboratory studies showing that birds (Hohtola et al., 1991), and more specifically Caprimulgiformes (Marshall, 1955; Lasiewski & Dawson, 1964; Peiponen, 1965; Dawson & Fisher, 1969), will only enter torpor when deprived of food for several days. However, field studies on a variety of species indicate that heterothermic responses may be a routine means of balancing energy requirements, and that energy emergencies or deficits are not necessary for torpor induction (Reinertsen, 1983; Brigham, 1992; Körtner et al., 2001; Turbill et al., 2003b; Schleucher, 2004). For instance, hummingbirds enter nocturnal torpor regularly during winter and while migrating, irrespective of  $T_a$  and nectar availability (Carpenter, 1974). Nonetheless, to date only frugivorous, nectarivorous, and insectivorous birds, those that would regularly experience seasonal food shortages, have been reported to employ torpor (McKechnie & Lovegrove, 2002). Aerial insectivores, including bats, swifts, swallows and nightjars, which rely on activity by their prey, may be among those most strongly affected by  $T_a$  dependent food availability (Racey & Swift, 1985). Torpor may also be employed during periods of prey shortage due to seasonal drought, even when not accompanied by low  $T_a$  (Bartels et al., 1998; Coburn & Geiser, 1998). As there is a direct correlation between low  $T_a$ , drought and reduced arthropod abundance and activity (King, 1974; Chapter 6), it is difficult to separate the influence of these factors on torpor use by avian insectivores. Food availability declines with  $T_a$ , while energy requirements increase (Speakman & Thomas, 2003). Few field studies have examined the relationship between torpor and  $T_a$  and/or arthropod abundance for free-ranging avian insectivores.

As an insectivorous bird that relies on activity by their prey, Australian owlet-nightjars (*Aegotheles cristatus*; 45 g) should be affected by the decrease in insect abundance during cold or drought (Racey & Swift, 1985; Brigham et al., 2000; Woods, 2002; Lane et al., 2004). Owlet-nightjars are non-migratory, cavity roosting, nocturnal Caprimulgiformes found in a variety of habitats throughout Australia, which have previously been found to regularly use torpor in winter (Brigham et al., 2000; Chapter 2). The purpose of my study is to compare thermoregulatory behaviour and daily torpor use of owlet-nightjars in a semi-arid desert habitat of central Australia with a cool, temperate eucalypt woodland on the Northern Tablelands of New South Wales.

Three main environmental factors differ between these habitats, all of which may influence torpor use:  $T_a$ , annual rainfall, and arthropod abundance. Due to lower levels of rainfall in the desert, arthropod abundance is likely lower. Thus, I predict torpor frequency and duration will be greater in the desert if torpor is strongly influenced by food availability. While similar winter minimum  $T_a$  (MIN  $T_a$ ) values occur at both sites, mean winter MIN  $T_a$  is lower in the eucalypt woodland. Thus, if torpor use is determined by low  $T_a$ , its frequency and duration should be greater in the eucalypt woodland. I included data from a third site in my comparison. This site is 150 km east of the desert site and while similar in habitat, vegetation, and  $T_a$ , it is irrigated regularly. I expected insect abundance at this site to be higher while winter  $T_a$  would be equivalent to the desert site, and therefore higher than the eucalypt woodland. Torpor frequency and depth was expected to be less at this irrigated desert site than at either of the other two sites. Furthermore, as  $T_a$  is the same at both desert sites, the irrigation area allows me to independently test for the influence of arthropod abundance on torpor use.

## **Methods**

### ***Study Sites***

My study was conducted at the three field locations during three winters (May to September 2004 – 2006) and I also incorporated data from three winters (May-September 1996, 1997 and 1999) at the eucalypt woodland site (below). Two of these locations (Ormiston Gorge (23°37'S, 132°43'E) and the Alice Springs Desert Park (Alice) (23°37'S, 132°43'E) are located in the semi-arid zone of central Australia and have been described in detail previously (Chapter 2). These two sites are separated by 150 km. The mean MIN  $T_a$  and maximum  $T_a$  (MAX  $T_a$ ) in Alice Springs for July are 4.0 °C and 19.9 °C and the mean annual rainfall is 282 mm (1941-2007, Australian Bureau of Meteorology). Ormiston Gorge represents a typically desert woodland site with mulga and riverine woodland habitats. I designated it as the desert (D) site for the current study. Parts of the Alice Springs Desert Park were irrigated once a fortnight for 4 hours on a rotating basis, so that at least one area of the park was being irrigated each day. This site was designated as irrigated desert (ID) for the current study.

During winter 2006 (June to September) I studied owlet-nightjars in the 218 ha Imbota Nature Reserve (30° 35' S, 151°45'E, 1000 m elevation), 10 km southeast of Armidale on the Northern Tablelands, New South Wales. The woodland is dominated by broadleaved stringybark (*Eucalyptus calignosa*), Blakely's red gum (*E. blakelyi*), and yellow box (*E.*

*melliodora*; Ford et al., 1986; National Parks & Wildlife Service NSW, 2002). Manna gum (*E. viminalis*) and fern leaf wattle (*Acacia filicifolia*) are also common. The understorey is open and the ground cover consists mainly of grasses (Ford et al., 1986). Until 1981, the reserve had been subject to tree-felling leaving an abundance of hollow stumps (Ford et al., 1985). The area around the woodland has been extensively cleared, with the exception of a few patches of woodland on adjacent private pastoral property (National Parks & Wildlife Service NSW, 2002). The mean daily MIN  $T_a$  and MAX  $T_a$  for Armidale in July are 1.0 °C and 13.2 °C (1857-1997, Australian Bureau of Meteorology). Mean annual rainfall is 790 mm and mean monthly rainfall in summer (93.8 mm) is almost double winter rainfall amounts (51.5 mm). This location was designated as the eucalypt woodland (EW) site. The photoperiod amongst all sites was similar throughout the winter, with dawn occurring ~30 minutes earlier at the eucalypt woodland site (sunrise = 5:51 h to 7:19 h depending on site and month).

### ***Ambient Temperature and Rainfall***

Small temperature data loggers (Thermochron iButtons®, Model DS1921,  $\pm 0.5^\circ\text{C}$ , Dallas Semiconductor Corp., Dallas, TX, U.S.A) were placed in the shade 1 m above the ground in a central position at each of the study sites to measure  $T_a$ . Weather stations at the Ormiston Gorge ranger station and at the Alice Springs Desert Park provided daily rainfall data. Daily rainfall data for Armidale were used as indicative of the eucalypt woodland site (Australian Bureau of Meteorology). Cloud cover as oktas (cloud coverage in eighths) recorded at 9:00 h was collected by the Australian Bureau of Meteorology for Armidale and Alice Springs.

### ***Telemetry***

Owlet-nightjars were caught by broadcasting taped calls to lure individuals into mist nets. Following capture I measured body mass and placed an alloy band (Australian Bird and Bat Banding Scheme Project 1418-8) on the right leg. Birds were generally fitted with an external radio transmitter (model PD-2T, Holohil Systems, Carp, Ontario, Canada) to measure skin temperature ( $T_{\text{skin}}$ ;  $n=20$  birds). External transmitters were attached using a back-pack-style harness made from elastic thread (Figure 5.1E in Kenward, 1987). Two birds in central Australia (one at each location) and one in the eucalypt woodland in 1999 were kept overnight to surgical implant internal transmitters (Sirtrack Ltd, Havelock North, New Zealand) to measure core  $T_b$ . Details of surgery are given in Chapter 2. No external characteristics allow reliable discrimination of gender for owlet-nightjars. The sex of birds caught in 2005 and

2006 was determined through DNA sexing using the shaft of feathers pulled from the chest area (Genetic Science Services, Fitzroy, Victoria, Australia).

Birds were tracked to day roosts using 3-element Yagi antennae and Merlin (Custom Electronics, Nokomis, U.S.A.) or Icom (IC\_R10, Icom, Bellevue, U.S.A.) receivers. Remote receiver/data logging stations were set up on high ground and/or by placing antennae in trees to receive the signal from birds in their roosts.  $T_{\text{skin}}$  or  $T_{\text{b}}$  was recorded every 10 minutes continuously when birds were in range of the receiver. Data were recorded using custom-made data loggers (Körtner & Geiser, 1998) or a Lotek SRX\_400 receiver/logger (Lotek Engineering, Aurora, Ontario, Canada) attached to a 3- or 5-element Yagi antennae. Data were downloaded to a laptop computer every 4-5 days. The custom-made data loggers measured the interval between two transmitter pulses and the Lotek recorded an event when it detected four consecutive pulses and provided  $T_{\text{b}}$  or  $T_{\text{skin}}$  based on the calibration curve entered into the system. Pulse rates recorded on loggers were confirmed by collecting data manually several times daily by using a receiver and timing 10 pulse intervals using a stopwatch.  $T_{\text{skin}}$  or  $T_{\text{b}}$  was estimated from pulse intervals using the calibration curve previously determined for each transmitter. Further details of telemetry are described in Chapter 2.

Acknowledgement: R. M. Brigham (Biology, University of Regina) and G. Körtner (Zoology, University of New England) contributed raw  $T_{\text{skin}}$  and  $T_{\text{b}}$  data to my study from five owl-nightjars monitored during the winters (May-September) of 1996, 1997, and 1999, collected using these same methods.

### ***Arthropod Sampling***

Pitfall traps and light traps were used to sample arthropods at all study sites. Pitfalls traps (diameter = 68 mm, depth = 150 mm), each containing 50 ml of 50% ethanol, were placed in a grid pattern consisting of three rows of four traps (12 traps per plot). Traps were placed at 10 m intervals. Arthropods were sampled in three different locations at each of the two study sites in central Australia, for a total of 36 traps per site. At the eucalypt woodland site, two plots were set-out in two different areas (24 traps in total). Vegetation and ground cover at these sampling plots is described in detail in Chapter 6. To sample nocturnal arthropods only, each pitfall trap was uncovered at dusk and covered at dawn. Traps were opened for two nights fortnightly at each site. Arthropods were removed from traps post-sampling and stored in 70% ethanol until being dried at 60°C for at least 12 hours before sorting.

Nocturnal aerial arthropods were sampled in the same plots using a ultra-violet light trap (Australian Entomological Supplies Pty. Ltd., Coorabell, NSW, Australia). Details of trap structure are given in Chapter 6. Each of the three plots at the two desert sites were sampled for aerial and terrestrial arthropods every fortnight. Additionally, each site was sampled during the new moon, with one site sampled for three nights prior and the other sampled for three nights post new moon (6 to 9 samples per site per month). The order of sampling was reversed each month. In the eucalypt woodland, two sites were sampled once each fortnight on the new and full moon (4 samples per month). Samples were removed at dawn and dried at 60°C for at least 12 h. All light and pitfall trap samples were weighed for dry biomass ( $\pm 0.01$  g) using a Mettler AE 260 balance (Mettler Instrumente AG, Switzerland). Arthropods  $<3$  mm long or  $>11$  mm diameter were excluded from analysis as these are not normally consumed by nightjars (Jackson, 2000; Jetz et al., 2003).

### ***Data Analysis***

Rock crevices are used as roosts at both desert sites (Chapter 2 and 3), but they are not available in the eucalypt woodland. This confounding factor was unexpected, and complicates the interpretation of the data on torpor as desert birds had the option to use roosts that allow them to use torpor less (Chapter 2). I controlled for this in my analysis. For comparisons amongst the desert sites and years, torpor use was compared between all birds at each site irrespective of roost. For comparisons between birds in the eucalypt woodland and those in the desert, only birds which used trees  $>95\%$  of bird-days were included. This excludes all data from the irrigated site in 2005. Data for each site and year in the desert are generally presented separately. However, as significant differences in torpor use were found between years, but not between sites in central Australia, data from the two sites were pooled for several of the statistical tests.

Only four owlet-nightjars were captured in the eucalypt woodland site in 2006, thus data published by Brigham et al. (2000) for five birds tracked in 1996, 1997 and 1999 at the same eucalypt woodland site were pooled with my data from 2006 for analysis unless otherwise noted. Due to climatic differences (lower rainfall and  $T_a$ ) between 2006 and the other years at this site (see climate results), the data are reported separately in some cases.

Mean  $\pm$  SE active  $T_{skin}$  for owlet-nightjars tagged with external transmitters was  $37.2 \pm 0.1$  °C. I followed Brigham et al. (2000) and defined owlet-nightjars as having entered torpor when

$T_{\text{skin}}$  fell below 30 °C for 20 minutes or more for birds with external transmitters (also see Reinertsen, 1996). Mean active  $T_b$  of owlet-nightjars with implanted transmitters was  $39.4 \pm 0.2$  °C and birds were defined as having entered torpor when  $T_b$  fell below 33 °C for 20 minutes or more (Chapter 2). Brigham et al. (2000) compared  $T_{\text{skin}}$  and  $T_b$  of an owlet-nightjar in captivity with both an external and internal transmitter attached and found the difference to be  $3.0 \pm 0.8$  °C. For comparison of minimum torpid  $T_{\text{skin}}$  (MIN  $T_{\text{skin}}$ ) amongst birds, 3 °C was subtracted from the minimum  $T_b$  of birds with internal transmitters to achieve the equivalent of  $T_{\text{skin}}$ . Days from which  $T_{\text{skin}}$  or  $T_b$  data were missing for more than a 3 h period during daylight hours (sunrise to sunset) were excluded from analysis of day-time torpor. The same procedure was used for night torpor bout analysis. Torpor-days are defined as days in which at least one bout of torpor occurred in a 24-h period. Torpor frequency for each site and year was compared using chi-square tests ( $\chi^2$ ) and two-way contingency tables (Lehner, 1996). Yates correction for continuity factor was used for all  $\chi^2$  tests with 1 degree of freedom to correct for bias (Zar, 1998). Torpor bout duration and torpid MIN  $T_{\text{skin}}$  were compared amongst sites and years using a one-way analysis of variance (ANOVA). Linear regression analysis was used to assess the relationship between torpid MIN  $T_{\text{skin}}$  and torpor bout duration, and between  $T_b$  and  $T_b - T_a$  for an owlet-nightjar in each habitat. Rates of passive re-warming from torpor bouts were calculated for the 25 morning torpor bouts with the lowest MIN  $T_{\text{skin}}/T_b$  in the desert in 2004 and 2005 and in the eucalypt woodland for all years combined. The overall slope of temperature increase during the arousal stage was calculated from the first point after the MIN  $T_{\text{skin}}/T_b$  to the MAX  $T_{\text{skin}}/T_b$  at the end of the bout.

Climate and arthropod biomass variables were compared amongst sites and years using Kruskal-Wallis ANOVAs. To investigate the potential effects of  $T_a$ , rainfall, cloud cover, and aerial and terrestrial arthropod biomass on torpor frequency, duration and MIN  $T_{\text{skin}}$  I used a correlation matrix. For several of the pairs of variables, the joint distribution was not bivariately normal (Quinn & Keough, 2002). Transforming the data was not a practical option due to negative  $T_a$  values that would have been excluded if the data were logarithmically or square-root transformed. Thus, pairs of variables were compared using a Spearman rank order correlation, which is 91% as powerful as a Pearson product moment correlation (Lehner, 1996). Many variables were influenced by collinearity, which prevented the use of multiple linear regression analysis (Quinn & Keough, 2002). I performed binomial logistic regression analysis using the only two uncorrelated variables,  $T_a$  and rainfall, to assess the likelihood of torpor occurring on any given day.

StatistiXL (version 1.6) was used for statistics on frequency and SigmaStat (version 2.0) was used for all other statistical tests. Numerical values are presented as means  $\pm$  SE for  $n$  = number of individuals and  $N$  = number of days observations recorded. An alpha value of 0.05 was used for all tests.

## Results

### *Climate*

Mean winter (May-September) MIN  $T_{as}$  for each year at the eucalypt woodland site were significantly lower than at the desert site in central Australia in 2004 and 2005 (Kruskal-Wallis ANOVA:  $H_5=231.14$ ,  $P<0.00001$ ; Figure 1). MIN  $T_a$  in the desert during winter averaged  $7.2 \pm 0.4$  °C, which was  $5.3 \pm 0.3$  °C greater than MIN  $T_a$  in the eucalypt woodland. At the eucalypt woodland site, the winter of 2006 was significantly colder than the other years. The single lowest daily MIN  $T_a$  in 2006 was  $-10.8$  °C, whereas the lowest daily  $T_a$  in 1996, 1997, and 1999 were  $-4.3$  °C,  $-4.4$  °C and  $-3.5$  °C, respectively. The daily MIN  $T_{as}$  in the desert were comparable, reaching as low as  $-4.0$  °C and  $-3.8$  °C in 2004 and 2005 respectively; however,  $T_{as}$  below zero were not as common. The MAX  $T_{as}$  in the desert were on average  $8.9 \pm 0.5$  °C higher than in the eucalypt woodland for all years ( $H_5=432.5$ ,  $P<0.00001$ ).

The average annual rainfall in Alice Springs is 282 mm, and the average winter (May-September) rainfall is 66.3 mm (1940-2007, Australian Bureau of Meteorology). The average annual rainfall for Ormiston Gorge is slightly higher at 333 mm (1972-2004, Ormiston Gorge Ranger Station). In both 2004 and 2005 above average winter rain occurred in central Australia. Heavy rains (120 mm) in mid-May 2004, preceded by a wetter than average year (420 mm), caused the usually dry Ormiston Creek to flow from 22 May 2004 until mid-June 2004 and small pools persisted throughout the river channel until the end of August 2004. In contrast, between June 2004 and May 2005 only 72 mm of rain fell in the area, making for dry conditions leading into winter 2005. From mid-June – mid-July 2005, 85 mm of rain fell, improving the situation for the second half of the winter, and overall there was no significant difference in rainfall between the winters of 2004 and 2005 at the desert sites (Figure 2). However, the creek remained dry and the permanent waterhole in Ormiston Gorge was less than one quarter the size of 2004 (see Plates 4 & 5, Chapter 6). The irrigated site at the Alice Springs Desert Park experienced similar low rainfall between 2004 and 2005. However, due to regular irrigation throughout the park it was expected that the differences in rainfall would have less impact on arthropod availability at this site. Nonetheless, due to the high level of

moisture in 2004, the difference between years in the desert was greater than the difference between sites, causing the focus of the comparison to shift. Thus, in subsequent analysis the irrigated desert and non-irrigated desert sites were often combined while the years are kept separate.

The eucalypt woodland site received significantly more rain than the desert from 1996-1999 ( $H_7=147.2$ ,  $P<0.00001$ ). However, 2006 was a dry year in the eucalypt woodland and rainfall amounts did not differ significantly from the desert. The mean winter rainfall (June-September) in Armidale is 251 mm (1857 to 1997, Australian Bureau of Meteorology). Thus, both 1999 and 2006 were below average years (Figure 2).

The number of days per month when cloud cover was  $>50\%$  at 09:00 h did not differ significantly between sites or years (ANOVA:  $F_{4,22}=2.72$ ,  $P=0.06$ ). The number of cloudy days per month ranged from only four days in the desert for August 2005 to 25 days in the eucalypt woodland in July 1999. Generally, there were fewer cloudy days in the desert. In 1999 the eucalypt woodland had twice ( $17.8 \pm 2.7$  days month<sup>-1</sup>) as many cloudy days as the desert in 2005 ( $8.2 \pm 1.3$  days month<sup>-1</sup>), but variation was great.

### ***Arthropod Biomass***

Aerial and terrestrial arthropod biomass was significantly lower at the eucalypt woodland site compared to both desert sites in 2004 and the irrigated site in 2005 (Kruskal-Wallis ANOVA: Aerial:  $H_4=23.3$ ,  $P<0.001$ ; Terrestrial:  $H_4=330.36$ ,  $P<0.0001$ ). Terrestrial arthropod biomass in the desert in 2005 was significantly lower than the irrigated desert site in 2005 and both sites in 2004 (Figure 3). The desert site in 2005 did not differ from the eucalypt woodland site for aerial or terrestrial biomass. For both desert sites in both years, aerial arthropod biomass increased near the end of winter (late August-September) due to a substantial increase in Lepidoptera abundance. Details of arthropod biomass and abundance at these sites are discussed in Chapter 6.

### ***Owlet-nightjar Captures***

Ten owlet-nightjars were captured in central Australia in 2004 (5 ID & 5 D) and data were collected for 9 individuals. One bird was never relocated after release (D). One bird was caught twice (D). This bird originally had an internal transmitter and was re-released with an external transmitter and, as a result of the difference in transmitter type, was analyzed as two separate birds (thus  $n = 5$  ID and  $n = 5$  D). Data were collected for one bird with an internal

transmitter at each site in 2004. In 2005, only six owlet-nightjars were caught (2 ID & 4 D) due to dry conditions and low bird abundance. One bird was immediately killed by a feral cat (*Felis catus*; D site), thus data were collected for 5 individuals in 2005. Data were collected at the eucalypt woodland site for two birds in 1996, three in 1997, one in 1999 (internal transmitter), and four in 2006.

Both sexes of owlet-nightjars are equally likely to be caught using playback (45% female, 55% male,  $n=22$ ,  $\chi^2_{0.05}=0.18$ ,  $P=1.00$ ) and both males and females were caught in 2005 (6 birds sexed = 4 males, 1 female, 1 undetermined) and in the eucalypt woodland in 2006 (4 birds sexed = 2 males, 1 female, 1 undetermined). Feather samples were not collected for birds in 2004, nor in the eucalypt woodland in 1996, 1997 and 1999, thus these data were not specifically analyzed by gender.

The body mass of owlet-nightjars captured at the desert sites in 2005 (ID= $40.4 \pm 1.3$  g,  $n=2$ ; D= $40.5 \pm 0.7$  g,  $n=3$ ) was significantly lower than in 2004 (ID= $47.8 \pm 1.1$  g,  $n=5$ ; D= $46.8 \pm 2.9$  g,  $n=5$ ), and the eucalypt woodland site in 2006 ( $52.2 \pm 2.2$  g,  $n=4$ ; ANOVA:  $F_{4,18}=4.39$ ,  $P<0.05$ ). Owlet-nightjar body mass in the eucalypt woodland in winter did not differ from summer mass of owlet-nightjars captured at this site for another study (Chapter 5;  $50.8 \pm 2.0$  g,  $n=12$ ;  $t$ -test:  $t_{19}=0.58$ ,  $P=0.57$ ). The body mass of birds caught in late winter at the woodland site was significantly less than those caught in early winter (June:  $50.58 \pm 1.66$ ,  $n=3$ ; versus August:  $40.84 \pm 1.25$ ,  $n=3$ ;  $t$ -test:  $t_4=4.68$ ,  $P<0.01$ ; see Chapter 5), but still within the normal range for owlet-nightjars (40-60 g; Holyoak, 2001).

### ***Torpor Use***

Radio-tagged desert birds were tracked from 10 May to 6 October 2004 and 1 June to 5 September 2005. Torpor bouts were recorded between 18 May and 13 September 2004 and 3 June to 16 August 2005. Eight of the 10 radio-tagged birds in the desert in 2004 entered torpor at least once for a total of 139 torpor bouts (121 torpor-days); occurring on 29% of the 418 bird-days that  $T_{\text{skin}}$  or  $T_{\text{b}}$  was recorded. Torpor frequency was greater in 2005, and all five desert birds entered torpor for a total of 98 torpor bouts (77 torpor-days), resulting in torpor occurrence of 57% for the 136 bird-days that  $T_{\text{skin}}$  was recorded. Torpor frequency did not differ between the two desert sites in either year (2004:  $\chi^2_{0.05}=0.4$ ,  $P=0.52$ ; 2005:  $\chi^2_{0.05}=1.9$ ,  $P=0.17$ ; Figure 4). Torpor frequency differed significantly between years at the desert site ( $\chi^2_{0.05}=32.5$ ,  $P<0.0001$ ), but not at the irrigated desert site ( $\chi^2_{0.05}=3.0$ ,  $P=0.09$ ).

The dates for which owlet-nightjars were tracked in the eucalypt woodland differed between years, but generally data were available from 1 May to 30 September and torpor bouts were recorded from 8 May until 8 September. Seven of the eight radio-tagged birds in the eucalypt woodland entered torpor for a total of 198 torpor bouts (140 torpor-days); resulting in torpor occurring on 50% of the 280 bird-days of monitoring. The one bird that did not enter torpor was caught near the end of winter (22 August 2006).

Torpor frequency differed significantly amongst sites for all roosts ( $X^2_{0.05,4}=47.5$ ,  $P<0.0001$ ) and for tree roosts ( $X^2_{0.05,4}=67.3$ ,  $P<0.0001$ ; Figure 4). For birds roosting in tree hollows, torpor frequency was greater in the eucalypt woodland and in the desert site in 2005 than for either desert site in 2004 ( $X^2_{0.05,4}=67.3$ ,  $P<0.0001$ ). Torpor use in the desert in 2005 exceeded that in the eucalypt woodland (96-99:  $X^2_{0.05,4}=13.6$ ,  $P<0.0001$ ; 2006:  $X^2_{0.05,4}=4.2$ ,  $P<0.05$ ; Figure 4). A comparison of torpor use by owlet-nightjars with internal transmitters showed that the owlet-nightjar (ONJ 60) in the eucalypt woodland (53% of bird-days) and the individual (ONJ 4) roosting in a tree hollow in the desert in 2004 (46% of bird-days) showed equivalent torpor frequency ( $X^2_{0.05}=0.3$ ,  $P=0.57$ ).

In all sites/years birds most frequently entered torpor in the morning between 06:00 h and 12:00 h (Day AM,  $N=317$ , 72.9% of torpor-days; Figure 5). The frequency of morning torpor bouts differed significantly among years in the desert and the eucalypt woodland ( $X^2_{0.05,2}=36.9$ ,  $P<0.0001$ ; Table 1). The mean time of torpor entry was  $89.5 \pm 16.2$  minutes after sunrise (05:51 to 07:19 h depending on the day and site). Time of entry did not differ significantly among sites (ANOVA:  $F_{2,15}=0.63$ ,  $P=0.55$ ). However, owlet-nightjars at the eucalypt woodland site aroused later from torpor bouts ( $282.8 \pm 23.8$  minutes after sunrise) than desert birds (2004:  $174.8 \pm 18.4$ ; 2005:  $230.2 \pm 7.8$  minutes after sunrise:  $F_{2,15}=6.98$ ,  $P<0.01$ ). This was not due to a difference in rewarming rates, which varied considerably amongst individual birds, but did not differ amongst sites (Figure 6). The rewarming rates of owlet-nightjars in tree hollows were not related to torpid MIN  $T_{\text{skin}}/T_{\text{b}}$  or MIN  $T_{\text{a}}$  during 2004, 2005 or at the eucalypt woodland site (ANCOVA: Site:  $F_{2,71}=0.18$ ,  $P=0.83$ ; MIN  $T_{\text{skin}}/T_{\text{b}}$ :  $F_{1,71}=0.00$ ,  $P=0.98$ , model  $R^2=0.01$ ; Site:  $F_{2,71}=0.37$ ,  $P=0.69$ ; MIN  $T_{\text{a}}$ :  $F_{1,71}=0.41$ ,  $P=0.52$ , model  $R^2=0.02$ ; Figure 6). Variation in rewarming rates amongst sites may have been increased by the differences in MIN  $T_{\text{skin}}/T_{\text{b}}$  amongst sites, as values were often higher in the desert in 2004 compared to 2005 and the eucalypt woodland. Rewarming from morning torpor generally coincided with increasing  $T_{\text{a}}$  (Figure 7), and ranged from 0.014 to 0.246 °C min<sup>-1</sup> and averaged  $0.067 \pm 0.008$  °C min<sup>-1</sup>.

Afternoon (12:00-18:00 h; mean start time: D=13:36 ± 14 minutes, EW=13:42 ± 8 minutes) torpor bouts occurred on only 6 occasions in the desert (2004: N=3 or 1.2% of bird-days; 2005: N=3 or 3.8% of bird-days), but were more common in the eucalypt woodland (N=44 or 15.7% of bird-days; Figure 5). However, the frequency of afternoon bouts did not differ statistically between sites ( $X^2_{0.05,2}=0.3$ ,  $P=0.60$ ). Afternoon bouts always followed an earlier morning bout in the desert and on 98% of occurrences (N=43) in the eucalypt woodland. Compared to single morning bouts only, afternoon bouts were significantly more likely to occur on colder days in the desert (2004: MIN  $T_a = 2.9 \pm 0.7$  °C,  $t_{14}=2.4$ ,  $P<0.05$ ; 2005:  $0.5 \pm 1.7$ °C,  $t_{14}=2.1$ ,  $P<0.05$ ) and in the eucalypt woodland in 2006 (MIN  $T_a = -6.7 \pm 1.0$  °C,  $t_{22}=2.8$ ,  $P<0.05$ ). However, MIN  $T_a$  had no effect on the occurrence of afternoon bouts in the eucalypt woodland from 1996 to 1999 ( $t_{63}=2.4$ ,  $P=0.39$ ). At the eucalypt woodland site bouts starting at dawn and lasting past 14:00 h were recorded on 23 occasions (8.2% of bird-days), whereas this only occurred on 5 occasions in the desert (0.9% of bird-days), as daytime  $T_a$  in the desert increases faster. Birds that remained in torpor until ~12:30 h (~300 minutes from dawn), did not re-enter torpor that afternoon.

It was not unusual for birds to exhibit more than one torpor bout per day, either as a morning bout followed by an afternoon bout, or a night bout followed by a morning bout (Figure 7). Bird-days on which more than one torpor bout occurred were significantly more common in the desert in 2005 (N=13, 16.3%) and the eucalypt woodland (N=50, 17.9%), than in the desert in 2004 (N=7, 2.8%;  $X^2_{0.05,2}=30.9$ ,  $P<0.0001$ ; Figure 5; Table 1). One desert bird in 2005 entered three torpor bouts in a 24-h period on two occasions, entering torpor at night, dawn and again in the afternoon (Figure 7b, 11 July). An owlet-nightjar in the eucalypt woodland (1997) also entered torpor three times during a 24-h period on five different occasions.

Night torpor bouts were more common in the eucalypt woodland and in the desert in 2005 than in the desert in 2004 ( $X^2_{0.05,2}=19.6$ ,  $P<0.0001$ ; Table 1). Night torpor appears to be more common for owlet-nightjars than previously thought (Brigham et al., 2000). Nighttime  $T_{skin}$  and  $T_b$  data recorded using data loggers were often missing values during the night when birds were far from the roost. By closely examining the data and including only nights when no more than three hours of data were missing, I calculated that night torpor bouts occurred on 28.4% of bird-nights (N=21) in the eucalypt woodland, and 5.7% (N=8) and 26.7% (N=17) of bird-nights in the desert in 2004 and 2005, respectively (Figure 5).

Irrespective of roost type, torpor bout duration was longer in the desert in 2005 and the eucalypt woodland in 2006 than at either desert site in 2004 ( $F_{3,12}=8.75$ ,  $P<0.01$ ; Figure 8 and Table 2). The longest torpor bout that occurred in the desert in 2004 was 480 minutes (8 h). The duration of the longest torpor bout in 2005 was 640 minutes (10.7 h), which occurred at night (beginning at 19:36 h) on 7 July 2005. On the coldest night for which  $T_{\text{skin}}$  data were recorded at the eucalypt woodland site (MIN  $T_a = -10.1$  °C), one owlet-nightjar reduced its  $T_{\text{skin}}$  to 22.3 °C and was in torpor from 1:26 h to 11:13 h (587 minutes, 9.8 h), which was the longest torpor bout recorded at this site. This bird entered torpor again from 13:15 h to 14:15 (60 minutes) on the same day. Oddly, two other owlet-nightjars that were radio-tagged during this period were both depredated by owls on this cold night.

There was a negative correlation between the duration of torpor bouts and torpid MIN  $T_{\text{skin}}$  ( $P<0.0001$ ,  $R^2=0.37$ ,  $N=417$ ; Figure 9). Mean MIN  $T_{\text{skin}}$  were higher in the desert in 2004 than in the eucalypt woodland or in the desert in 2005 ( $F_{3,12}=5.58$ ,  $P<0.05$ ; Figure 10 and Table 2). The lowest MIN  $T_{\text{skin}}$  during a torpor bout was 18.6 °C, which occurred at 7:31 h on 11 July 2005 when MIN  $T_a$  was a relatively warm 7 °C (Figure 7). The lowest  $T_{\text{skin}}$  recorded in 2004 was 21.7 °C. The lowest  $T_b$  measured for a bird with an internal transmitter in the desert was 24.8 °C in 2004. The lowest MIN  $T_{\text{skin}}$  recorded in the eucalypt woodland was 19.5 °C which occurred at 9:36 h when the minimum  $T_a$  (MIN  $T_a$ ) was -1.5°C. The lowest  $T_b$  measured for the woodland bird with the internal transmitter was 19.4 °C. The mean torpid MIN  $T_b$  of the owlet-nightjar with an internal transmitter in the eucalypt woodland ( $28.9 \pm 0.1$  °C) was lower than that of the tree hollow roosting desert bird with an internal transmitter in 2004 ( $31.2 \pm 0.3$  °C; Mann-Whitney  $U$ -test:  $T=945.0$ ,  $P<0.00001$ ).

Torpid owlet-nightjars typically thermoregulate at low  $T_a$ . However, a comparison of minimum  $T_b - T_a$  as a function of  $T_a$  between two birds with internal transmitters suggests that some birds do maintain higher  $T_b$ s at low  $T_a$ s than others (ANCOVA: Owlet-nightjar:  $F_{1,8361}=61.58$ ,  $P<0.001$ ;  $T_a$ :  $F_{1,8361}=18\ 000$ ,  $P<0.001$ ; Owlet-nightjar\* $T_a$ :  $F_{1,8361}=26.73$ ,  $P<0.001$ ; model  $R^2=0.81$ ; Figure 11). Although, the range of  $T_a$ s birds were exposed to differed, an owlet-nightjar roosting in a tree hollow at the desert site in 2004 (ONJ 4) regularly maintained  $T_b$  20 to 33 °C above  $T_a$  at  $T_a<10$  °C (Figure 11a). Nonetheless, ONJ 4 entered torpor on 23 bird-days (46%), although the lowest minimum  $T_b$  was only 26.5 °C. In contrast, an owlet-nightjar monitored in the eucalypt woodland in 1999 (ONJ 60), regularly

reduced  $T_b$  to within 15 °C of  $T_a$  at  $T_a < 10$  °C (Figure 11b). ONJ 60 entered torpor on 33 bird-days (53%) and reduced its  $T_b$  as low as 22.4°C.

### ***Effects of Climate and Arthropod Abundance on Torpor***

A correlation matrix comparing monthly climate variables and mean monthly arthropod biomass to mean monthly torpor frequency, torpid MIN  $T_{skin}$  and duration indicated that several factors were correlated (Table 3). In fact, the only factor not correlated with the other variables was rainfall amount. As expected, minimum monthly  $T_a$  was correlated with both aerial and terrestrial biomass. Higher  $T_a$  was associated with increased arthropod abundance (also see Chapter 6). Likewise the number of days with >50% cloud cover correlated with arthropod abundance, but this may be due to the correlation between  $T_a$  and cloud cover. Both  $T_a$  and aerial and terrestrial arthropod abundance was correlate with all measures of torpor. Thus, lower  $T_a$ , and hence lower arthropod abundance, resulted in increased torpor frequency, increased torpor duration, and lower torpid MIN  $T_{skin}$ .

Because of the collinearity between variables, it is difficult to separate their effects. Modeling was not possible (Quinn & Keough, 2002), except to compare the only two uncorrelated variables,  $T_a$  and rainfall. Binomial logistic regression analysis of the effect of rainfall and  $T_a$  on torpor indicated that  $T_a$  had a significant likelihood of predicting torpor occurrence on a given day while rainfall did not (Likelihood ratio: 77.4,  $P < 0.0001$ , Wald statistic:  $T_a = 60.0$ ,  $P < 0.0001$ , Rain = 2.24,  $P = 0.13$ , N = 395).

**Table 1:** Frequency of torpor bouts in the morning (Day AM) and at night, and for the number of days when more than one torpor bout occurred (>1 bout) at the combined desert sites in 2004 and 2005 and the eucalypt woodland site for all years (EW). The  $\chi^2$  value with Yates correction and the  $P$  value for each comparison from a 2 x 2 contingency table are given. Values relate to torpor frequency (%) presented in Figure 5.

	2004		2005	
	$\chi^2$	$P$	$\chi^2$	$P$
<b>DAY AM</b>				
2005	35.3	<0.0001		
EW	81.2	<0.0001	21.5	<0.0001
<b>NIGHT</b>				
2005	13.0	<0.0001		
EW	15.5	<0.0001	0.0	0.99
<b>&gt;1 BOUT</b>				
2005	16.6	<0.0001		
EW	29.0	<0.0001	0.0	0.87

**Table 2:** Physiological variables of torpor in free-ranging Australian owl-nightjars (*Aegotheles cristatus*) at the irrigated desert site in 2004 and 2005 (ID-2004, ID-2005), at the desert site in 2004 and 2005 (D-2004, D-2005), and at the eucalypt woodland site from 1996 to 1999 and 2006 (EW-96-99, EW-2006). Data are presented for birds in either roost type (rock + tree roosts) and for those using tree roosts only. Values are given as mean  $\pm$  SE and range of values (minimum – maximum) for all observations (N). n = number of individuals.

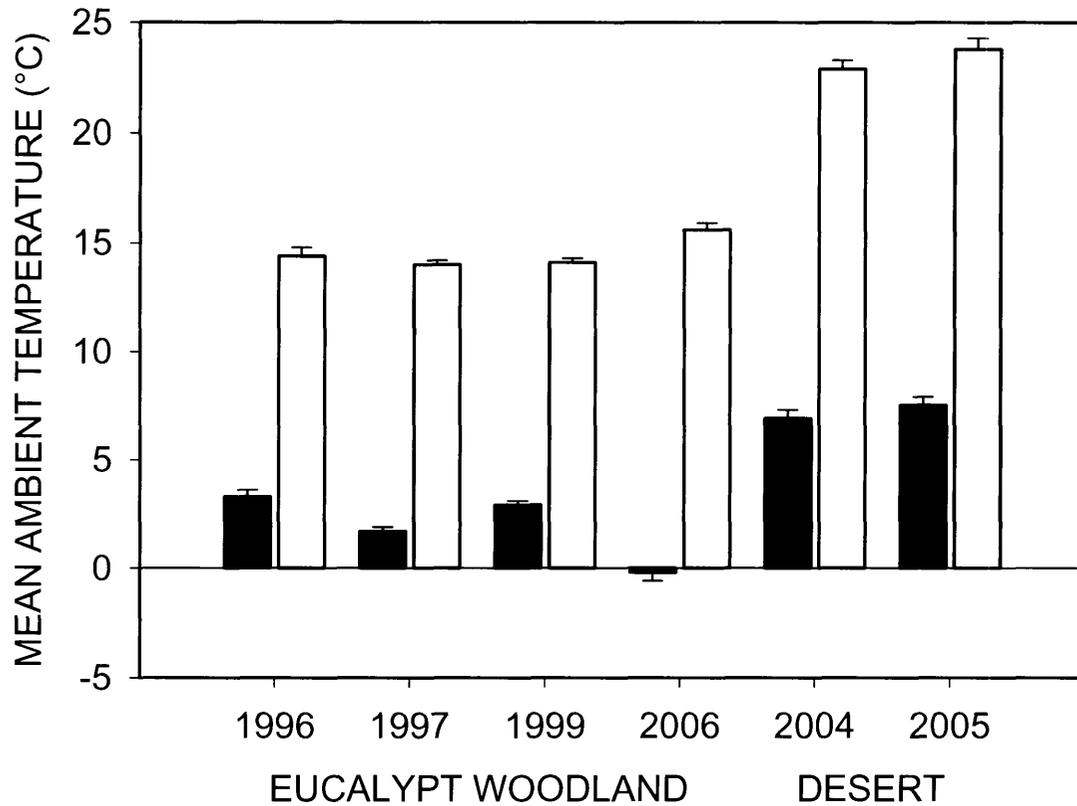
	<b>ID-2004</b>	<b>ID-2005</b>	<b>D-2004</b>	<b>D-2005</b>	<b>EW-96-99</b>	<b>EW-2006</b>
<b>Rock + Tree Roosts</b>	n = 3 N = 68	n = 2 N = 21	n = 5 N = 70	n = 3 N = 77		
Mean Minimum Torpid $T_{\text{skin}}$ ( $^{\circ}\text{C}$ )	27.4 $\pm$ 0.4	26.2 $\pm$ 0.6	27.7 $\pm$ 0.3	24.8 $\pm$ 0.4		
Range Torpid $T_{\text{skin}}$ ( $^{\circ}\text{C}$ )	21.8-29.6	21.5-29.6	21.7-29.9	18.6-29.9		
Mean Torpor Duration (minutes)	141.4 $\pm$ 9.1	198.6 $\pm$ 31.7	155.6 $\pm$ 11.7	220.9 $\pm$ 15.3		
Range Torpor Duration (minutes)	20-429	20-541	20-480	20-640		
<b>Tree Roosts</b>	n = 2 N = 54	n = 0	n = 3 N = 32	n = 2 N = 75	n = 4 N = 142	n = 4 N = 57
Mean Minimum Torpid $T_{\text{skin}}$ ( $^{\circ}\text{C}$ )	27.5 $\pm$ 0.2		27.9 $\pm$ 0.3	24.7 $\pm$ 0.4	26.1 $\pm$ 0.2	24.5 $\pm$ 0.2
Range Torpid $T_{\text{skin}}$ ( $^{\circ}\text{C}$ )	22.6-29.6		21.7-29.9	18.6-29.9	19.4-29.7	20.6-29.7
Mean Torpor Duration (minutes)	148.7 $\pm$ 10.2		146.5 $\pm$ 11.9	224.2 $\pm$ 16.1	169.7 $\pm$ 18.8	252.4 $\pm$ 26.3
Range Torpor Duration (minutes)	30-429		30-480	20-640	21-530	20-587

**Table 3:** Correlation matrix showing Spearman rank order correlation coefficients ( $r_s$ ) and  $P$  values for monthly means of minimum ambient temperature ( $T_a$ , °C), rainfall (mm), aerial and terrestrial arthropod biomass (g), minimum torpid  $T_{skin}$  (°C), and torpor bout duration (minutes) at each site. Cloud cover indicates the number of days per month with >50% cloud cover and torpor frequency is the percent of bird-days per month torpor was entered. Data are for owlet-nightjars in tree roosts only ( $n = 15$  birds,  $N = 33$  observations (months)).

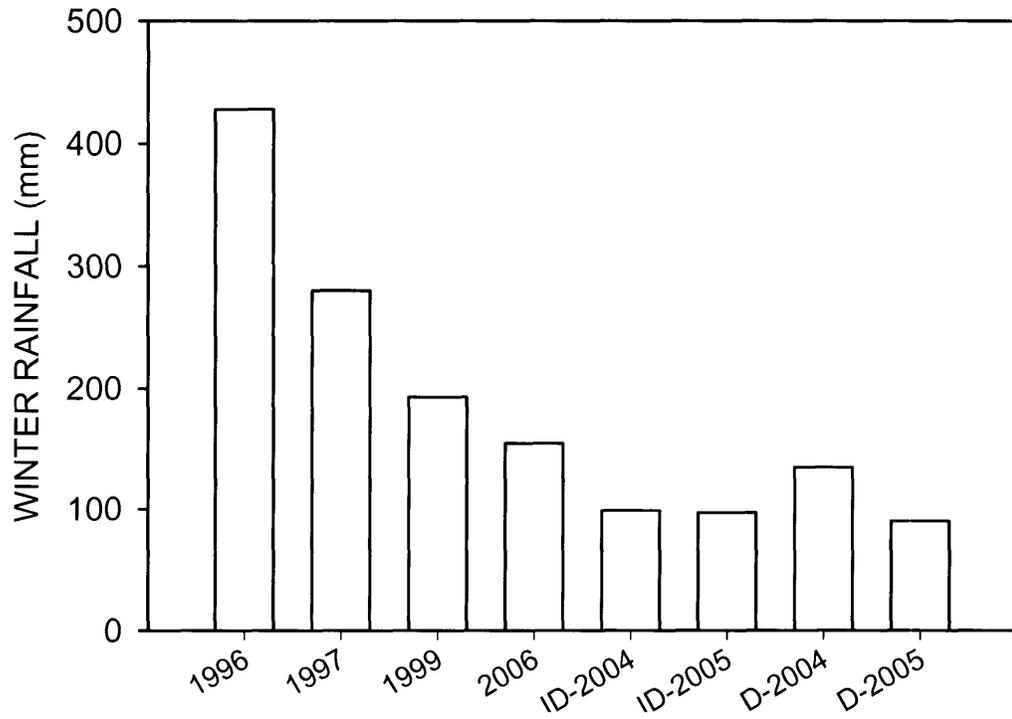
	<b>Rain (mm)</b>	<b>Cloud Cover</b>	<b>Aerial Arthropod Biomass (g)</b>	<b>Terrestrial Arthropod Biomass (g)</b>	<b>Torpor Frequency (%)</b>	<b>Torpid Minimum <math>T_{skin}</math> (°C)</b>	<b>Torpor Duration (minutes)</b>
<b>Minimum <math>T_a</math></b>	-0.241 <i>P</i> =0.18	-0.685 <i>P</i> <0.00001	0.844 <i>P</i> <0.00001	0.716 <i>P</i> <0.00001	-0.445 <i>P</i> <0.01	0.468 <i>P</i> <0.01	-0.429 <i>P</i> <0.05
<b>Rain</b>		0.364 <i>P</i> =0.06	-0.139 <i>P</i> =0.48	-0.662 <i>P</i> <0.00001	-0.176 <i>P</i> =0.32	-0.212 <i>P</i> =0.26	0.113 <i>P</i> =0.54
<b>Cloud Cover</b>			-0.812 <i>P</i> <0.00001	-0.682 <i>P</i> <0.00001	0.391 <i>P</i> <0.05	-0.240 <i>P</i> =0.23	0.226 <i>P</i> =0.25
<b>Aerial Arthropod Biomass</b>				0.677 <i>P</i> <0.00001	-0.447 <i>P</i> <0.05	0.430 <i>P</i> <0.05	-0.511 <i>P</i> <0.01
<b>Terrestrial Arthropod Biomass</b>					-0.329 <i>P</i> =0.07	0.528 <i>P</i> <0.01	-0.448 <i>P</i> <0.05
<b>Torpor Frequency</b>						-0.713 <i>P</i> <0.0001	0.721 <i>P</i> <0.00001
<b>Torpid Minimum <math>T_{skin}</math></b>							-0.810 <i>P</i> <0.00001

**Table 4:** Summary of physiological variables of torpor by owlet-nightjars in tree roosts, climate variables, and arthropod biomass at the two desert sites combined in 2004, the desert site in 2005, and the eucalypt woodland (EW) site years combined. n = number of individuals and N = number of torpor bouts recorded.

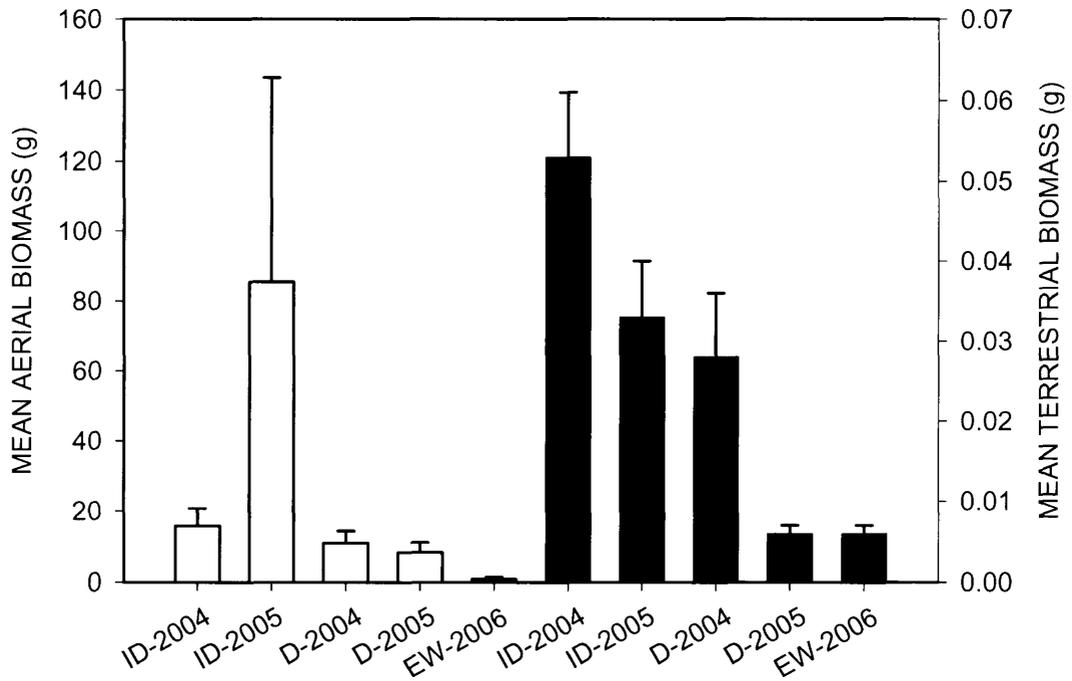
	<b>2004</b> <b>n = 5, N = 78</b>	<b>2005</b> <b>n = 2, N = 58</b>	<b>EW</b> <b>n = 8, N = 136</b>	<b>Significant Differences</b>
<b>Torpor Frequency (%)</b>	32	73	50	2005 > EW > 2004
<b>Torpid Minimum T<sub>skin</sub> (°C)</b>	28.1	25.0	25.3	2004 > EW & 2005
<b>Torpor Duration (minutes)</b>	125	222	201	2005 > 2004
<b>Mean Minimum T<sub>a</sub> (°C)</b>	6.9	7.5	1.9	2004 & 2005 > EW
<b>Total Rain (mm)</b>	117	90	264	EW > 2004 & 2005
<b>Mean Aerial Arthropods (g)</b>	13.1	6.3	0.80	2004 > 2005 > EW
<b>Mean Terrestrial Arthropods (g)</b>	0.041	0.006	0.006	2004 > 2005 & EW



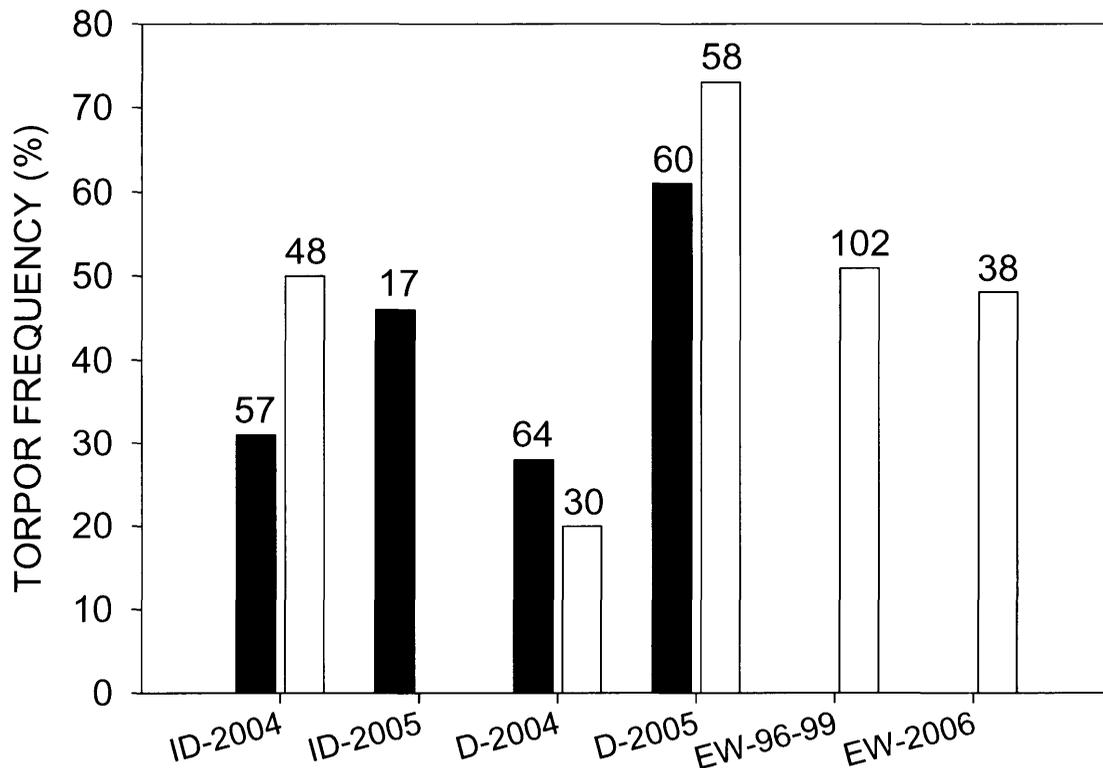
**Figure 1:** Mean  $\pm$  SE of minimum (black bars) and maximum (white bars) ambient temperatures ( $T_a$ , °C) for each winter (May-September) at the desert and eucalypt woodland sites that torpor data was collected on owlet-nightjars. Mean winter MIN and MAX  $T_a$  for all years in the eucalypt woodland were significantly lower than both years in the desert (Kruskal-Wallis ANOVA: MIN  $T_a$ :  $H_5=231.14$ ,  $P<0.00001$ ; MAX  $T_a$ :  $H_5=432.47$ ,  $P<0.00001$ ). MIN and MAX  $T_a$  did not differ between years in the desert. MIN  $T_a$  in winter 2006 was significantly less than for all other years in the eucalypt woodland.



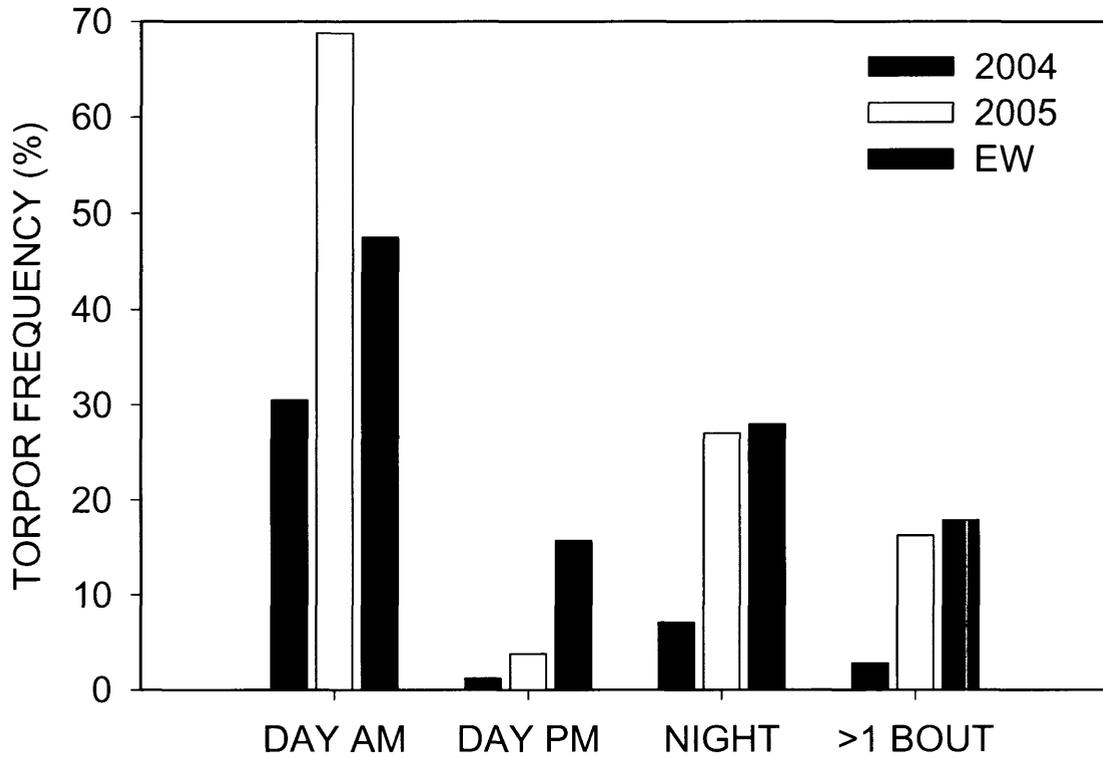
**Figure 2:** Sum of winter rainfall (mm; May-September) at the eucalypt woodland site for 1996, 1997, 1999 and 2006, at the irrigated desert (ID) and desert (D) sites during 2004 and 2005. The eucalypt woodland during 1996, 1997 and 1999 had significantly more rainfall than 2004 and 2005 at both desert sites (Kruskal-Wallis ANOVA:  $H_7=147.16$ ,  $P<0.00001$ ). The eucalypt woodland had significantly less rainfall in 2006 than 1996.



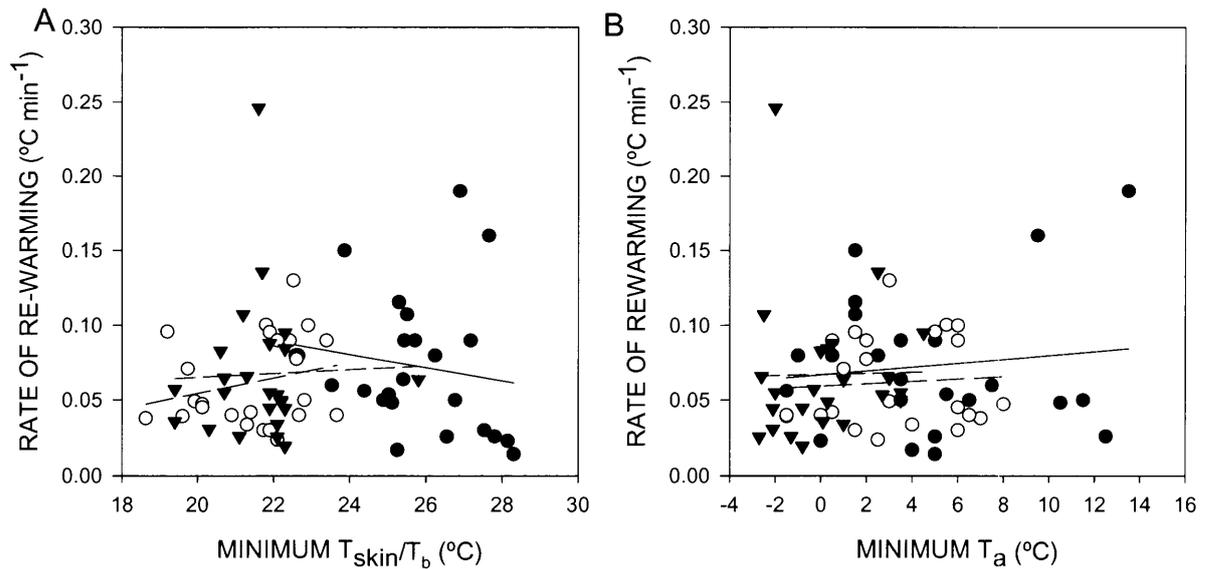
**Figure 3:** Mean  $\pm$  SE of aerial (white bars) and terrestrial (black bars) arthropod dry biomass (g) collected in light and pitfall traps during winter (June-September) for the irrigated desert (ID) in 2004 and 2005, desert (D) in 2004 and 2005, and at the eucalypt woodland (EW) site in 2006. The aerial arthropod dry biomass at sites ID-2004, ID-2005 and D-2004 was significantly greater than at the EW site (Kruskal-Wallis ANOVA:  $H_4=23.3$ ,  $P<0.001$ ). Terrestrial arthropod biomass was significantly lower at the desert site in 2005 and the eucalypt woodland site than at all other sites, and the biomass at the desert site in 2004 was lower than the irrigated desert site in both years ( $H_4=330.4$ ,  $P<0.00001$ ).



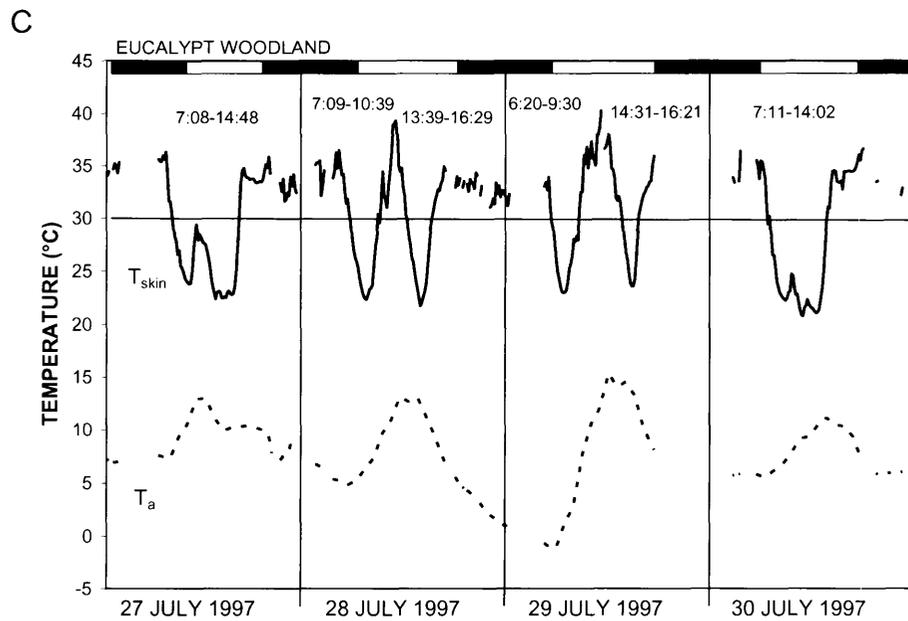
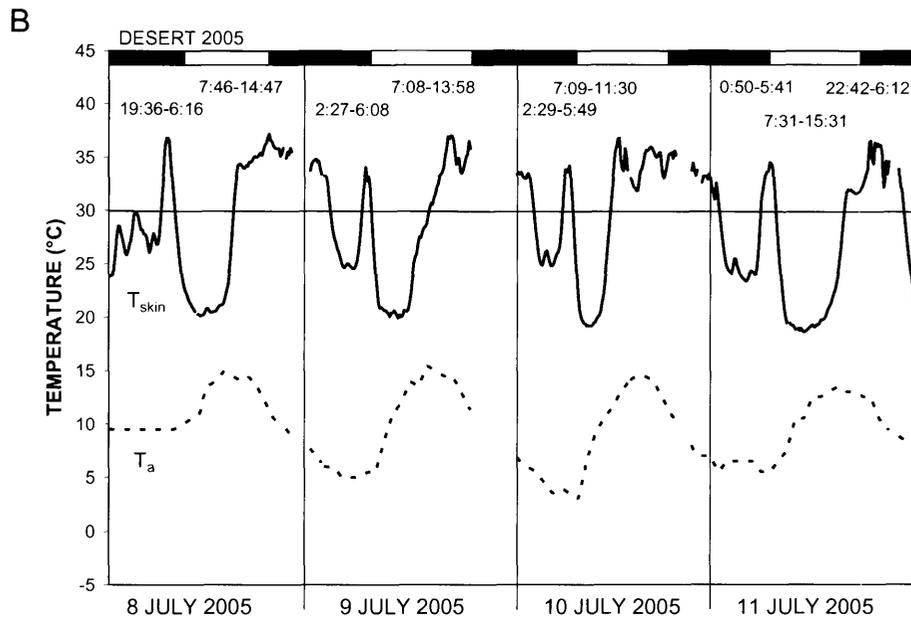
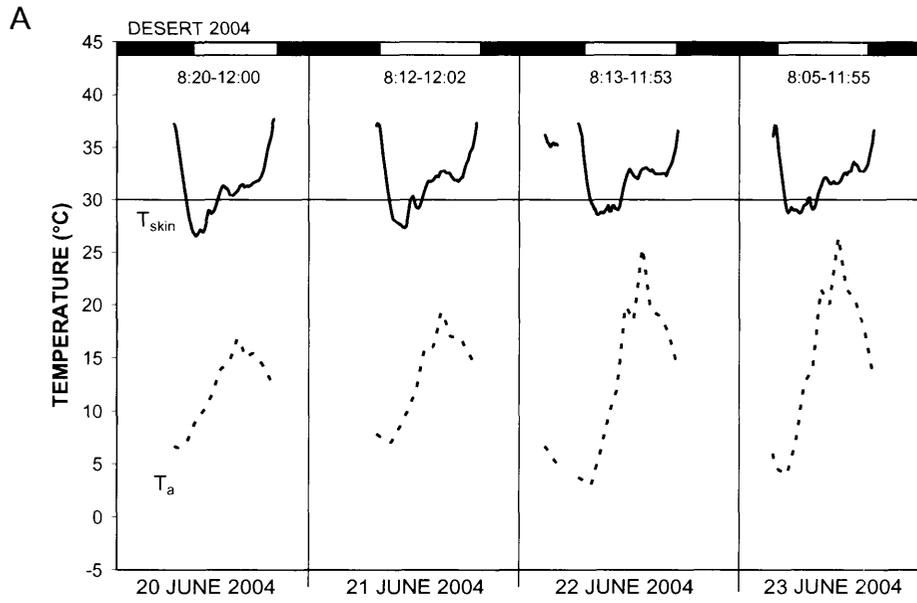
**Figure 4:** Torpor frequency as a percentage of the number of days or nights data were collected for all birds in both rock and tree roosts (black bars) and for birds in tree roosts only (white bars). The x-axis labels are for the irrigated desert (ID) in 2004 and 2005, desert (D) in 2004 and 2005, and at the eucalypt woodland (EW) site from 1996-1999 and in 2006. No birds used only tree roosts at the irrigated desert in 2005 and none used rock crevice roosts in the eucalypt woodland. Numbers above the bars represent the total number of torpor bouts (N). Sample sizes of individuals (n) are given in Table 2. Torpor frequency differed significantly amongst sites for all roosts ( $\chi^2_{0.05,4}=47.5$ ,  $P<0.0001$ ) and for tree roosts ( $\chi^2_{0.05,4}=67.3$ ,  $P<0.00001$ ). Torpor frequency did not differ between the two desert sites in either year (2004:  $\chi^2_{0.05}=0.4$ ,  $P=0.52$ ; 2005:  $\chi^2=1.9$ ,  $P=0.17$ ). Torpor frequency differed significantly between years at the desert site ( $\chi^2=32.5$ ,  $P<0.0001$ ), but not at the irrigated desert site ( $\chi^2_{0.05}=3.0$ ,  $P=0.09$ ). Torpor frequency at the eucalypt woodland site during both time periods was significantly greater than D-2004 (96-99:  $\chi^2_{0.05,4}=29.5$ ,  $P<0.0001$ ; 2006:  $\chi^2_{0.05,4}=26.9$ ,  $P<0.0001$ ) and less than D-2005 (96-99:  $\chi^2_{0.05,4}=13.6$ ,  $P<0.0001$ ; 2006:  $\chi^2_{0.05,4}=4.2$ ,  $P<0.05$ ).



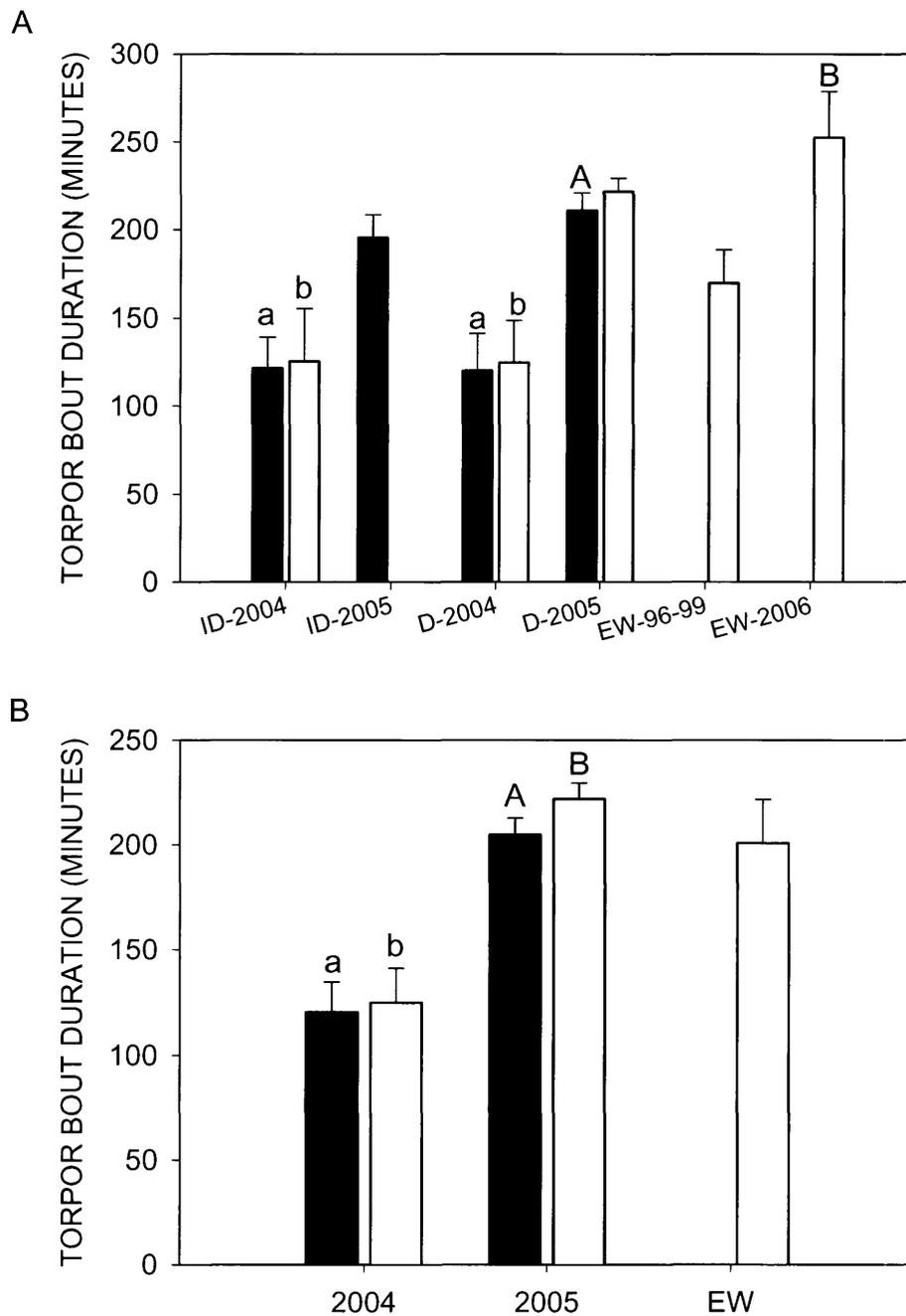
**Figure 5:** Torpor frequency as a percentage of the number of days or nights data were collected for birds using tree roosts at the desert sites combined for 2004 ( $n=5$ ) and 2005 ( $n=2$ ) and the eucalypt woodland site (EW,  $n=8$ ). The frequency of morning (Day AM: 6:00-12:00 h;  $X^2_{0.05,2}=36.9$ ,  $P<0.0001$ ) and night bouts ( $X^2_2=19.6$ ,  $P<0.0001$ ) differed amongst sites, but the frequency of afternoon bouts (Day PM: 12:00-18:00 h) did not ( $X^2_2=0.3$ ,  $P=0.60$ ). The number of days when more than one torpor bout occurred (>1 bout) differed significantly amongst sites ( $X^2_{0.05,2}=30.9$ ,  $P<0.0001$ ). See Table 1 for a pairwise comparison of sites for morning, night and > 1 bout per day.



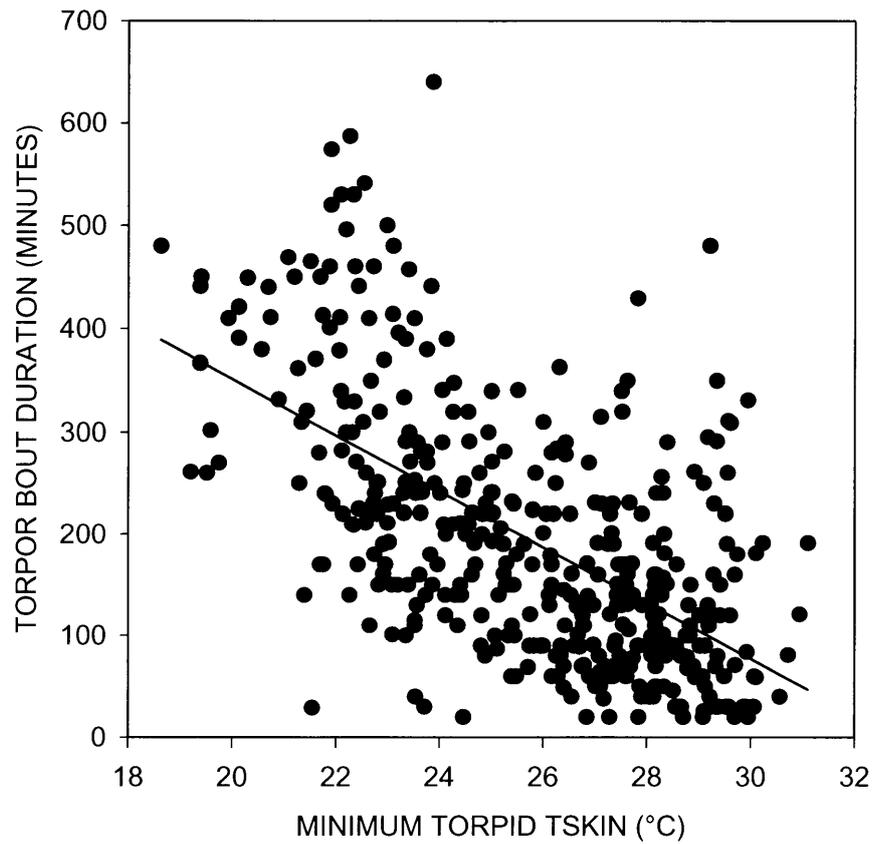
**Figure 6:** Rate of re-warming ( $^{\circ}\text{C min}^{-1}$ ) for birds roosting in tree hollows in central Australian in 2004 (filled circle, solid line), 2005 (circle, short dashed line), and in the eucalypt woodland (EW, triangle, long dashed line). The ANCOVA models indicated no significant relationship between rate of re-warming and A) MIN  $T_a$  ( $^{\circ}\text{C}$ ) or B) MIN  $T_{\text{skin}/T_b}$  ( $^{\circ}\text{C}$ ), either for sites separately (below) or combined (MIN  $T_{\text{skin}/T_b}$ :  $P=0.50$ , MIN  $T_a$ :  $P=0.48$ ). The rate of owllet-nightjar re-warming did not differ amongst sites/years for MIN  $T_a$  or MIN  $T_{\text{skin}/T_b}$ . A) ANCOVA: Site:  $F_{2,71}=0.37$ ,  $P=0.69$ ; MIN  $T_a$ :  $F_{1,71}=0.41$ ,  $P=0.52$ ; model  $R^2=0.02$ ; Linear regression for 2004: Rate= $0.067 - 0.001$  (MIN  $T_a$ ),  $F_{1,23}=0.32$ ,  $P=0.58$ ; 2005: Rate= $0.059 + 0.001$  (MIN  $T_a$ ),  $F_{1,23}=0.12$ ,  $P=0.74$ ; EW: Rate= $0.186 - 0.004$  (MIN  $T_a$ ),  $F_{1,23}=0.54$ ,  $P=0.47$ . B) ANCOVA: Site:  $F_{2,71}=0.18$ ,  $P=0.83$ ; MIN  $T_{\text{skin}/T_b}$ :  $F_{1,71}=0.00$ ,  $P=0.98$ ; model  $R^2=0.01$ ; Linear regression for 2004: Rate= $0.186 - 0.004$  (MIN  $T_a$ ),  $F_{1,23}=0.54$ ,  $P=0.47$ ; 2005: Rate= $-0.050 + 0.005$  (MIN  $T_a$ ),  $F_{1,23}=1.37$ ,  $P=0.25$ ; EW: Rate= $0.039 + 0.001$  (MIN  $T_a$ ),  $F_{1,23}=0.03$ ,  $P=0.87$ .



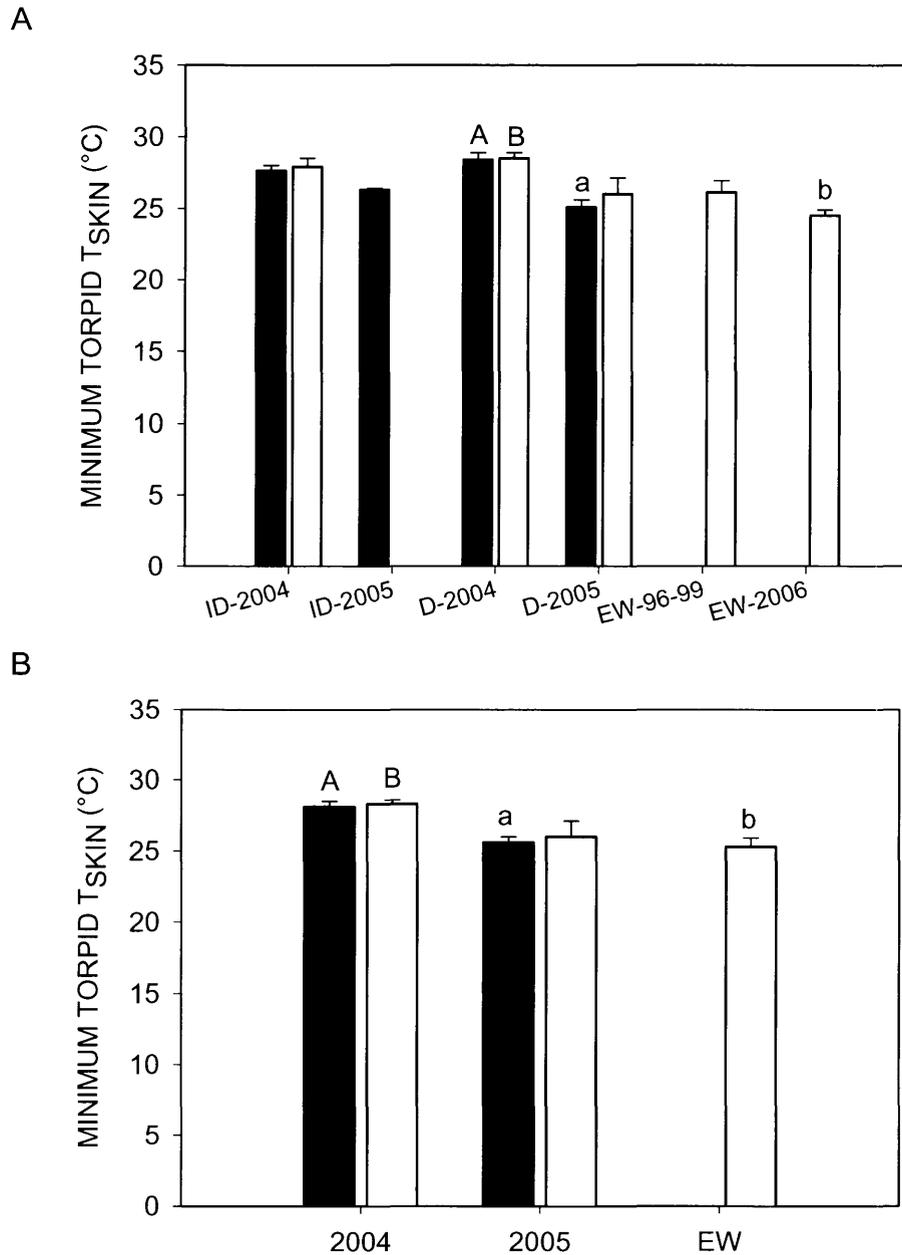
**Figure 7:** Examples of torpor bout patterns used by individual owlet-nightjars roosting in tree hollows in central Australia in 2004 and 2005 and at the eucalypt woodland site showing  $T_{skin}$  (solid line) and  $T_a$  (dotted line). Torpor bouts in the desert were longer and deeper in 2005 than in 2004 and the occurrence of more than one bout per day was more frequent. The same pattern of multiple deep frequent torpor bouts occurred in the eucalypt woodland. Start and end times of torpor bouts are labeled above each bout. Dark and light bars at the top of each figure correspond to scotophase (night) and photophase (day).



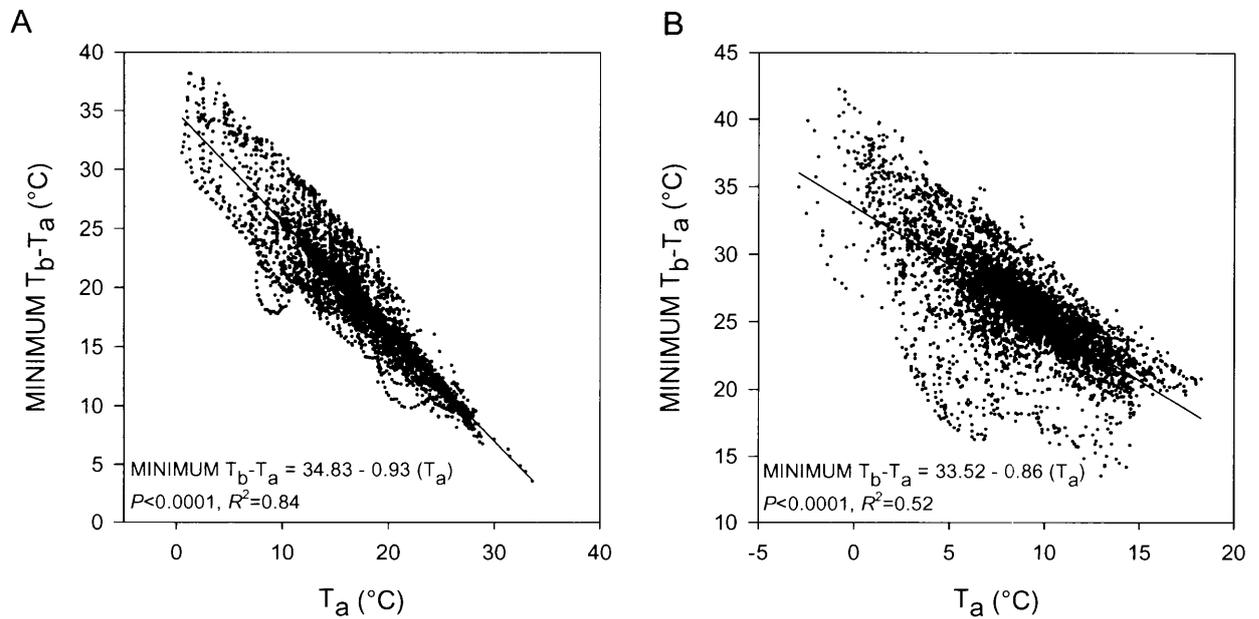
**Figure 8:** Mean  $\pm$  SE torpor bout duration (minutes) for birds in both rock and tree roosts (black bars) and tree roosts only (white bars). Letters above the bars indicate significant differences (i.e. 'a' is significantly less than 'A'). A) The mean torpor bout duration at the desert site in 2005 (D-2005) was significantly longer than both desert sites in 2004 for birds in rock and tree roosts (ANOVA:  $F_{3,12}=8.75$ ,  $P<0.01$ ). Mean torpor bout duration in tree roosts was significantly longer at the eucalypt woodland site in 2006 than at either desert site in 2004 ( $F_{4,14}=5.24$ ,  $P<0.05$ ). X-axis labels are as in Figure 4. Samples sizes are given in Table 2. B) Mean torpor bout duration for the irrigated desert and desert sites combined for each year. Bout duration was significantly greater in 2005 than in 2004 in the desert irrespective of roost type (Rock + Tree:  $t$ -test:  $t_{11}=4.44$ ,  $P<0.001$ ; Tree:  $F_{2,13}=4.49$ ,  $P<0.05$ ). Roost type had no significant effect on torpor bout duration (Chapter 2).



**Figure 9:** Torpor bout duration (minutes) is significantly inversely related to the minimum torpid  $T_{\text{skin}}$  (°C). Torpor Bout Duration =  $900.54 - 27.45 (\text{Minimum } T_{\text{skin}})$ ,  $P < 0.0001$ ,  $R^2 = 0.37$ ,  $N = 417$ .



**Figure 10:** Mean  $\pm$  SE minimum torpid  $T_{\text{skin}}$  ( $^{\circ}\text{C}$ ) for birds in both rock and tree roosts (black bars) and tree roosts only (white bars). Letters above the bars indicate significant differences (i.e. 'a' is significantly less than 'A'). A) The minimum torpid  $T_{\text{skin}}$  at the desert site in 2005 (D-2005) was significantly lower than for the desert site in 2004 for roost types combined (ANOVA:  $F_{3,12}=5.58$ ,  $P<0.05$ ). The minimum torpid  $T_{\text{skin}}$  at the eucalypt woodland site in 2006 (EW-2006) was significantly lower than the desert site in 2004 (D-2004) for tree roosts (ANOVA:  $F_{4,13}=4.58$ ,  $P<0.05$ ). X-axis labels are the same as in Figure 4. Sample sizes are given in Table 2. B) Minimum torpid  $T_{\text{skin}}$  differed significantly between years in the desert for rock and tree roosts combined ( $t$ -test:  $t_{11}=4.44$ ,  $P<0.001$ ). Minimum torpid  $T_{\text{skin}}$  for birds in the eucalypt woodland was less than the desert in 2004 ( $F_{2,13}=7.59$ ,  $P<0.01$ ). Roost type had no significant effect on the minimum torpid  $T_{\text{skin}}$  (Chapter 2).



**Figure 11:** Plots of  $T_b - T_a$  as a function of  $T_a$  for all  $T_b$  values collected for two individual owlet-nightjars with internal transmitters during day and night. A) An owlet-nightjar (ONJ 4) at the desert site in 2004. B) An owlet-nightjar (ONJ 60) at the eucalypt woodland site in 1999. The slopes and intercept of the regression lines differ significantly between the two birds and with  $T_a$  (ANCOVA: Owlet-nightjar:  $F_{1,8361} = 61.58$ ,  $P < 0.001$ ;  $T_a$ :  $F_{1,8361} = 18\ 000$ ,  $P < 0.001$ ; Owlet-nightjar\* $T_a$ :  $F_{1,8361} = 26.73$ ,  $P < 0.001$ ; model  $R^2 = 0.81$ ).

## Discussion

### *Effects of Climate and Arthropod Abundance on Torpor*

Arthropod abundance was lower in the eucalypt woodland than anticipated. Evidently, lower winter  $T_a$  reduced arthropod availability at this site. Thus, both aerial and terrestrial arthropod biomass in the eucalypt woodland and the desert in 2005 were statistically equivalent. Heavy rain in early winter 2004 increased arthropod abundance in the desert and negated the expected differences between the irrigated and non-irrigated sites. However, this rainfall did allow me to compare a wet with a normal-to-dry winter in the desert. Thus, although site variables were not as expected, a valid comparison of the relationship between torpor use,  $T_a$  and arthropod availability is possible by comparing years in the desert and the eucalypt woodland.

Owlet-nightjars entered daily torpor regularly at all sites, but torpor frequency, depth and duration were greater at the two sites with lower arthropod abundance (desert 2005 and eucalypt woodland; Figure 3). These two sites differed significantly in rainfall and  $T_a$ , suggesting that the similarity in prey availability was the major factor determining torpor occurrence (Table 4). As expected, there was a strong correlation between  $T_a$  and arthropod biomass (Table 3); however, if  $T_a$  alone determines the expression of torpor I would expect its use to be greater at the colder eucalypt woodland site only, where  $T_a$  was consistently lower than in the desert. As expected, torpor use was lowest in the desert in 2004, the site/year where  $T_a$  was moderate and prey abundance high.

### *$T_a$ and Solar Radiation*

It seems probable that on most days  $T_a$  alone does not represent a thermoregulatory challenge for owlet-nightjars. Owlet-nightjars possess feather insulation with low thermal conductance (Chapter 5), and are able to use cavity roosts with warmer microclimates than external  $T_a$  to reduce energy costs (Walsberg, 1986; Chapter 2). Owlet-nightjars may also use solar radiation to reduce the effect of low morning  $T_a$ s and/or an unsuccessful night of foraging, and basking is not uncommon (Geiser & Drury, 2003; Geiser et al., 2004). Basking, typically at the entrance to tree hollows, was observed more often in the eucalypt woodland (EW:  $n=4$ ,  $N=12$ ; D:  $n=2$ ,  $N=3$ ), suggesting that birds at this site may be more reliant on solar radiation to arouse and maintain  $T_{skin}$  than in the desert. One individual in the woodland (ONJ 32) was found basking exposed on a gravel road on three consecutive mornings. In total, ONJ 32 was observed basking on six occasions during the 15 days it was tracked (40%), and entered

torpor on only 40% of bird-day mornings. Night torpor was more frequent for ONJ 32 (50% of bird-nights) and this bird was known to arouse from torpor and change roosts at dawn to move to a sunnier location. ONJ 32 was recorded in torpor ( $T_{\text{skin}} = 26.3\text{ }^{\circ}\text{C}$ ) on only one occasion while basking. These findings suggest that ONJ 32 had adapted a successful basking strategy to reduce torpor use. In contrast, two other individuals tagged during the same time period in the eucalypt woodland entered torpor at dawn on 88 and 93% of bird-days and only one bird was observed basking on a single occasion. This bird was recorded basking with a  $T_{\text{skin}}$  of  $21.2\text{ }^{\circ}\text{C}$  at the entrance to a tree hollow on a morning when MIN  $T_{\text{a}}$  was  $-6.7\text{ }^{\circ}\text{C}$ , and was unresponsive to noise. Owlet-nightjars have been observed basking on gravel roadways on cold winter mornings elsewhere on the Northern Tablelands (D. Page, personal communication). Approaching birds without causing disturbance is difficult, and thus basking behaviour by owlet-nightjars is likely more common than reported here. This method of thermoregulation would serve as a practical alternative to daytime torpor use, and would facilitate torpor arousal (Mzilikazi et al., 2002; McKechnie & Wolf, 2004b). Because of the frequency of basking behaviour, I included cloud cover as a variable that may influence torpor use. Cloud cover was correlated with torpor frequency; however, it is difficult separate the result from the influence increased cloud cover has on  $T_{\text{a}}$ .

Periods of low nocturnal  $T_{\text{a}}$  may have a greater impact on small diurnal birds, which are inactive during the colder night period and do not have the opportunity to take advantage of solar radiation during their rest-phase like nocturnal birds can. While torpor seems relatively rare in small birds, especially passerines, a pattern of shallow nocturnal hypothermia, where  $T_{\text{b}}$  is reduced by several degrees is common (Reinertsen, 1983; Bartholomew et al., 1983; Clark & Dukas, 2000; McKechnie & Lovegrove, 2003; Dolby et al., 2004; Maddocks & Geiser, 2007). However, several small diurnal avian species, such as hummingbirds, enter torpor each night, reducing  $T_{\text{b}}$  to as low as  $5\text{ }^{\circ}\text{C}$ . For these species, torpor appears to be an innate response to conserve energy stores, and may be unrelated to daily  $T_{\text{a}}$  or food availability (Carpenter & Hixon, 1988). Manakins (*Manacus vitellinus* and *Pipra mentalis*), small (15 g) tropical frugivorous passerines (Pipridae) also use nocturnal torpor regularly, reducing  $T_{\text{b}}$  to  $27\text{ }^{\circ}\text{C}$  at  $T_{\text{a}}$  of  $15\text{ }^{\circ}\text{C}$  without food restrictions (Bartholomew et al., 1983). Tropical female Puerto Rican todies (5-7 g, *Todus mexicanus*, Todidae) enter torpor during the warm breeding season when food is abundant (Merola-Zwartjes & Ligon, 2000), and populations of Andean hillstar hummingbirds (*Oreotrochilus estella estella*) enter nocturnal torpor during winter daily, irrespective of  $T_{\text{a}}$  and nectar availability (Carpenter, 1974). Carpenter (1974) concluded that torpor was part of their circannian cycle and that

hummingbirds were genetically programmed to enter torpor immediately at dusk to save energy should it be needed later for thermoregulation. The occurrence of torpor is less predictable for nocturnal avian species, whether they enter torpor during their nocturnal rest-phase (Körtner et al., 2001) or during the daytime (Brigham, 1992; Brigham et al., 2000; Brigham et al., 2006). Nocturnal species may have an advantage by being active during the colder periods of the night, when activity associated with foraging generates heat and reduces thermoregulatory costs (Webster & Weathers, 1990). Thus, entering torpor daily is not necessary, and the use of torpor is determined by environmental factors, which in the case of owlet-nightjars, appears to be prey availability. Limitation in food supply combined with cold stress is postulated as the major cause of torpor in birds (Schleucher, 2004).

#### *Arthropod Availability*

Low arthropod abundance at both the eucalypt woodland site and the desert site in 2005 was correlated with increased torpor frequency and duration, and lower torpid MIN  $T_{\text{skin}}$  in both locations (Tables 3 and 4). Aerial and terrestrial arthropod abundance was low, but statistically equivalent at the two sites. A difference in arthropod abundance also explains the disparity in torpor use between the two years in the desert despite no difference in  $T_a$ . The desert flourished during winter of 2004, with creeks flowing, vegetation flowering, and relatively high arthropod abundance resulting in low torpor frequency and shorter, shallower bouts. In the desert in 2005, despite mid-winter rains, conditions were harsher. Creeks were dry, permanent water holes were shrinking (Chapter 6) and diurnal and nocturnal wildlife activity was reduced (G. Edwards, NRETA Alice Springs, personal communication). Terrestrial arthropod abundance was lower at both desert sites and aerial arthropod abundance was less in the desert site than in 2004. Aerial arthropod abundance, in the form of high numbers of Lepidoptera after the rains (mid-July), was high at the irrigated site (Chapter 6). Moths seem to have been drawn to this site, possibly by the irrigation systems promoting flowering vegetation. Nonetheless, torpor depth was lower and duration longer at the irrigated desert site in 2005 than in 2004 (Table 2). This may be due to the poorer condition of the owlet-nightjars after a dry year leading into the winter. The body mass of owlet-nightjars captured in 2005 were on average 7.4 g (15%) less than in 2004. These findings suggest that while torpor naturally occurs in owlet-nightjars at low  $T_a$ , a reduction in prey increases the frequency and depth of this energy saving mechanism.

Many laboratory studies have examined the effect of a restricted diet, a period of fasting, and/or a reduction in body mass on torpor use in animals (Marshall, 1955; Lasiewski &

Dawson, 1964; Peiponen, 1965; Dawson & Fisher, 1969; Dawson & Hudson, 1970; Ligon, 1970; Calder & King, 1974; Prinzinger et al., 1981; Hohtola et al., 1991; Bech et al., 1997; Song et al., 1998; Lovegrove et al., 1999b). A restricted diet typically results in increased torpor frequency, depth and duration in both mammals and birds. However, differences in torpor patterns differ between captive and free-ranging animals (Geiser et al., 2000; Geiser et al., 2007). Few field studies have examined the effect of food availability on free-ranging birds, and I know of only two that quantitatively demonstrated the effect of reduced food resources on torpor independently from  $T_a$ . In a semi-natural field study, Bech et al. (1997) caught three species of hummingbirds (*Amazilia versicolor*, *Melanotrochilus fuscus*, *Euptomena macroura*) at artificial feeders and deprived them of food for varying periods until sunset, keeping them in cages overnight to examine torpor use. All three species entered torpor, but torpor frequency and duration was positively related to the duration of fasting time before sunset and negatively related to the body mass of the individual. Secondly, Woods & Brigham (2004) used artificial lighting to investigate the effect of aerial insect abundance on the use of torpor by common poorwills (*Phalaenoptilus nuttalli*). They found that torpor frequency decreased 38% at the site with supplemental illumination, and hence greater prey availability. Previously, Brigham (1992) had reported that  $T_a$  at twilight was the main determinant of torpor entry in common poorwills, but noted that foraging activity by poorwills was less on nights when torpor was used. Woods & Brigham (2004) suggested that it was likely the reduction of twilight insect activity levels by low  $T_a$  that was influencing poorwill torpor more than the low  $T_a$  itself. Similarly, it is more likely the influence of  $T_a$  on arthropod availability, rather than a direct effect of  $T_a$ , which resulted in the correlation between  $T_a$  and torpor use in my study.

Previously, I reported that torpid MIN  $T_{skin}$  and torpor bout duration appeared to be unrelated to roost microclimate, and suggested that it may be influenced by prey abundance (Chapter 2) or diet instead (see below). The lower torpid MIN  $T_{skin}$  in the desert in 2005 ( $24.7 \pm 0.4$  °C) and in the eucalypt woodland ( $24.5 \pm 0.2$  °C), compared to the desert in 2004 ( $27.7 \pm 0.3$  °C), likely reflects that paucity of prey items at these sites/years and the greater need to conserve energy. The energy saved by the reducing metabolic rate below basal during daily torpor in small heterotherms is largely determined by  $T_b$  (Song et al., 1995; Geiser, 2004a). Thus, even a 3 °C decrease in  $T_{skin}$  would likely mean substantial metabolic energy savings for a small bird. The MIN  $T_b$  threshold during torpor is controlled by the animal and torpid endotherms are able to increase their heat production to prevent  $T_b$  from falling below this threshold (Bartholomew, 1982). Although the  $T_b$  threshold varies widely among species, the average

minimum  $T_b$  during daily torpor for birds is 18.6 °C (Geiser & Ruf, 1995), and for most bird species metabolic heat production rises when  $T_b$  has fallen to about 20 °C (Reinertsen & Haftorn, 1983). Reinertsen & Haftorn (1983) postulated that below 20 °C birds may no longer be capable of spontaneous arousal; however, the common poorwill is capable of arousing from  $T_{skin} < 3$  °C (Brigham, 1992). While owlet-nightjars were capable of reducing their MIN  $T_{skin}$  during torpor to below 20 °C, they usually maintained MIN  $T_{skin} \sim 26$  °C. This  $T_{skin}$  may represent the threshold for owlet-nightjars that allows for maximum energy conservation with minimal heat production. The MIN  $T_{skin}$  of owlet-nightjars was inversely related to the duration of torpor bouts, thus, owlet-nightjars at sites/years with low prey abundance also spent longer in torpor, increasing energy conservation still further. A reduction in food supply increases torpor duration in both mammals (Tucker, 1962) and birds (Hiebert, 1992) in the laboratory.

Although desert 2005 and eucalypt woodland birds did not differ significantly in MIN  $T_{skin}$ , owlet-nightjars in the eucalypt woodland may have a greater capability to lower their  $T_{skin}$  further based on their diet. The diet of owlet-nightjars in the woodland differs from that in the desert; they eat twice the biomass of Coleoptera (49% versus 25%; Chapter 6). Coleoptera are high (22.3%) in linoleic acid, an unsaturated essential fatty acid (EFA) that may facilitate the use of torpor (Schalk & Brigham, 1995). Body fats must remain fluid to be metabolized, and the melting point of animal fat greatly decreases as the degree of fatty acid unsaturation increases (Munro & Thomas, 2004). EFAs cannot be synthesized by animals, and must be acquired in the diet. Thus, a diet high in EFA allows for a decrease in  $T_b$ , and therefore, the duration of torpor bouts (Geiser & Kenagy, 1987; Schalk & Brigham, 1995; Falkenstein et al., 2001). This difference in diet may enhance the ability of owlet-nightjar in the colder woodland to enter deeper, longer torpor bouts during periods of low prey abundance.

Although food availability influenced the use of torpor in this study, a critical food shortage or period of fasting was not required to stimulate torpor in free-ranging owlet-nightjars. All birds were in good condition when captured. One of the owlet-nightjars captured in June 2006 in the eucalypt woodland with a body mass of 51.3 g had previously been captured in February 2006 (52.5 g) and was captured again in September 2006 (51.5 g). This individual used torpor on 93% of bird-days during June-July, despite its fit condition and high body mass. Many laboratory studies on Caprimulgiformes have noted that a period of fasting and mass loss was required to 'force' nightjars and other avian species into torpor (Marshall, 1955; Lasiewski & Dawson, 1964; Peiponen, 1965; Dawson & Fisher, 1969; Dawson &

Hudson, 1970; Ligon, 1970; Calder & King, 1974; Prinzinger et al., 1981; Hohtola et al., 1991). However, several species readily enter torpor in the field under favourable environmental conditions and no acute reduction in food availability (Carpenter & Hixon, 1988; Brigham, 1992; Körtner et al., 2001; Lane et al., 2004; Schleucher, 2004; Woods & Brigham, 2004; McKechnie et al., 2007). This discrepancy in the use of torpor between free-ranging and captive birds is likely due to captivity-induced stress (Geiser et al., 2000; Körtner et al., 2001; Schleucher & Prinzinger, 2006). Both non-fasting tawny frogmouths (*Podargus strigoides*) and owlet-nightjars would not enter torpor in the laboratory (Geiser et al., 2000; L. I. Doucette, unpublished data), but readily do so in the wild (Körtner et al., 2000; Körtner et al., 2001).

### *Rainfall*

Rainfall was not correlated with any torpor measure (Table 3), and there was no relationship between rainfall amounts on a given day and the occurrence of torpor in my study. Owlet-nightjars are active on nights with periodic to continuous light rainfall (L. Doucette, unpublished data), but would likely seek shelter during very heavy falls. Rain and overcast skies resulted in warmer winter nights, and the aerial arthropod abundance was greater in light traps at all locations on wet nights. Increased arthropod activity provides better foraging opportunities, which may offset increased thermoregulation costs by wet birds. Laboratory studies have shown that rainfall at  $T_a$ s of 10 to 15 °C caused a decrease in  $T_b$  and a 14% increase in metabolism in American kestrels (*Falco sparverius*; Wilson et al., 2004) and 10% in bald eagles (*Haliaeetus leucocephalus*; Stalmaster & Gessaman, 1984). Thus, the metabolic costs associated with exposure to rain would likely be greater for the smaller owlet-nightjars. Nonetheless, owlet-nightjars often roost in hollow stumps or dead snags open at the top, fully exposed to weather during the day. This occurs most commonly during the summer, when rainfall is greatest in the eucalypt woodland (monthly mean = 94 mm), as birds nest in stumps (Brigham et al., 1997; Brigham & Geiser, 1997). Thermoregulation is important to birds incubating eggs or brooding nestlings (Kissner & Brigham, 1993), and presumably these exposed nest locations would not be used if rain caused a significant energetic dilemma.

Owlet-nightjars have the option to return to cavity roosts to shelter from the rain during the night, but to do so would reduce foraging time. Rain was a significant predictor of torpor in sugar gliders (*Petaurus breviceps*), another cavity user at the eucalypt woodland site, due to a reduction in foraging activity (Körtner & Geiser, 2000b; Christian, 2007). However, rainfall

appears to be relevant for owlet-nightjars only in terms of its relationship to arthropod abundance.

### ***Torpor use in Arid Environments***

Torpor frequency is expected to be greater in animals that experience variability and unpredictability in food supply, such as insectivores in semi-arid regions that may experience a reduction in food availability during droughts (Lovegrove et al., 1999b). Torpor is especially pronounced in small insectivorous mammals living in arid areas as food availability decreases during dry or drought conditions, while their need for food and water increases (Geiser, 2004b). Torpor significantly reduces evaporative water loss (EWL) and influences the lengths of torpor bouts in mammals (Thomas & Geiser, 1997; Geiser, 2004b). However, few studies have examined the use of torpor by desert birds (although see Schleucher, 2001a; 2001b), and as birds are better adapted for water retention, a reduction of EWL during torpor may be less crucial for them compared to arid zone mammals. Birds typically have lower respiratory water losses and excrete up to 10 times less water per mg of nitrogenous waste than similar-sized mammals (Serventy, 1971; Astheimer & Buttemer, 2002). Arid zone birds also have lower resting basal metabolic rates (BMR) and EWL, which reduce both energy and water requirements, than species from mesic habitats (Dawson & Bennett, 1973; Tieleman & Williams, 2000), although this is controversial (Williams & Tieleman, 2002; Williams & Tieleman, 2005). Tieleman et al. (2003) demonstrated that BMR and EWL in 12 species of lark (Alaudidae) decreased as aridity of the area they inhabited increased (also see Tieleman & Williams, 2000). However, Cooper et al. (2002) found no difference in the water economy, measured as the ratio of EWL to oxygen consumption, between arid zone and forest-dwelling cockatoos and corellas. Nonetheless, birds with lower BMRs, and hence EWLs, such as owlet-nightjars (Chapter 5), should be better suited to arid environments. Spotted nightjars (*Eurostopodus argus*), another species of Caprimulgiformes, have metabolic rates 68% of those predicted and are well suited to arid conditions in central Australia (Dawson & Fisher, 1969). Thus, the lower BMR of owlet-nightjars may suitably adapt them to the desert environment without the need to increase torpor use, which explains the lack of difference between the mesic and arid habitats. It is also possible that conditions were not dry enough in the desert in 2004 to significantly affect the birds, and that the drier conditions in 2005, in addition to the lower arthropod abundance, contributed to the increased use of torpor. Further studies on the physiology and ecology of arid zone Caprimulgiformes to determine how they cope with drought and intense heat are required.

### ***Daily Torpor Patterns***

While data on torpor could not be analyzed by sex due to lack of gender data for 1996, 1997, 1999 and 2004, it is relevant to note that torpor occurred in both sexes and there was no apparent difference in MIN  $T_{\text{skin}}$  between genders. Torpor frequency by the female caught in the eucalypt woodland in 2006 was less than the two males, but this bird also spent more time basking. In contrast, the female monitored in the desert in 2005 used torpor more frequently than any of the males; however, this bird was tracked during a colder portion of the winter and only roosted in tree hollows.

Torpor patterns and periodicity were similar between sites and years. Owlet-nightjars predominantly enter torpor during the daytime rest phase and only used torpor on the coldest nights ( $<5^{\circ}\text{C}$ ). However, owlet-nightjars used night torpor more frequently than previously thought (up to 26.7% of bird-nights; Brigham et al., 2000). The frequency of nocturnal torpor in habitats with low prey abundance suggests that owlet-nightjars may use torpor at night when foraging is no longer profitable. Körtner & Geiser (2000a) suggested that torpor is only likely to commence in the normal activity phase during times of adverse weather conditions and reduced food availability (also see Körtner et al., 2001). Birds never remained in torpor past sunset, when insect availability was normally highest (Racey & Swift, 1985), and only entered torpor before midnight (within 6 hours of sunset) on six occasions in the desert and one in the eucalypt woodland. Night torpor was rarely used in the desert in 2004 (5.7% of bird-nights) where prey abundance was greater.

While the most common torpor pattern of owlet-nightjars was a single morning bout, a bimodal pattern of two torpor bouts per day, or at least a lowering of  $T_{\text{skin}}$  twice per day with a midday arousal, occurred in both habitats. Synchronizing arousal with the warmest part of the day greatly reduces the cost of torpor, as arousal is the most energetically expensive part of the bout (Körtner & Geiser, 2000a; Schmid, 2000; Geiser & Drury, 2003). Owlet-nightjars in poorly insulated tree hollows are able to take advantage of increasing diurnal  $T_a$  for passive rewarming (Lovegrove et al., 1999a; Geiser et al., 2004; Chapter 2), which explains arousal from torpor near midday. Even common poorwills, which may remain inactive for several consecutive days during winter, arouse from torpor regularly on sunny days through passive solar warming, and re-enter torpor at sunset (Woods & Brigham, 2004).

Owlet-nightjars which enter two torpor bouts during daytime will typically re-enter torpor in late-morning to early afternoon, sometimes only 60 minutes after arousal from the morning bout. It is this pattern of re-entry that is difficult to explain. While the longest torpor bouts at each site commenced at night, owlet-nightjars did occasionally enter torpor in the morning and remain in torpor throughout the day (e.g. 530 minute bout in EW from 7:12-16:02 h). Thus, it is not passive re-warming with  $T_a$  that mandates their arousal. This is supported by a similar pattern of more than one torpor bout interspersed with short periods of arousal that occur in hummingbirds during the night (Bech et al., 1997) and in Australian microbats during summer (Turbill et al., 2003a; Turbill et al., 2003b). One feature of torpor which all sites and years had in common was that if a bird entered torpor at dawn, and remained in torpor until at least 12:30 h (~300 minutes after sunrise adjusted for site differences), a second bout did not occur that day (N=62). However, night bouts of even greater length still resulted in a second or even third bout within 24-h. Thus, it appears that birds that wait until afternoon when  $T_a$  is higher to arouse do not re-enter torpor, while those that arouse mid-morning may re-enter torpor in the afternoon. Afternoon or double torpor bouts occur on colder days than single morning bouts, and occurred more often at the eucalypt woodland site (15.7% of bird-days compared to <3.8% in the desert), where  $T_a$  was significantly lower. Thus, the decision to re-enter torpor may depend on  $T_a$ , or possibly available energy reserves (Hiebert, 1992).

But why should owlet-nightjars incur the high energetic cost of two arousals rather than remaining in torpor for a longer period? The bimodal temporal pattern of two torpor bouts per day occurs every day during summer in Australian microbats (Turbill et al., 2003a; 2003b). Turbill et al. (2003a) proposed that a period of arousal during the warmest part of the day may facilitate physiological processes such as spermatogenesis. However, as owlet-nightjars spend less time in torpor compared to bats, and never enter torpor bouts for longer than one day, warming at midday does not seem physiologically necessary. One possibility is that once the  $T_b$  set point is reached the metabolic rate increases and metabolic processes provide the stimulus for arousal (Geiser & Kenagy, 1988). Unlike most species, the torpor bout curve for owlet-nightjars often does not flatten at the lowest  $T_b$ , and arousal generally commences immediately following the lowest  $T_b$  (Figure 7). A second possibility is that there is a trade-off between torpor duration and the risk of predation (Welton et al., 2002). Bats use shallower, shorter torpor bouts when in exposed cavity roosts (rock crevice) compared to roosts with lower risk, such as the attic of a building (Lausen & Barclay, 2006). Owlet-nightjars may also use shorter daytime bouts to remain alert and reduce predation risk. Although rates of re-warming were highly variable amongst individuals, owlet-nightjars

rewarm slower than most other species of birds (McKechnie & Wolf, 2004a), and thus would be unable to react to disturbance or predation (Carpenter & Hixon, 1988).

### ***Conclusion***

Owlet-nightjars used torpor regularly during winter at low  $T_a$ , but torpor bouts were more frequent, deeper, and longer in habitats with reduced prey availability. My results suggest that torpor use is a physiological adaptation by owlet-nightjars to conserve energy reserves throughout winter, even in the moderate climate of the desert. Birds using torpor frequently during winter maintained high body mass, indicating that a state of pronounced energetic emergencies did not occur. My findings support the findings of field studies on free-ranging birds which quantitatively demonstrated the effect of reduced food resources on torpor independently from  $T_a$  (Bech et al., 1997; Woods & Brigham, 2004).

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## CHAPTER 5

### Seasonal Variation in Energetics of the Australian Owlet-Nightjar (*Aegotheles cristatus*)

#### Abstract

Many birds living in regions with seasonal fluctuations in ambient temperatures ( $T_a$ ) typically respond to cold by increasing insulation and adjusting metabolic rate. Although Australian birds experience relatively mild winters, most do not migrate and therefore must cope with cold winter weather and a reduction in food supply. Seasonal variation in thermal physiology has not been studied for the Caprimulgiformes, an order of birds that generally have basal metabolic rates (BMR) lower than predicted for their body mass. I measured the metabolic rate and thermal conductance of Australian owlet-nightjars (*Aegotheles cristatus*) during summer and winter using open-flow respirometry. Body mass did not vary seasonally, but body temperature ( $T_b$ ) was higher in summer ( $38.2 \pm 0.3$  °C) than winter-acclimatized ( $37.1 \pm 0.5$  °C) birds. Within the thermoneutral zone (TNZ; 31.3 to 34.8 °C), there was no seasonal difference in BMR or thermal conductance (C). Below the TNZ, resting metabolic rate (RMR) increased linearly with decreasing  $T_a$ , and RMR and C were higher for summer than winter-acclimatized birds. The mean mass-specific BMR of owlet-nightjars ( $1.27 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$ ) was close to the allometrically predicted value for a 45g Caprimulgiformes, but well below that predicted for birds overall. My results suggest that owlet-nightjars do not adjust BMR during winter. Instead, they increase plumage insulation to cope with low winter  $T_a$ , which is reflected in the seasonal difference in RMR and C below the TNZ. The use of thermally insulated cavity roosts may further reduce their need for seasonal adjustments in thermal physiological.

#### Introduction

Thermoregulatory responses of birds to cold can include increasing insulation, behavioural thermoregulation, and augmenting heat production (Calder & King, 1974). Birds are limited in the degree to which they can increase plumage and fat deposits for insulation (Scholander et al., 1950a), presumably due to the necessity of maintaining a body mass that allows for efficient flight. Thus, increasing insulation in winter may not be adequate to offset the added energetic costs of keeping warm at low ambient temperatures ( $T_a$ ), especially in cold climates at high latitudes or altitudes. Selecting an appropriate microclimate, such as a cavity roost or a roost warmed by solar radiation will also play a role in reducing the energetic demands

imposed by low  $T_{as}$  (Walsberg, 1985; Lovegrove et al., 1991). However, it has been proposed that many species can only achieve a thermal balance during winter by adjusting heat production and basal metabolic rate (BMR; Calder & King, 1974). For several decades there has been an ongoing debate over whether the BMR of birds should be higher in winter to maintain body temperature ( $T_b$ ) at low  $T_{as}$  (e.g. Weathers & Caccamise, 1978), or lower to reduce energy expenditure for thermoregulation (e.g. King, 1974). Others propose that birds should exhibit no seasonal variation in BMR, either because they are able to produce adequate insulation to maintain a constant  $T_b$  without adjusting their BMR (Scholander et al., 1950a), or because the increased energetic costs associated with breeding and raising young during summer are comparable to the energetic demands of winter (Masman et al., 1986), a situation that would be most likely to occur in regions with mild to moderate winter climates.

In Australia, the few studies on seasonal variation of bird thermal physiology have all been restricted to small diurnal passerines less than 15 g. The outcome of these studies are conflicting, with species inhabiting milder or arid climates in Western Australia increasing their BMR during winter (Collins & Briffa, 1983; Ambrose & Bradshaw, 1988), while those in regions with greater seasonal variation in  $T_a$  exhibiting no seasonal variation or a lower winter BMR (Maddocks & Geiser, 2000; Lill et al., 2006). This contrasts with most studies on birds in North America where winter BMR was higher than summer BMR (Pohl & West, 1973; Swanson, 1991; Cooper & Swanson, 1994; Cooper, 2002; Liknes et al., 2002). Resting metabolic rate (RMR) and thermal conductance (C) below the thermoneutral zone (TNZ) was lower in winter for the two Australian species in which it was measured (Maddocks & Geiser, 2000; Lill et al., 2006). The body mass (BM) of passerines in these studies did not differ seasonally or was only slightly higher for birds during winter (Maddocks & Geiser, 2000; Lill et al., 2006).

Australian owlet-nightjars (*Aegotheles cristatus*; ~45 g) are sexually monomorphic birds of the order Caprimulgiformes whose range encompasses all of Australia, including Tasmania. They occupy a range of habitats from tropical rainforests to temperate woodlands, highlands, and deserts. Owlet-nightjars are sedentary nocturnal insectivores that roost singly in cavities year round. Caprimulgiformes are one order of birds which have lower BMRs than expected from allometric equations and body mass (BM; Bennett & Harvey, 1987), and are one of the few orders of birds capable of reducing metabolic rate (MR) and  $T_b$  during torpor (McKechnie & Lovegrove, 2002). Sedentary birds from seasonally variable environments have been found to have lower BMRs than those from more moderate climates (White et al.,

2007). My purpose was to determine whether the BMR of one species of owl-nightjar (Aegothelidae) was comparable to other families of Caprimulgiformes and whether its thermal physiology varied with season in a region that experienced a substantial disparity in seasonal  $T_a$ . Mine is the first study to: 1) assess seasonal variation in thermal energetics for a species of Caprimulgiformes; 2) determine the BMR for a species of the family Aegothelidae.

## **Methods**

### ***Experimental Procedures***

Open flow respirometry was used to measure the MR of owl-nightjars at  $T_a$  ranging from 0 to 35 °C during summer and winter. The owl-nightjars used in this study were captured at Imbota Nature Reserve (30° 35' S, 151°45'E, 1000 m elevation), 10 km southeast of Armidale on the Northern Tablelands, New South Wales during summer (December 2005 to February 2006) and winter (June to August 2006). The mean daily minimum and maximum temperatures for Armidale are 13.0 °C and 26.6 °C in summer and 1.0 °C and 13.2 °C in winter (1857-1997, Australian Bureau of Meteorology). Mean monthly rainfall in summer (93.8 mm) is almost double of that in winter (51.5 mm).

Individual owl-nightjars were captured in the evening by broadcasting taped owl-nightjar calls to lure individuals into mist nets. After capture, birds were immediately transported to the laboratory and kept in dark boxes overnight. Metabolic experiments commenced the following morning. Only one bird was measured at a time, except for one occasion when two birds were caught simultaneously and measured together (separate chambers) the following day. The sex of individuals was unknown as there are no external characteristics which can reliably be used to determine gender of owl-nightjars. The sex of birds was later determined based on DNA extracted from the shaft of feathers pulled from the chest area (Genetic Science Services, Fitzroy, Victoria). The sex of two of the birds could not be determined, thus these birds were excluded from analysis by sex. Each bird was examined for signs of feather moult and details of stages and location of moulting feathers were recorded based on descriptors cited on the Moulting Recording Sheet, Australian Bird Banding Scheme. All summer birds were caught after the completion of the breeding season (February) with the exception of one individual caught in late-December whose young were known to have fledged successfully the previous week.

The BM was measured for each bird at the start and end of the experiment and a linear rate of mass loss was assumed for calculation of mass-specific MR. A pre-calibrated temperature-

sensitive external radio-transmitter (model PD-2T, Holohil Systems, Carp, Ontario, Canada) was attached to the interscapular region of each owlet-nightjar using an elastic harness (Figure 5.1E in Kenward, 1987) prior to commencement of metabolic readings to measure skin temperature ( $T_{\text{skin}}$ ). The transmitters had previously been calibrated based on pulse rate against a mercury thermometer to the nearest 0.1 °C for temperatures from 0 °C to 40 °C in a water bath. Cloacal temperatures for measurement of core  $T_b$  were measured to the nearest 0.1 °C at the start and end of each experiment and at each major change in  $T_a$  using a pre-calibrated fine thermocouple inserted 1.5 to 2 cm into the cloaca, and read with an Omega digital thermometer accurate to within  $\pm 0.1$  °C. (Model HH-71 T, Omega Engineering Inc., Stamford, Connecticut).

Seven different adult owlet-nightjars were measured in summer and six in winter. Owlet-nightjars were placed in the chamber at 8:00 h. Birds were not fed and were post-absorptive, given that at least 10 hours had elapsed since their last potential feed (prior to latest capture at 22:00 h).  $T_a$  ( $\pm 0.1$  °C) was measured using a thermocouple inserted 1 cm into the respirometry chamber. The thermocouple signal was amplified and recorded with an Omega multiplex thermocouple thermometer (DP 116, Omega Engineering Inc., Stamford, Connecticut).  $T_a$  was increased about every two hours to record MR at 0 °C, 8 °C, 17 °C and 28 °C. During the final two hours  $T_a$  was gradually increased in 2-5 °C intervals from 28 °C to 36 °C to define the thermoneutral zone. Thus, birds were in the metabolic chamber for approximately 10 hours. After the completion of metabolic measurements, birds were released at night at the point of capture.

Ideally, BMR is measured over an eight to ten hour period. However, owlet-nightjars are difficult to maintain in captivity and require force feeding several times daily. Thus, to minimize stress which would confound BMR results (McKechnie & Wolf, 2004), all of the measurements were conducted in one day and the birds released as quickly as possible. The option of using additional individuals to measure BMR separately from RMR was not possible as owlet-nightjars are difficult to capture, requiring up to 10 nights of mist-netting per bird captured during winter (Chapter 7). Keeping owlet-nightjars under thermoneutral conditions for a longer period may have resulted in a marginally lower BMR. However, altering the protocol would not have affected the seasonal comparison as time used to measure BMR during both seasons was identical.

### ***Respirometry***

Birds were placed in respirometry chambers (diameter= 120 mm, length = 205 mm, volume =2.0 l) made from air-tight acrylic containers with rubber seals. Each chamber had three short copper tubes affixed for air inlet and outlet, and a third opening for the thermocouple to measure  $T_a$ . The chambers were placed horizontally inside a temperature-controlled cabinet ( $\pm 0.5$  °C) and covered with a layer of fabric to dim the lighting and create the effect of a cavity or tree hollow. A small piece of oven-dried bark was placed in the bottom of the chamber for the bird to stand on. No perch was provided given that owllet-nightjars lie flat in hollows (Doucette, 2007). Light in the chamber was provided by a shaded 15 W bulb.

To measure oxygen consumption, I used a single channel oxygen analyzer (FOX, Sable Systems International Inc., Las Vegas, USA), placed inside an insulated foam box in a temperature-controlled room at  $19 \pm 2$  °C. A sub-sampling design was used to keep the rate of flow of the sample air through the analyzer constant ( $125 \text{ ml min}^{-1}$ ) throughout the measurements. Outside air was pumped through silica gel to remove moisture while rotameters (Aarlborg 7908, New York, USA) controlled the rate of airflow to the chambers. After passing through the chamber, excurrent air was dried again using silica gel and the flow rate of air was measured using a mass flow meter (Omega FMA-5606, Stamford, USA). A flow rate of  $800 \text{ ml min}^{-1}$  was maintained throughout the experiments, which was sufficient to maintain the oxygen content in the excurrent air above 20%. The excurrent air from the chamber was sampled every three minutes for three readings, followed by a six minute sampling of a reference channel of dried outside air. Channel changes were controlled by a solenoid valve connected to a computer. Thus, one measurement for each bird was obtained every three to nine minutes (Coburn & Geiser, 1998; Geiser & Brigham, 2000; Geiser et al., 2003). Measurements of  $T_{\text{skin}}$  and  $T_a$  were taken simultaneously to those of MR. Digital data from the oxygen analyzer were transferred to a computer via a serial connection. Millivolt outputs from the flow meter and analogue output of the oxygen analyzer were transferred to a computer via a 14 bit A/D converter. Transmitter signals were received by a VHF/UHF scanning receiver (FRG-9600, Yaesu Musen Co. Ltd., Tokyo, Japan) and transferred to a computer. Data acquisition and processing were performed using software written by G. Körtner, B. Lovegrove and T. Ruf.

### ***Data Analysis***

The rate of oxygen consumption of birds was calculated using equation 3a of Withers (1977a). A RQ of 0.85 was assumed for all measurements, which would have resulted in a

maximum error of  $\pm 3\%$  if the RQ was actually 0.7 or 1.0 (Withers, 1977a). RMRs were calculated for each individual as the average of the six consecutive lowest  $\text{VO}_2$  values (i.e. over 21 minutes) in normothermic resting individuals at each  $T_a$ . Only data from the final 75 minutes of testing once the chamber had reached the designated  $T_a$  were considered in the analysis. BMRs were determined as the minimum RMR within the range of  $T_a$ s measured. The lower critical temperature ( $T_{lc}$ ) and upper critical temperature ( $T_{uc}$ ) defining the thermoneutral zone (TNZ) were determined by calculating a regression equation for the increasing RMR values for each individual below the TNZ and determining the intercept with the mean BMR for that individual. The  $T_{uc}$  is technically the point where evaporative water loss (EWL) increases (Pough et al., 2005), however, as EWL was not measured in my study the above method achieves the best possible estimation. Mass-specific thermal wet conductance was calculated using the equation  $\text{Conductance} = \text{MR}/(T_b - T_a)$  (Scholander et al., 1950b; Lasiewski et al., 1967; Schleucher & Withers, 2001).

RMR regression lines were compared using analysis of covariance (ANCOVA), with  $T_a$  as a covariate, and means were compared using Student's  $t$ -tests performed using Minitab Statistical Software (version 13.1). Numerical values are presented as means  $\pm$  SE for  $n$  individuals. An alpha value of 0.05 was employed for all tests.

## Results

The average BM of owlet-nightjars did not differ between summer ( $45.56 \pm 0.89$  g,  $n=7$ ) and winter ( $45.71 \pm 2.37$ ,  $n=6$ ;  $t$ -test:  $t_{11} = 0.06$ ,  $P=0.95$ ), nor between sexes (males:  $n=6$ ,  $45.21 \pm 1.77$  g; females:  $n=4$ ,  $47.25 \pm 2.68$ ;  $t_8=0.67$ ,  $P=0.52$ ). However, BM decreased significantly during the winter (June:  $50.58 \pm 1.66$ ,  $n=3$ ; August:  $40.84 \pm 1.25$ ,  $n=3$ ;  $t$ -test:  $t_4=4.68$ ,  $P<0.01$ ).

Below the TNZ, mass-specific RMR was negatively correlated with  $T_a$  during both summer and winter ( $F_{1,49}=200.31$ ,  $P<0.0001$ ). Winter RMRs were significantly lower than those measured in summer ( $F_{1,49}=26.03$ ,  $P<0.0001$ ; Figure 1). Below the  $T_{lc}$ , RMR increased with decreasing  $T_a$  at a rate of  $0.08 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1} \text{ }^\circ\text{C}^{-1}$  for birds in summer and  $0.06 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1} \text{ }^\circ\text{C}^{-1}$  for birds in winter (Figure 1).

The TNZ did not differ between summer ( $31.7$  to  $34.8^\circ\text{C}$ ) and winter ( $31.3$  to  $34.0^\circ\text{C}$ ;  $T_{lc}$   $t$ -test:  $t_8=0.34$ ,  $P=0.74$ ). The overall range of the TNZ was only slightly less in winter ( $0.7^\circ\text{C}$ ). Within the TNZ there was no difference in mass-specific BMR between summer ( $1.29 \pm 0.07$

ml O<sub>2</sub> g<sup>-1</sup> h<sup>-1</sup>, n=7) and winter (1.24 ± 0.08 ml O<sub>2</sub> g<sup>-1</sup> h<sup>-1</sup>, n=5;  $t_{10}= 0.41$ ,  $P=0.69$ ), or in whole animal BMR between seasons (summer: 63.10 ± 5.53 ml O<sub>2</sub> h<sup>-1</sup>; winter: 51.08 ± 1.87 ml O<sub>2</sub> h<sup>-1</sup>,  $t_{10}= 1.76$ ,  $P=0.11$ ). Likewise, birds measured in early winter (June: 1.15 ± 0.11 ml O<sub>2</sub> g<sup>-1</sup> h<sup>-1</sup>) exhibited no difference in BMR compared to those in late August (1.37 ± 0.03 ml O<sub>2</sub> g<sup>-1</sup> h<sup>-1</sup>;  $t_3=1.48$ ,  $P=0.24$ ). Mass-specific BMR did not differ between sexes (male: 1.21 ± 0.06 ml O<sub>2</sub> g<sup>-1</sup> h<sup>-1</sup>, n=6; female: 1.23 ± 0.09 ml O<sub>2</sub> g<sup>-1</sup> h<sup>-1</sup>, n=4;  $t_8=0.15$ ,  $P=0.88$ ). The mean BMR for owlet-nightjars was below the values predicted for birds (passerine + non-passerine) by recent scaling curves (Reynolds & Lee, 1996; Rezende et al., 2002; McKechnie et al., 2006), but were similar to published values for other species of Caprimulgiformes (Figure 2; Table 1).

No winter-caught owlet-nightjars exhibited any sign of moult and all had dense plumage. Four of the seven birds captured during summer were in active moult of most their body feathers (e.g. breast, flanks and back) and two of these birds were also moulting flight feathers (birds caught in early to mid-February). One bird caught in late December showed no moult activity and two birds caught in late February showed only slight moult of body feathers and were likely nearing the completion of the moult cycle. Although the four actively moulting birds did have slightly higher mass-specific BMRs in the TNZ (1.35 ± 0.21 ml O<sub>2</sub> g<sup>-1</sup> h<sup>-1</sup>), these did not differ significantly from birds not or only slightly moulting (1.30 ± 0.18 ml O<sub>2</sub> g<sup>-1</sup> h<sup>-1</sup>;  $t_5=0.32$ ,  $P=0.76$ ). Even at 0 °C the RMR of actively moulting birds (4.04 ± 0.22 ml O<sub>2</sub> g<sup>-1</sup> h<sup>-1</sup>) was not significantly higher than non-moulting birds in summer (3.51 ± 0.05 ml O<sub>2</sub> g<sup>-1</sup> h<sup>-1</sup>), although it did differ significantly from the RMR at T<sub>a</sub> 0 °C of winter birds (3.00 ± 0.16 ml O<sub>2</sub> g<sup>-1</sup> h<sup>-1</sup>; ANOVA:  $F_{2,11}=9.57$ ,  $P<0.01$ ). The RMR values for the pre-moulting December bird fell within the range of RMR values for the six other summer birds at all measurement T<sub>a</sub>.

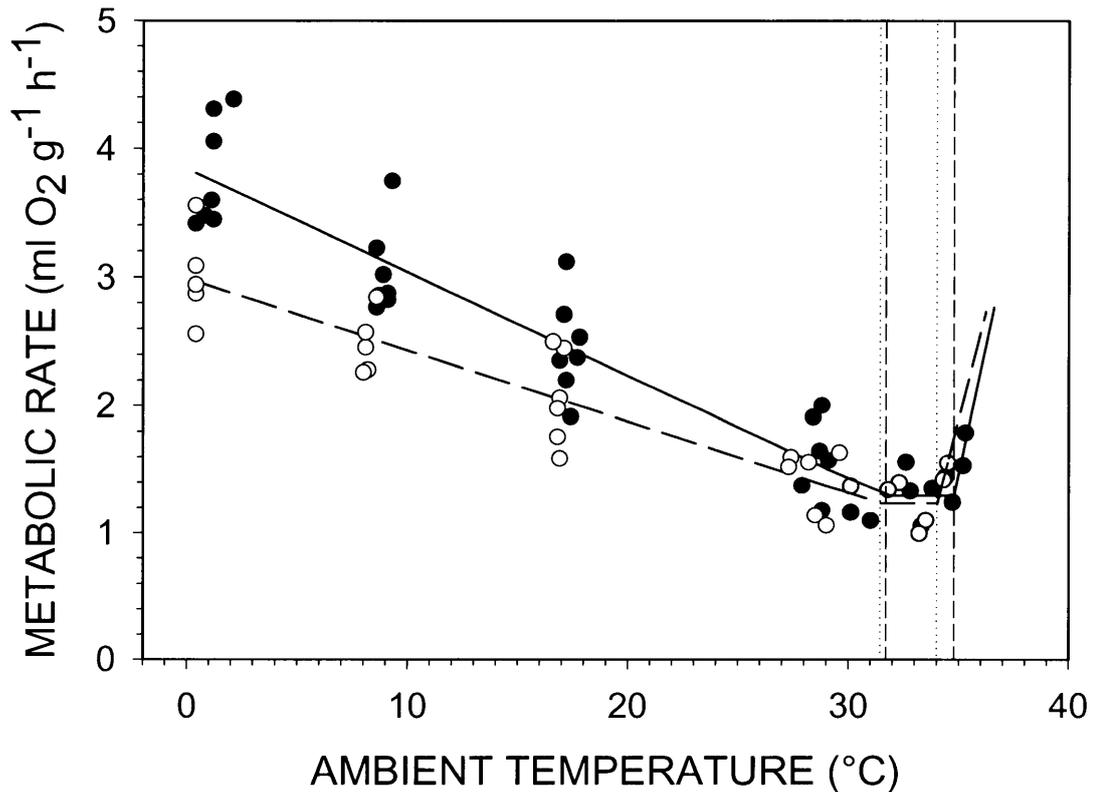
Core T<sub>b</sub> was not correlated with T<sub>a</sub> below the TNZ ( $F_{1,45}=5.19$ ,  $P=0.14$ ), but was significantly lower in winter than in summer ( $F_{1,45}=5.19$ ,  $P<0.05$ ; model R<sup>2</sup>=0.15; Figure 3a). Conversely, T<sub>skin</sub> was positively correlated with T<sub>a</sub> ( $F_{1,43}=35.25$ ,  $P<0.0001$ ), but did not differ between seasons ( $F_{1,43}=0.48$ ,  $P=0.49$ ; model R<sup>2</sup>=0.47; Figure 3b). Within the TNZ, summer T<sub>b</sub> (38.2 ± 0.3 °C) did not differ from winter T<sub>b</sub> (37.1 ± 0.5 °C;  $t_9=2.08$ ,  $P=0.07$ ). Likewise, there was no difference in T<sub>skin</sub> by season within the TNZ (summer: 37.6 ± 0.4 °C; winter: 37.7 ± 0.2 °C  $t_{10}=0.11$ ,  $P=0.91$ ). There was a significant positive relationship between T<sub>skin</sub> and T<sub>b</sub> (Linear Regression:  $F_{1,56}=14.20$ ,  $P<0.0005$ ; Figure 4). The mean difference between T<sub>skin</sub> and T<sub>b</sub> was 0.7 ± 0.2 °C. The difference between T<sub>b</sub> and T<sub>skin</sub> ranged from a minimum of 0.1 °C to a

maximum of 6.7 °C. Values of  $T_b$  ranged from 34.0 to 39.0 °C and  $T_{skin}$  values ranged from 32.0 to 38.8 °C.

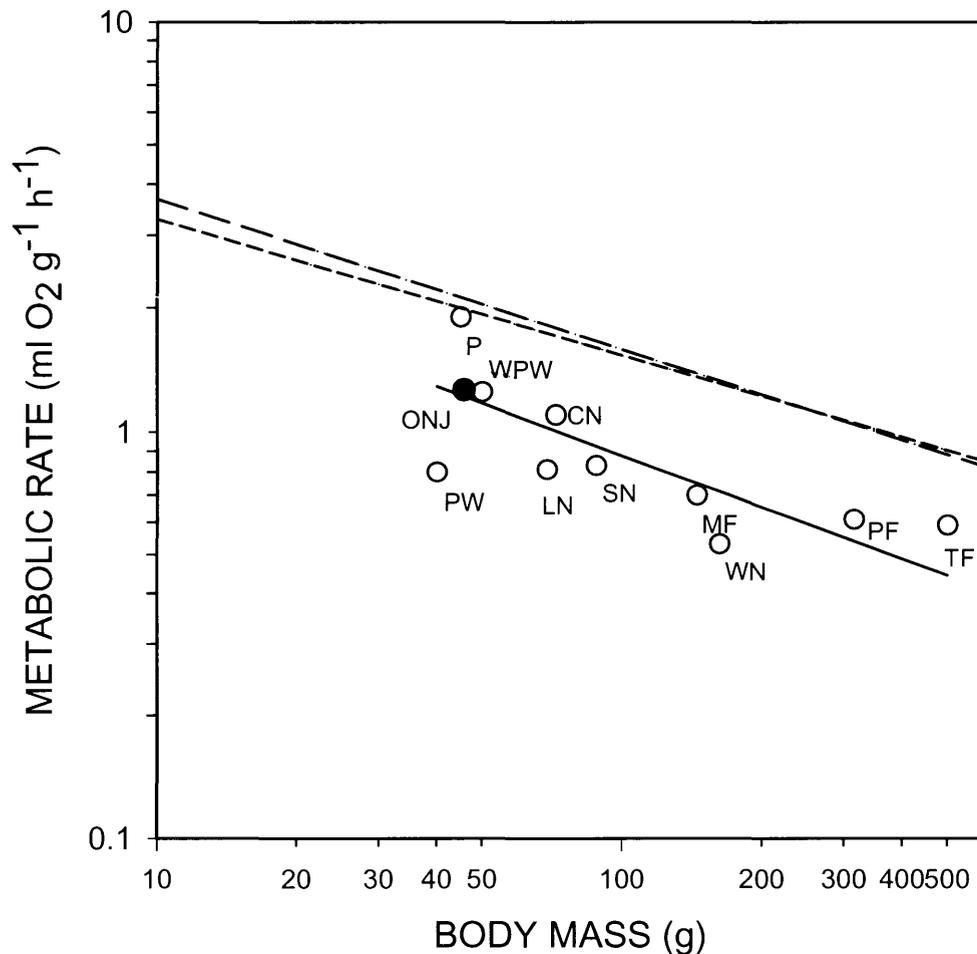
Thermal conductance ( $C$ ) below the TNZ was positively correlated with  $T_a$  in both summer and winter ( $F_{1,49}=112.09$ ,  $P<0.0001$ ) and was higher in summer than in winter ( $F_{1,49}=7.93$ ,  $P<0.01$ ; model  $R^2=0.72$ ; Figure 5). Mean minimum  $C$  values at  $T_a$  0 °C were significantly greater in summer ( $0.106 \pm 0.005$  ml O<sub>2</sub> g<sup>-1</sup> h<sup>-1</sup> °C<sup>-1</sup>) versus winter ( $0.085 \pm 0.004$  ml O<sub>2</sub> g<sup>-1</sup> h<sup>-1</sup> °C<sup>-1</sup>;  $t_{10}=3.12$ ,  $P<0.01$ ), but did not differ between seasons within the TNZ (summer:  $0.228 \pm 0.025$  ml O<sub>2</sub> g<sup>-1</sup> h<sup>-1</sup> °C<sup>-1</sup>; winter:  $0.282 \pm 0.039$  ml O<sub>2</sub> g<sup>-1</sup> h<sup>-1</sup> °C<sup>-1</sup>,  $t_9=1.21$ ,  $P=0.26$ ).

**Table 1:** Published body mass and basal metabolic rate (BMR) values for Caprimulgiformes as plotted in Figure 2.

Species	Abbrev.	Mass (g)	BMR (ml O <sub>2</sub> g <sup>-1</sup> h <sup>-1</sup> )	Reference
<b>Camprimulgidae</b>				
Common Poorwill ( <i>Phalaenoptilus nuttallii</i> )	PW	40	0.80	Bartholomew et al. 1962
Whip-poor-will ( <i>Caprimulgus vociferous</i> )	WPW	50	1.25	Lane et al. 2004
Common Nighthawk ( <i>Chordeiles minor</i> )	CN	80	1.10	Lasiewski & Dawson 1964
Spotted Nightjar ( <i>Eurostopodus argus</i> )	SN	90	0.83	Dawson & Fisher 1969
White-throated Nightjar ( <i>Eurostopodus mysticalis</i> )	WN	162	0.53	McNab & Bonaccorso 1995
Large-tailed Nightjar ( <i>Caprimulgus macrurus</i> )	LN	70	0.81	McNab & Bonaccorso 1995
Pauraque ( <i>Nyctidromus albicollis</i> )	P	45	1.9	Scholander et al. 1950
<b>Podargidae</b>				
Tawny Frogmouth ( <i>Podargus strigoides</i> )	TF	500	0.59	Bech & Nicol 1999
Marbled Frogmouth ( <i>Podargus ocellatus</i> )	MF	145	0.70	Lasiewski et al. 1970
Papuan Frogmouth ( <i>Podargus papuensis</i> )	PF	315	0.61	McNab & Bonaccorso 1995
<b>Aegotheidae</b>				
Australian Owlet-Nightjar ( <i>Aegotheles cristatus</i> )	ONJ	45	1.27	This study



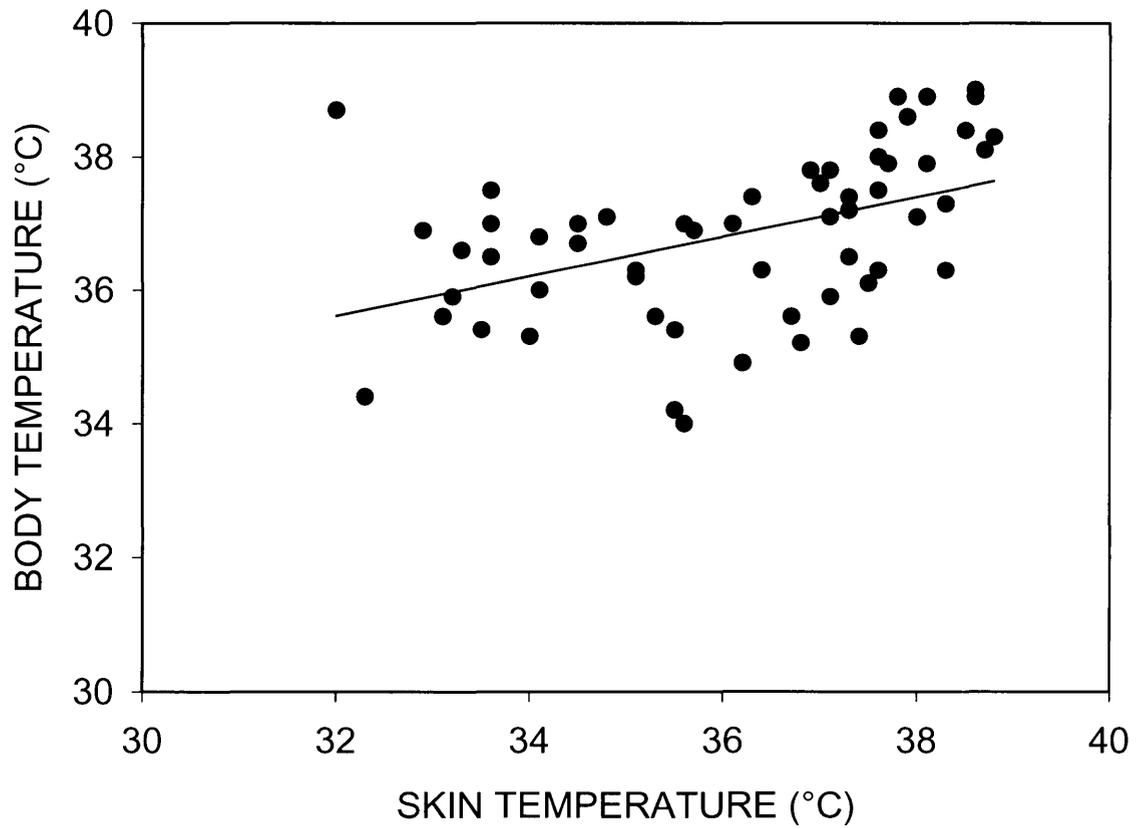
**Figure 1:** Mass-specific metabolic rate of resting owlet-nightjars over a range of ambient temperatures ( $T_a$ ) during summer (● solid line;  $n=7$ ) and winter (○ dashed line;  $n=6$ ). Each point represents a measurement for one individual. The vertical lines represent the upper ( $T_{lc}$ ) and lower ( $T_{uc}$ ) critical temperatures of the thermoneutral zone (TNZ) for summer (dashed line) and winter (dotted line). Below the TNZ, RMR increased with  $T_a$  and differed significantly with season (ANCOVA:  $T_a$ :  $F_{1,49}=200.31$ ,  $P<0.0001$ ; season:  $F_{1,49}=26.03$ ,  $P<0.0001$ ;  $T_a$ \*season:  $F_{1,49}=6.78$ ,  $P<0.05$ ; model  $R^2=0.84$ ); Linear regression for summer:  $RMR=3.84 - 0.08 (T_a)$ ,  $F_{1,27}=134.62$ ,  $P<0.0001$ ; winter:  $RMR=2.99 - 0.06 (T_a)$ ,  $F_{1,21}=84.49$ ,  $P<0.0001$ . Within the TNZ ( $31.7-34.8$  °C summer;  $31.3-34.0$  °C winter) the BMR was  $1.29 \pm 0.19$  ml  $O_2$   $g^{-1}$   $h^{-1}$  in summer-acclimatized birds and  $1.24 \pm 0.18$  ml  $O_2$   $g^{-1}$   $h^{-1}$  in winter-acclimatized birds.



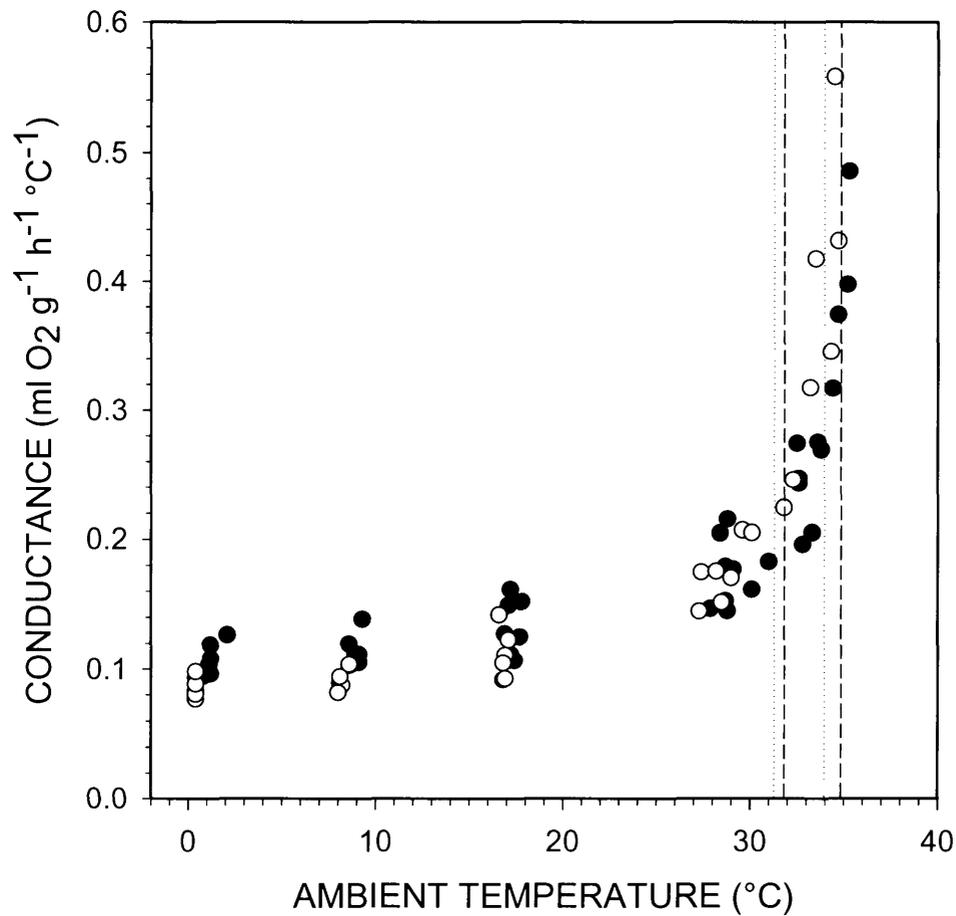
**Figure 2:** Basal metabolic rate (BMR) of nightjars ( $\circ$ ) (Caprimulgiformes) as a function of  $\log_{10}$  body mass (BM). The solid black line represents the resulting significant regression ( $\text{BMR} = 6.13 \text{ BM}^{-0.422}$ ;  $F_{1,9}=6.95$ ,  $P<0.05$ ,  $R^2=0.46$ ,  $n=10$ , excludes value obtained for owlet-nightjars). The published BMR values and corresponding BM values of the Caprimulgiformes plotted, and the full species names for the abbreviated data labels, are given in Table 1. The mean of both summer and winter BMR values obtained for Australian owlet-nightjars ( $\bullet$ ) in the current study ( $1.27 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$ ) was only 3% higher than that predicted by the nightjar regression line ( $1.23 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$ ). The BMR values for nightjars, with the possible exception of the pauraque (*Nyctidromus albicollis*), are below those predicted by recent equations for scaling of avian metabolism by Reynolds and Lee (1996; short dashed line;  $\text{BMR} = 7.01 \text{ BM}^{-0.330}$ ), Rezende et al. (2002; long dashed line;  $\text{BMR} = 8.51 \text{ BM}^{-0.365}$ ), and McKechnie et al.'s (2006) recent equation for wild-caught birds (solid grey line;  $\text{BMR} = 3.83 \text{ BM}^{-0.256}$ ).



**Figure 3:** Body temperature ( $T_b$ ; A) and skin temperature ( $T_{skin}$ ; B) of owlet-nightjars during summer (● solid line;  $n=7$ ) and winter (○ dashed line;  $n=6$ ).  $T_b$  was measured using a pre-calibrated fine thermocouple inserted 1.5 to 2 cm into the cloaca. A temperature-sensitive radio-transmitter was attached to the interscapular region of each owlet-nightjar using an elastic harness to measure  $T_{skin}$ . Each point represents the value for a single individual. Vertical lines represent the upper ( $T_{lc}$ ) and lower ( $T_{uc}$ ) critical temperatures of the thermoneutral zone (TNZ) for summer (dashed line) and winter (dotted line). A) Below the TNZ,  $T_b$  did not vary significantly with ambient temperature ( $T_a$ ), but  $T_b$  was significantly higher in summer than in winter (ANCOVA:  $T_a$ :  $F_{1,45}=2.27$ ,  $P=0.14$ ; season:  $F_{1,45}=5.19$ ,  $P<0.05$ ; model  $R^2=0.15$ ; Linear regressions for summer:  $T_b=36.39 + 0.02 (T_a)$ ,  $F_{1,27}=0.78$ ,  $P=0.38$ ; winter:  $T_b=35.50 + 0.03 (T_a)$ ,  $F_{1,17}=1.57$ ,  $P=0.23$ ; B) Below the TNZ,  $T_{skin}$  decreased with decreasing  $T_a$  (ANCOVA:  $F_{1,43}=35.25$ ,  $P<0.0001$ ), but did not differ between seasons ( $F_{1,45}=0.48$ ,  $P=0.49$ ; model  $R^2=0.47$ ). Linear regression:  $T_{skin}=33.67 + 0.11 (T_a)$ ,  $F_{1,43}=35.97$ ,  $P<0.0001$ ,  $R^2=0.68$ .



**Figure 4:** Plot of simultaneously collected  $T_{\text{skin}}$  and  $T_{\text{b}}$  values measured using an external temperature-sensitive radio transmitter and a thermocouple placed 1.5 cm into the cloaca during laboratory experiments at  $T_{\text{a}}$  0 °C to 36 °C. Linear Regression:  $T_{\text{b}} = 26.08 + 0.30(T_{\text{skin}})$ , ( $F_{1,56}=14.20$ ,  $P<0.0005$ ,  $R^2=0.45$ ,  $n=13$  birds at steady state,  $N=56$ ).



**Figure 5:** Thermal conductance ( $\text{ml O}_2 \text{ g}^{-1} \text{ h}^{-1} \text{ }^\circ\text{C}^{-1}$ ) of owlet-nightjars as a function of ambient temperature ( $T_a$ ) during summer ( $\bullet$  solid line;  $n=7$ ) and winter ( $\circ$  dashed line;  $n=6$ ). The vertical lines represent the upper ( $T_{ic}$ ) and lower ( $T_{uc}$ ) critical temperatures of the thermoneutral zone (TNZ) for summer (dashed line) and winter (dotted line). Below the TNZ, conductance values increased with ambient temperature ( $T_a$ ) and differed significantly with season (ANCOVA:  $T_a$ :  $F_{1,49}=112.09$ ,  $P<0.0001$ ; season:  $F_{1,49}=7.93$ ,  $P<0.01$ ; model  $R^2=0.72$ ).

## **Discussion**

No seasonal adjustments in mean BM or BMR by owlet-nightjars were apparent in my study, despite the cold  $T_a$ s experienced at the high altitude of Armidale during winter. Below the TNZ, however, RMR and C values were higher in summer-acclimatized than winter-acclimatized birds. The difference in RMR and C between winter and summer birds became greater with decreasing  $T_a$ . Irrespective of the annual cycle, RMR increased with decreasing  $T_a$ , as the regulation of a high  $T_b$  became energetically more expensive with an increasing difference between  $T_b$  and  $T_a$ , thus, increasing heat loss (Calder & King, 1974). Although birds had higher BM at the beginning of winter, presumably due to an increase in fat deposits, these were spent by mid-winter, and there was no difference between early and late winter BMR. Thus, the lower RMR and C during winter is most likely attributable to better insulating plumage, which would reduce C and enable birds to maintain  $T_b$  at low  $T_a$  with lower energetic costs. While  $T_b$  was higher in summer relative to winter birds; there was considerable variation.

### ***Seasonal Variation of BMR***

Species and populations that experience a greater seasonal range of  $T_a$ s, such as those at high latitudes, high altitudes and non-migratory species, are predicted to show greater seasonal thermal acclimatization in the form of increased insulation and changes to MRs (Calder & King, 1974; Weathers, 1979). Large changes in seasonal  $T_a$  are generally compensated for by increases in tissue (fat deposits) and the amount of plumage or fur insulation in birds and mammals (Calder & Booser, 1973). Animals with adequate insulation should be able to maintain a constant  $T_b$  without increasing their BMR over a wider range of  $T_a$  (Scholander et al., 1950a). However, species differ in their capacity to increase fat stores and insulation during winter, an effect which appears to be correlated with the climate the species inhabits (Dawson & Marsh, 1989; Swanson, 1991; Liknes et al., 2002). There are also small-body-size constraints associated with carrying extra mass (Scholander et al., 1950a), and constraints imposed by requirements for flight. Physiological adjustments to BMR may be required to cope with low  $T_a$ s for some species. Yet there is still considerable controversy about whether the BMR of birds should be higher in winter to maintain  $T_b$  at low  $T_a$ s (Weathers & Caccamise, 1978), or lower to reduce energy expenditure for thermoregulation (King, 1974).

Weathers & Caccamise (1978) suggested that the BMR of small birds (< 100 g) may be 50% higher in winter than in summer to maintain  $T_b$  at low  $T_a$ s. Studies conducted in North America generally support this theory, BMR is usually (e.g. Dawson & Carey, 1976), higher

in winter-acclimatized passerines (see also Dawson & O'Connor, 1996). The BMRs of American goldfinches (*Carduelis tristis*; 13 g; Liknes et al., 2002), black-capped chickadees (*Parus atricapillus*; 13 g; Cooper & Swanson, 1994), mountain chickadees (*Poecile gambeli*; 11 g; Cooper, 2002), juniper titmice (*Baeolophus griseus*; 17 g; Cooper, 2002), common redpoll (*Acanthis flammea*; 12-15 g; Pohl & West, 1973), and dark-eyed juncos (*Junco hyemalis*; 18 g; Swanson, 1991) was higher in winter than in summer. Similarly, Broggi et al. (2004) found that BMRs of great tits (*Parus major*) were higher in a more northerly population in Finland than in a southern population in Sweden (also see Broggi et al., 2007). Liknes et al. (2002) suggested that the increased size of the large pectoralis muscle and increased fat stores in Nearctic birds during winter provides them with a larger energy reservoir to draw upon during cold exposure, which could in turn accommodate a higher winter BMR. However, Lovegrove et al. (1991) proposed that a reduction in body mass in winter that did not sacrifice an animal's ability to maintain thermal balance should be advantageous as would decrease the absolute energy requirements of the animal. Data on seasonal differences in body mass of the North American species studied were inconsistent. Winter acclimatized American goldfinches and dark-eyed juncos were heavier than summer birds, however, mountain chickadees declined in mass during winter, and there were no seasonal differences in BM for black-capped chickadees and juniper titmice (Swanson, 1991; Cooper & Swanson, 1994; Cooper, 2002; Liknes et al., 2002). Some of this variation may be explained by the stage of winter (i.e. early or late) when measurements were made, the extremes of winter conditions, and the degree to which the winter fat deposits may have been used.

The limited numbers of studies on seasonal variation of BMR in small Australian birds have produced conflicting results, suggesting that different species are using different strategies for seasonal physiology. Winter-acclimatized Australian silver-eyes (*Zosterops lateralis*; 11 g) caught at the same location as my study, had mass-specific BMRs 20% lower than that of summer-acclimatized birds (Maddocks & Geiser, 2000). However, superb fairy-wrens (*Malurus cyaneus*; 9 g) near Melbourne exhibited no difference in seasonal BMR (Lill et al., 2006). There was no seasonal difference in BM of silvereyes, but the BM of fairy-wrens was significantly, albeit slightly, higher in winter. Conversely, Collins and Briffa (1983) found that the metabolic costs of a perching Australian nectivore (*Lichmera indistincta*; 7 to 12 g) in Western Australia were higher in winter than in summer. Ambrose and Bradshaw (1988) likewise found that white-browed scrubwrens (*Sericornis frontalis*; 11-15 g) living in arid regions increased BMR during winter.

The accumulated data suggests that variation in the severity of winter temperatures results in birds employing distinct physiological strategies in different climates. While increased insulation may provide adequate protection from cold exposure in the moderate winter climates of Australia (minimum  $T_a$  0 to 13 °C, Maddocks and Geiser, 2000; monthly winter mean minimum  $T_a$  = -1.5 to 4 °C for my study), this may not be sufficient in the colder temperate climates of North America (winter mean = -8.2 °C; Liknes et al., 2002). Thus, birds found in temperate regions may need to increase energy reserves and BMR during winter to survive colder conditions. Moreover, different populations of a species distributed over a wide geographic range differ in the extent of their seasonal variation in BMR. For example, house finches (*Carpodacus mexicanus*) in California that experience mild winters exhibit little seasonal BMR variation, whereas those in Colorado, where winters are more severe birds increase fat deposits as well as BMR (Dawson et al., 1983; Dawson & Marsh, 1989). Similarly, Broggi et al. (2007) found that the harshness of winter conditions in a given year at least partially influenced BMR of great tits in Finland. Even so, birds wintering in relatively mild winter climates can substantial increase BM and BMR. Fat stores of the dark-eyed junco in Oregon, USA increased by 9% in winter, plumage mass increased by 32%, and BMR increased by 9%, despite mild winter conditions (Swanson, 1991).

Theoretically, the increased body mass due to added tissue and plumage during winter should actually result in lower mass-specific BMRs based on the scaling of bird metabolic rate to BM (Reynolds & Lee, 1996; Rezende et al., 2002; McKechnie et al., 2006). A reduction in BMR should also reduce the overall energy expenditure (King, 1974; Cooper & Geiser, 2008). In moderate climates, the energy expended on breeding and raising offspring may exceed the thermal costs of colder winter  $T_a$ s. Bryant (1997) compared BMR of 58 species of birds year-round and found that BMRs were lower and equal for birds moulting or wintering (i.e. not laying, incubating or rearing young) and increased during the breeding season. (Note, however, that BMR is generally measured in non-reproductive individuals). This supports the 'increased demand hypothesis', suggesting that breeding results in a substantial increase in adult energy demand resulting in a higher BMR during the breeding season (Masman et al., 1986). My summer measurements for owl-nightjars were obtained after the breeding season, and, thus, were unaffected by the increased costs of raising young. Hence, perhaps it is not surprising that BMR values were similar for summer and winter. Most of the summer birds were moulting; however, for birds that sequentially moult feathers this may not have had a

significant effect on BMR (see discussion on moulting below; Brown & Bryant, 1996; Bryant, 1997; Buttemer et al., 2003).

The lack of seasonal variation in BM and BMR that I found for owlet-nightjars could also be the result of the larger BM of owlet-nightjars (45 g) relative to most other species studied, or due to their nocturnal habits. While food availability decreases in winter for almost all non-predatory birds, diurnal species are further disadvantaged by shorter day length which limits the time available for foraging and imposes long periods of nocturnal fasting (Dawson & Hudson, 1970). In contrast, nocturnal birds have the advantage of longer periods of darkness for foraging to maintain energy stores. Winter energy expenditure of nocturnal species may be further reduced by selecting roosts exposed to solar radiation during the diurnal rest phase (see discussion below). To my knowledge, mine is the first study to compare seasonal energetics for a nocturnal insectivore. Clearly, more research is required to determine if nocturnal, non-predatory species are less affected by reduced winter food resources than diurnal species.

### ***The Thermoneutral Zone and Critical Thermal Levels***

Cold-acclimatized animals may be able to maintain a higher MR at low  $T_{as}$  (Geiser et al., 2003), and the increased cold tolerance is manifested in a shift of the TNZ towards lower  $T_{as}$ . However, the TNZ was similar for winter-acclimatized and summer-acclimatized owlet-nightjars, thus the change in insulation of winter-acclimatized birds is not reflected in a shift in the TNZ to a lower value. A winter  $T_{lc}$  of 31.3 °C seems high for a 45 g bird. Perhaps roosting in well-insulated cavities with moderate thermal microclimates has relaxed the selection for cold tolerance of this species. The  $T_{uc}$  of 34.8 °C for summer birds is also relatively low, although the  $T_{uc}$  of silvereyes at the same site was only 33.6 °C (Maddocks & Geiser, 2000). The highest  $T_a$  ever recorded in Armidale was 36.5 °C and the mean daily maximum  $T_a$  in the hottest month, January, is only 27.1 °C (1857- 1997, Australian Bureau of Meteorology). Thus, owlet-nightjars in this region would rarely need to increase RMR in response to high  $T_{as}$ .

A low BMR should minimize the production of endogenous heat, reducing the problem of having to lose heat at high  $T_a$  (Bartholomew, 1982b), and thus increase the  $T_{uc}$ . Caprimulgids are known to tolerate high  $T_a$  (>35 °C) without large increases in RMR because they can cool by evaporating water using gular fluttering. This is the process of fluttering the highly vascularized gular area, including the floor of the mouth and the anterior part of the

esophagus, by rapid muscle contraction or by movement of the hyoid apparatus (Bartholomew, 1982a). Gular fluttering has the advantage of consuming little energy, and thus little heat production, and does not result in alkalosis as panting can. Panting also requires more energy than gular fluttering (Bartholomew, 1982a). Owls (Strigidae) also use gular fluttering to lower  $T_b$  and in some species gular fluttering may commence at  $T_{as}$  as low as 32.5 °C (Ganey et al., 1993). However, frogmouths (Podargidae) do not use gular fluttering, but pant at very high  $T_{as}$ . Above  $T_{as}$  of 40 °C Papuan frogmouths (*Podargus papuensis*) pant to enhance evaporative cooling (Lasiewski et al., 1970). At  $T_{as}$  of 46.8 °C Papuan frogmouths lost heat solely by panting at rates that previously had only been seen in birds using gular fluttering (EWL/HP = 1.8; Lasiewski et al., 1970). I found no evidence that owlet-nightjars use gular fluttering, but they may pant at high  $T_{as}$ . The  $T_{as}$  during the current laboratory study did not exceed 36 °C and did not induce panting in any adult owlet-nightjars. However, two nine-day-old thermoregulating chicks exposed to a range of  $T_{as}$  began panting at  $T_a > 38$  °C (L. Doucette, unpublished data).

### ***Body and Skin Temperature***

$T_b$  was higher in summer-acclimatized compared to winter-acclimatized owlet-nightjars. Other small birds which employ regulated hypothermia or torpor at low  $T_{as}$  have been found to have lower  $T_b$  during winter than in summer (Chaplin, 1974). However, the reverse was found for the small mammal (*Sminthopsis macroura*), which was able to maintain a higher MR and consequently a higher  $T_b$  at low  $T_a$  after several weeks of acclimation to cold in the laboratory (Geiser et al., 2003). Maddocks & Geiser (2000) and Buttemer et al. (2003) found little variation in  $T_b$  with  $T_a$  in two species of Australian birds that differed extensively in body mass (17 g to 350 g).

The variation in individual  $T_{bs}$  in the current study was substantial, ranging from 34 to 38 °C at  $T_{as}$  below the TNZ (Figure 3a). Individual common nighthawks (*Chordeiles minor*) also maintain  $T_b$  within a range of several degrees (34 to 40 °C) during rest (Lasiewski & Dawson, 1964), as do many species of passerines (Reinertsen, 1983; Bartholomew et al., 1983; Clark & Dukas, 2000; Schleucher, 2001; McKechnie & Lovegrove, 2003; Dolby et al., 2004). The slightly higher  $T_{bs}$  observed at  $T_a$  0 °C in my study may be due to the relatively short exposure time at low  $T_a$  (150 to 180 minutes) when this measurement was taken. Birds may have initially maintained a higher  $T_b$  at the lowest  $T_{as}$  with increases in MR, than slightly relaxed both MR and  $T_b$  as  $T_a$  increased. Lovegrove et al. (1991) found a similar increase in  $T_b$  at a  $T_a$  of 0 °C for small rodents (*Thallomys paedulus* and *Aethomys namaquensis*).

As has been found previously for owlet-nightjars (Brigham et al., 2000), there was a highly significant correlation between  $T_{\text{skin}}$  and  $T_b$  (Figure 4), confirming that  $T_{\text{skin}}$  is a reliable indicator of core  $T_b$ . On average,  $T_{\text{skin}}$  underestimated  $T_b$  by  $0.7 \pm 0.2$  °C across all  $T_{\text{as}}$  measured (Figures 4). However,  $T_{\text{skin}}$  is a better predictor of  $T_b$  at higher  $T_{\text{as}}$  (>10 °C) than at low  $T_{\text{as}}$  (<10 °C; Figure 4; also see Willis & Brigham, 2003). Using internal and external temperature-sensitive transmitters on the same bird concurrently, Brigham et al. (2000) found that  $T_{\text{skin}}$  underestimated  $T_b$  by  $3.0 \pm 0.8$  °C ( $R^2=0.85$ ,  $N=11014$ ) for an owlet-nightjar held in an outdoor aviary during winter in Armidale. Likewise, comparisons of  $T_{\text{skin}}$  and  $T_b$  with the concurrent placement of thermocouples against the skin and inserted in the cloaca of nestling oilbirds (*Steatornis caripensis*; Thomas et al., 1993) and herring gulls (*Larus argentatus*; Lustick et al., 1979) indicated that  $T_{\text{skin}}$  underestimated  $T_b$  by <3 °C. Lustick et al. (1979) also noted that  $T_{\text{skin}}$  was a better predictor of  $T_b$  at higher body temperatures, increasing from a difference of 1.0% at  $T_{\text{skin}}$  35 °C to 17.8% at  $T_{\text{skin}}$  15 °C. In contrast to  $T_b$ ,  $T_{\text{skin}}$  was correlated to  $T_a$  but showed no seasonal differences (Figure 3b).  $T_{\text{skin}}$  can be expected to vary slightly more with  $T_a$  than  $T_b$ . Rautenberg (1986) reported a substantial decrease in  $T_{\text{skin}}$  from 40 °C to 32° C at  $T_a$  of -20 °C in pigeons (Columbidae).

$T_a$  likely influenced  $T_{\text{skin}}$  more in this study than typically seen in field studies of birds with external temperature-sensitive transmitters (Chapter 2), as the transmitters were freshly attached. In field studies,  $T_{\text{skin}}$  readings are less accurate in the first 24 h after the bird is released as it takes time for the transmitter to work its way through the bird's plumage and achieve good contact with the skin. For example, five of 13 birds released with external backpack style transmitters attached showed significantly lower active  $T_{\text{skin}}$  on the first day of release ( $36.4 \pm 0.5$  °C) compared to five days after release ( $38.4 \pm 0.3$  °C;  $t$ -test:  $t_4=115.87$ ,  $P<0.0001$ ). One to two days after a bird was released in the field backpack-mounted transmitters were no longer visible and feathers lay flat on the bird's back. Although the feathers were pushed aside during transmitter attachment in the current study, the contact achieved and degree of plumage coverage was poorer than seen in the field, with feathers remaining ruffled and the transmitters visible. Removal of feathers under and around the transmitter in this study would have compromised the birds' insulation, and thus the metabolic results. Ideally, external transmitters should be attached several days before readings commence.

### ***Conductance***

Mean minimum C values for owlet-nightjars were significantly lower in winter compared to summer birds. This is presumably due to an increase in winter plumage. The mean minimum C values for owlet-nightjars at 0 °C during summer (0.106 ml O<sub>2</sub> g<sup>-1</sup> h<sup>-1</sup>°C<sup>-1</sup>) and winter (0.085 ml O<sub>2</sub> g<sup>-1</sup> h<sup>-1</sup>°C<sup>-1</sup>) were 26% and 41% lower, respectively, than the minimum C values predicted for a 45 g bird at rest (0.143 ml O<sub>2</sub> g<sup>-1</sup> h<sup>-1</sup>°C<sup>-1</sup>;  $\log_{10}C = -0.0028 - 0.5094 \log_{10}BM$ ) (Schleucher & Withers, 2001; Figure 5). This indicates that owlet-nightjars gained extensive thermal benefits from their insulative plumage, which at least in part explains why seasonal adjustments to BMR were apparently not required. For allometric reasons, an increase in feather insulation tends to incur a greater increase in cold resistance for larger birds than for smaller birds (Dawson & O'Connor, 1996), thus owlet-nightjars appear to fall in the category of large birds in this respect.

Behavioural thermoregulation through the selection of thermally buffered cavity roosts should assist owlet-nightjars in dealing with low winter T<sub>a</sub> (Walsberg, 1986; Lovegrove et al., 1991; Chapter 2). Mammals that shelter in hollows or burrows during cold and/or wet weather tend to have sparser coats and greater C than those species that live in exposed tree tops (Cooper et al., 2006). For example, koalas have long, dense pelts and low C while numbats have sparse, thin pelts and high C (Cooper et al., 2006). Thus, it is surprising that owlet-nightjars have such dense plumage while tawny frogmouths (*Podargus strigoides*), large Australian birds that roost exposed to the elements, had C values very close to the allometrically predicted value for birds of their size (Bech & Nicol, 1999), and thus proportionally higher than owlet-nightjars. The low conductance of owlet-nightjar plumage may reflect the insulation requirements of this much smaller species during nocturnal activity while T<sub>a,s</sub> are at their lowest, precluding the advantages of using cavity roosts. Thermal conductance is 35% to 60% higher for mammals relative to birds (Aschoff, 1981; Schleucher & Withers, 2001), illustrating the excellent thermal insulating properties of feathers.

### ***Energetic Costs of Moulting***

Feather moult has two possible influences on avian metabolic rate. First, feather loss is expected to decrease thermal insulation and increase evaporative heat transfer resulting in greater conductance at temperatures below the TNZ (Murphy, 1996). Second, the production of new feathers increases energetic demands and should be exhibited as an increase in BMR within the TNZ (Robin et al., 1988; Buttemer et al., 2003). In my study, the BMR of moulting

and non-moulting summer birds did not differ. Thus, it appears that the energy cost of the synthesis of new feathers is not great enough to detect in a large bird. However, decreased insulation during moult may explain the 20% higher C and increased RMR below the TNZ in summer versus winter birds.

A review of BMR during moult compared to pre- and post-moult periods in seven species of birds showed variation among species (King, 1974). The increase in BMR during moult ranged from 0% to 45% and was greatest for domestic fowl derived from tropical populations. More recently, a comparison of the cost of feather production for seven species of birds (13 g to 2900 g) found a negative correlation with body mass and a positive correlation with BMR (Lindstrom et al., 1993). The cost of mass-specific feather production was directly proportional to mass-specific BMR. Thus, large species and those with low BMRs should have a lower mass-specific cost of feather production. At one extreme, Lindstrom et al. (1993) found that two species of small passerines in Lapland increased their BMR by 106% (*Lusinia s. sveica*, 17 g, 39.7 kJ d<sup>-1</sup> to 83.8 kJ d<sup>-1</sup>) and 111% (*Carduelis f. flammea*, 13 g, 26.8 kJ d<sup>-1</sup> to 55.3 kJ d<sup>-1</sup>) during the peak moult period. However, the larger 270 g long-eared owl (*Asio otus*; Wijnandts, 1984) and the 570 g Mexican spotted owl (*Strix occidentalis lucida*; Ganey et al., 1993) exhibited a more moderate 30% and 18% increase in BMR during moult, respectively. No difference was found in the mass-specific BMR of kookaburras (*Dacelo novaeguineae*; 340 g) or the much smaller 65 g dippers (*Cinclus cinclus*) during moult compared to non-moult (Brown & Bryant, 1996; Buttemer et al., 2003). The BMR of kookaburras is very low (0.64 ml O<sub>2</sub> g<sup>-1</sup> h<sup>-1</sup>; Buttemer et al., 2003), which combined with its large size, may explain the lack of increase in BMR during moult. Likewise, a combination of large size and low BMR of owlet-nightjars may explain the low energetic costs of moult in this species.

### ***Low BMR of Caprimulgiformes***

Nocturnal birds, including frogmouths (Podargidae), nightjars (Caprimulgidae), kiwis (Apterygidae), and owls (Strigidae) have significantly lower relative BMRs than diurnal birds (Bennett & Harvey, 1987; Hohtola et al., 1994). The tendency for nocturnal birds to have lower BMRs extends to nocturnal species within taxonomic groups which contain mostly diurnal members. For example, nocturnal Eurasian woodcocks (*Scolopax rusticola*, Charadriiformes, 317 g) had low BMRs (0.68 ml O<sub>2</sub> g<sup>-1</sup> h<sup>-1</sup>), which were 40% below those predicted for shorebirds during winter in the temperate zone (Duriez et al., 2004) and 35% lower than the BMR predicted for 317 g birds by Rezende et al. (2002). Duriez et al. (2004)

suggested that this was due to a combination of nocturnal life and living in a sheltered habitat (forests) compared to other shorebirds. Bennett and Harvey (1987) suggested that low relative BMR in nocturnal birds is an adaptive response to the higher  $T_a$ s encountered during the day when the birds are resting. Nocturnal birds may choose a site with a favorable microclimate and sun exposure during the rest phase and hence reduce thermoregulatory costs by basking to raise or maintain  $T_a$ , as seen for some species of small mammals (Geiser & Drury, 2003; Warnecke et al., 2008). Diurnal birds do not have this opportunity to maintain  $T_b$  through solar heating while at rest during the night. This hypothesis is supported by data for tropical diurnal species that forage in the sun and have BMRs averaging 25% lower than expected (Weathers, 1979). Heat generated by nocturnal birds during night activity may also substitute for thermoregulatory expenditure at night (Webster & Weathers, 1990; also see Cooper & Sonsthagen, 2007).

The mean BMR of owlet-nightjars in my study ( $1.27 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$ ) was 37% and 41% lower than predicted for birds by Reynolds and Lee (1996) and Rezende et al. (2002) respectively. However, owlet-nightjar BMR was only 12% lower than predicted ( $1.45 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$ ) based on the equation of McKechnie et al. (2006) on data from wild-caught birds only. This equation has a shallower slope that takes into account migratory tendency, habitat aridity, phylogenetic relatedness, and whether birds were captive-raised or wild caught (McKechnie et al., 2006). While this equation indicates that Caprimulgiformes have BMRs much closer to those found for other birds, all species except for the pauraque (*Nyctidromus albicollis*) still have BMRs below that predicted for other birds. The disparity in BMR between Caprimulgiformes and other avian taxa is greater for species with higher BMs based on the McKechnie et al. (2006) equation (Figure 2).

My data represent the first BMR measurement reported for Aegothelidae. The value falls within 3% of the allometric curve for Caprimulgiformes (Figure 2). Owlet-nightjar BMR is almost identical to that found for whip-poor-wills (*Caprimulgus vociferous*; 50 g), a migratory North American species. The BMR for whip-poor-wills was measured for birds caught in South Dakota during summer when  $T_a$  ranged from 5 to 25 °C (Lane et al., 2004). Given that this species migrates to the southern USA during winter, it likely experiences similar  $T_a$  year round. Conditions experienced by owlet-nightjars in my study are more similar to those experienced by whip-poor-wills, compared to the similarly size tropical pauraque (45 g) studied near the equator in Panama (Scholander et al., 1950a), which had a higher BMR than all other nightjars measured. Generally, the BMRs of tropical birds and birds from arid

regions are lower compared to species from higher latitudes, but there is species-specific variations (Weathers, 1979; Bennett & Harvey, 1987; Dawson & O'Connor, 1996). The BMR of common poorwills (*Phalaenoptilus nuttallii*; 40 g) is much lower than that of owl-nightjars or whip-poor-wills, and is 64% lower than the predicted allometric value for birds of its size (Bartholomew et al., 1957; 1962; Withers, 1977b; Brigham, 1992; Csada & Brigham, 1994; Rezende et al., 2002; Woods & Brigham, 2004). The low BMR of poorwills may explain the long torpor bouts used by this species (McNab, 1983), however, Cooper & Geiser (2008) found no correlation between low BMR and torpor use by birds. The paucity of data on heterothermy and torpor use in birds makes this issue difficult to resolve and the area requires further investigation.

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## CHAPTER 6

### A Comparison of Diet and Foraging Tactics of Australian Owlet-Nightjars in Desert and Woodland Habitats

#### Abstract

Seasonal shifts in the foraging behaviours of birds in response to changes in prey abundance are well known, but few studies have examined geographic differences in diet and foraging ecology for a species occurring in diverse habitat types. I compared the diet and inferred foraging tactics of the Australian owlet-nightjar (*Aegotheles cristatus*), a sedentary nocturnal insectivore, in a cool temperate eucalypt woodland and two desert habitats, one with and one without irrigation. Faecal samples were collected and analyzed from birds and cavity roosts at three locations. Light and pitfall traps were used to sample prey availability and composition. The ratio of trapped aerial-to-terrestrial arthropod biomass was comparable at all sites. Wholly terrestrial arthropods comprised 44-52% and 51% of the diet in the desert and woodland habitats, respectively. Lepidoptera were most abundant by biomass at both locations; however, none were found in the diet of woodland birds, compared to 18-30% at desert sites. Coleoptera dominated the woodland diet in both summer (43%) and winter (48%), yet represented less than 13% of the winter arthropod biomass. Since low nocturnal ambient temperatures likely restricted flight of Coleoptera in winter, I suggest that owlet-nightjars primarily obtained them by foraging on the ground. Thus, the diet of woodland owlet-nightjars in winter could be composed entirely of terrestrial-caught arthropods. Greater terrestrial foraging in the woodland habitat suggests that owlet-nightjars may be using optimal foraging strategies to obtain sustenance with minimum energy expenditure. Habitat differences in foraging by owlet-nightjars may also be influenced by vulnerability to predation when foraging on the exposed ground.

#### Introduction

Optimal foraging theory predicts that animals will select foods that deliver the maximum net benefit or fitness payoff (Lacher et al., 1982). Thus, the decision to select or reject a particular food item should depend on the availability of alternate food types with a greater benefit. However, availability reflects ease of capture as well as abundance. Foraging behaviour of birds is influenced by time and energy spent searching for and handling prey, as well as the energy content of the prey item (Stephens & Krebs, 1986). For insectivorous birds, the energetic costs associated with capturing prey vary widely depending on the prey type and the

hunting technique, with aerial foraging being the most costly, followed by sallying, and perch-and-pounce techniques (Goldstein, 1990). Searching and hunting techniques may be further constrained by seasonal shifts in prey abundance and activity levels.

Several studies have compared foraging behaviour and diet shifts of birds as a function of seasons (Willson, 1970; Ford et al., 1990; Poulaine et al., 1992; Borghesio & Laiolo, 2004). Birds in the northern hemisphere frequently adjust foraging behaviours in response to seasonal changes in foliage structure (Willson, 1970), the presence of snow or ice covering substrates (Ulfstrand, 1976), and food scarcity. However, few studies have investigated seasonal foraging shifts at low latitudes where seasonal climatic differences are less extreme. Those that have mainly focused on species occurring within a single (Ford et al., 1990; Borghesio & Laiolo, 2004) or similar habitat types (Poulaine et al., 1992). Food resources and availability differ between diverse habitats, and allopatric populations would be expected to adapt foraging behaviours to their locale (Doucette, 2001; Mumme et al., 2006). Geographic differences in resource use could affect activity and breeding patterns of local populations (Rautenbach et al., 1988; Dugger & Petrie, 2000), and lead to evolutionary divergence in other aspects of behaviour and physiology (Foster & Endler, 1999).

Australian owlet-nightjars (*Aegotheles cristatus*) differ from the majority of birds in that they inhabit a variety of different habitat types. This makes them an ideal species to investigate geographic variation in diet and foraging tactics and how it relates to climate, prey availability and habitat structure. However, little is known about their diet or foraging. It has been proposed that they mainly forage on aerial arthropods (Brigham et al., 1999), as do most species of Caprimulgiformes (Brigham & Barclay, 1995; Brigham & Fenton, 1991; Jackson, 2003c), but anecdotal reports based on the stomach contents of road-killed individuals suggest otherwise (Lea & Gray, 1935; Serventy, 1936; Webb, 1989; Rose, 1973; Rose, 1997; Jones, 2004). The purpose of my study is to quantify the diet of owlet-nightjars in distinct habitats: a semi-arid desert and a temperate, high-altitude, eucalypt woodland that differ in climate, arthropod availability, and vegetation structure. I predict that decreased abundance of aerial prey during periods of low temperature or dry conditions will result in a shift from aerial to terrestrial foraging for this species.

## **Methods**

### ***Study Sites***

This study was conducted at three field locations, two in the semi-arid zone of central Australia and one in temperate eucalypt woodlands on the Northern Tablelands of New South Wales. The two locations in central Australia, Ormiston Gorge (23°37'S, 132°43'E) and the Alice Springs Desert Park (23°37'S, 132°43'E) have been described in detail previously (Chapter 2). Sampling was conducted during the winter of 2004 and 2005 (June to September) at both sites. The mean minimum and maximum ambient temperatures ( $T_a$ ) in Alice Springs for July are 4.0 °C and 19.9 °C and the mean annual rainfall is 282 mm (1941-2007, Australian Bureau of Meteorology). Ormiston Gorge is a desert woodland site with mulga and riverine woodland habitats. It is designated as the desert (D) site in the current study. Areas at the Alice Springs Desert Park were irrigated once a fortnight for 4 hours on a rotating basis, so that at least one area of the park was irrigated each day. Thus, this site is designated as irrigated desert (ID).

I studied owllet-nightjars year-round (November 2005 to November 2006) in the 218 ha Imbota Nature Reserve (30° 35' S, 151°45'E, 1000 m elevation), 10 km southeast of Armidale on the Northern Tablelands, New South Wales. This location was described in detail previously (Chapter 4) and is designated as the eucalypt woodland (EW) site. The Armidale region is temperate with cold winters due to its elevation and distance from the coast. The mean daily minimum and maximum  $T_a$  for Armidale are 13.0 °C and 26.6 °C in summer and 1.0 °C and 13.2 °C in winter (1857-1997, Australian Bureau of Meteorology). Mean annual rainfall is 790 mm and mean monthly summer quantities (93.8 mm) are typically double winter amounts (51.5 mm).

### ***Ambient Temperature and Rainfall***

I deployed small temperature data loggers (Thermochron iButtons®, Model DS1921,  $\pm 0.5^\circ\text{C}$ , Dallas Semiconductor Corp., Dallas, TX, U.S.A) in the shade 1 m above the ground in a central position at each of the study sites to measure  $T_a$ . Weather stations at the Ormiston Gorge ranger station and the Alice Springs Desert Park provided daily rainfall data. Daily rainfall data for the eucalypt woodland were obtained from the Australian Bureau of Meteorology data for Armidale.

## ***Diet***

Owlet-nightjars were caught by broadcasting taped calls to lure individuals into mist nets. Faecal samples produced by birds during handling were collected. Birds were fitted with radio-transmitters and tracked to diurnal cavity roosts for another study (Chapters 2-4). Accessible roosts, such as rock crevices and stumps, were regularly checked for faecal pellets.

Faecal samples were dried at 100 °C for 24 hours. Each pellet was placed in a petri dish and teased apart using 10% KOH and 70% ethanol (see Pavey et al., 2001 for further details). The material was systematically searched for identifiable fragments under a low-power (6.4x-40x) binocular microscope. Arthropods were identified to the lowest taxonomic level possible. Formicidae were typically identified to genus and caste. The number of fragments in each faecal pellet was recorded. The percentage by volume of each order in each pellet was visually estimated to the nearest 5%.

*Acknowledgement:* Faecal samples were analyzed by C.J. Burwell (Curator of Entomology, Queensland Museum, Brisbane) and C.R. Pavey (Biodiversity Conservation, Parks and Wildlife Service, Alice Springs) and data provided to me as the number of fragments and percent volume of each arthropod order in each pellet.

## ***Arthropod Sampling***

Pitfall and light traps were used to sample arthropods at all study sites. Pitfalls traps (diameter = 68 mm, depth = 150 mm), each containing 50 ml of 50% ethanol, were placed in a grid pattern consisting of three rows of four traps each placed at 10 m intervals (12 traps per plot). To focus on nocturnal arthropods only, each pitfall trap was uncovered at dusk and covered at dawn. Traps were opened for two nights fortnightly. Arthropods were removed from traps post-sampling and stored in 70% ethanol. Samples were later dried at 60 °C for a minimum of 12 hours.

Three plots were placed in three different habitats at each of the two study sites in central Australia, for a total of 36 traps per site. At the desert site, plot 1 was on the edge of a river channel with an under-story consisting of grasses and an upper-story of tall river red gums (*Eucalyptus camaldulensis*). The habitat of plot 2 had sand substrate with mulga shrubs (*Acacia aneura*), and plot 3 was in a habitat consisting of hard, rocky substrate with *Acacia* sp. upper-story and an under-storey of spinifex grasses (*Triodia brizoides*, *T. longiceps*; Plate 1). The three habitats where arthropods were sampled in the irrigated desert site all had an

upper-storey of *A. aneura* (Plate 2). Plot 2 was more open than plot 1. Plot 3, located outside the park fence, had a dense under-storey of invasive buffel grass (*Cenchrus ciliaris*). Plots 1 and 2 were irrigated once a fortnight. Plot 3 was not irrigated nor the weeds controlled. At the eucalypt woodland site, two structurally similar plots in two different areas of the reserve were samples with a total of 24 traps. The two habitats where arthropods were sampled had similar upper-stories of *Eucalyptus sp.* with an open under-story. Ground cover at plot 1 consisted of mixed grasses and plot 2 was on higher ground with a ground cover of leaf litter (Plate 3).

Nocturnal aerial arthropods were sampled using an ultra violet light trap (Australian Entomological Supplies Pty. Ltd., Coorabell, NSW, Australia). The trap consisted of a large white funnel atop a bucket, upon which fitted an 8 W black ultra-violet light tube attached to three clear plastic vanes, which allowed a 360° exposure to attract arthropods. A small bottle with a wick contained ethyl acetate was used as an anesthetic to kill the arthropods entering the trap. The trap was suspended 0.5 to 1 m above the ground. Aerial arthropods in each plot for both desert sites were sampled every fortnight. Additionally, arthropods were sampled during the new moon, with one site sampled for three nights prior and the other sampled for three nights post new moon (6 to 9 samples per site per month). The order that sites were sampled was reversed each month. In the eucalypt woodland, two sites were sampled once each fortnight on the new and full moon periods (4 samples per month) during winter and monthly on the new moon throughout the rest of the year. Samples were removed at dawn and dried at 60 °C for a minimum of 12 hours.

All light and pitfall sampling collected on a new moon (one sample set per month at each location) were sorted to order and individual arthropods counted. Arthropods <3 mm in length or >11 mm diameter were excluded from analysis as these were outside the range of prey sizes normally consumed by nightjars (Jackson, 2000b; Jetz et al., 2003). The dry mass of each order per sample was measured to  $\pm 0.0001$  g using a Mettler AE 260 balance (Mettler Instrumente AG, Switzerland). The remaining samples were weighed after drying for biomass  $\pm 0.01$  g.

### ***Crepuscular Foraging Behaviour***

Owlet-nightjars roosting in tree hollows were observed exiting roosts at dusk against a backlit sky and the time recorded. Occasionally, birds were tracked to their roosts at dawn. Roost departure and return times were calculated in relation to sunset or sunrise and civil and

nautical twilight. Civil twilight begins in the evening when the centre of the sun is at a depression angle of  $6^\circ$  below the horizon until nautical twilight when the centre of the sun is at a depression angle of  $12^\circ$  (GeoScience Australia). In the absence of moonlight, illumination during civil twilight is such that large objects can be seen but no detail is discernible (GeoScience Australia). During nautical twilight (no moonlight) it is dark for normal practical purposes (GeoScience Australia). The end of evening nautical twilight defines when 'true night' begins and the crepuscular period (civil and nautical twilight) ends (Brigham et al., 1999).

### ***Data Analysis***

Arthropod samples from pitfall and light traps were treated as separate data sets because the two techniques sample different types of arthropods, and because the biomasses collected are likely to differ as light traps are attractant-traps and pitfalls are not. Aerial arthropod abundance was assessed from July to September for all sites and years. Terrestrial arthropod abundance was sampled from June to September for all sites except the irrigated desert in 2005, for which only August and September data were collected. Samples from June to September were designated winter samples to correspond with diet samples collected during the same period. Similarly, arthropods sampled in the eucalypt woodland from November to February were classified as summer to compare to faecal samples collected simultaneously. To compare the seasonal availability of arthropods within the eucalypt woodland throughout the year I grouped samples by true seasons: summer (December-February), autumn (March-May), winter (June-August), and spring (September-November). Given that some taxa, including Coleoptera and Blattodea, can be trapped and captured by owl-nightjars both aerially and on the ground, my analyses comparing aerial and terrestrial prey were performed with and without these taxa included.

A general linear model (GLM) using month and site as factors was performed on biomass of terrestrial and aerial samples separately. Biomass data were not normally distributed (Lehner, 1996), therefore I used Kruskal-Wallis analysis of variance (Kruskal Wallis ANOVA) to compare biomass at sites by month, between seasons at the eucalypt woodland site, between aerial-to-terrestrial biomass ratios by site, and the proportions of different arthropod orders at sites and in the diet. An analysis of covariance (ANCOVA) was used to investigate the influence of  $T_a$  on log aerial and log terrestrial biomass. The relationship between aerial and terrestrial arthropod availability and volume of these groups in the diet was evaluated with Spearman rank correlations.

To determine the energy content of the diet, the mean dry mass of an individual in each arthropod order was calculated by dividing the total dry biomass by the total number of individuals collected at each site. Using published values of arthropod water content (Bell, 1990), the mean wet mass of an individual from each order was determined. Based on published values of energy content per gram (Bell, 1990) the energy available from each individual arthropod was calculated separately for the desert and eucalypt woodland sites. The minimum number of individual arthropods required per day to support the energy requirements of a 45 g owlet-nightjar was calculated based on the owlet-nightjar basal metabolic rate of  $1.27 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$  or  $27.6 \text{ kJ day}^{-1}$  (Chapter 5) for each site separately.

All statistical tests were performed using either Minitab Statistical Software (version 13.1) or SigmaStat (version 2.0) software. Numerical values are presented as means  $\pm$  SE for  $n$  = number of individual birds and  $N$  = number of traps or number of faecal pellets. An alpha value of 0.05 was used for all tests.

## **Results**

### ***Ambient Temperature and Rainfall***

Mean monthly minimum  $T_{as}$  for the eucalypt woodland site were on average  $8.4 \pm 0.6$  °C lower than the desert sites throughout the year and were always below 0 °C in winter ( $-1.3 \pm 0.2$  °C; Figure 1). Mean monthly minimum  $T_a$  in the desert during winter averaged  $5.0 \pm 0.3$  °C. However, minimum  $T_{as}$  reached during winter were the same in the desert and at the eucalypt woodland site. The range of minimum and maximum  $T_a$  on arthropod collection dates was  $+1.0$  to  $+32.5$  °C and  $-1.7$  to  $+33.6$  °C for the irrigated desert site in 2004 and 2005, respectively,  $-0.5$  to  $+33.0$  °C and  $-0.5$  to  $+29.6$  °C for the desert in 2004 and 2005, respectively, and  $-0.6$  to  $11.8$  °C and  $+11.8$  to  $29.4$  °C for the eucalypt woodland in winter and summer. Notably, maximum  $T_{as}$  reached in the desert in winter were more than 20 °C higher than at the eucalypt woodland site, which translated into higher evening  $T_{as}$ .

The mean annual rainfall at Ormiston Gorge (D) is 333 mm (1972-2004, Ormiston Gorge Ranger Station). However, heavy rains (120 mm) in mid-May 2004, preceded by a wetter than normal year (420 mm), caused the usually dry Ormiston Creek to flow from 22 May 2004 until mid-June 2004 and small pools persisted throughout the river channel until the end of August 2004 (Plate 4). In contrast, between June 2004 and May 2005 only 72 mm of rain fell in the area leading to dry conditions at the onset of winter. From mid-June – mid-July 2005,

85 mm of rain fell, making the second half of the winter wetter (Figure 1). However, the creek remained dry and the permanent waterhole in Ormiston Gorge was less than one quarter the size of 2004 (Plate 5). The Alice Springs Desert Park (ID) experienced the same low rainfall between 2004 and 2005. However, due to regular irrigation I expected that the differences in rainfall would have less impact on arthropod availability at this site. Total annual rainfall at the eucalypt woodland site in 2006 was approximately double (614 mm) that of the desert sites (214 to 328 mm).

### ***Comparison of Arthropod Biomass between Study Sites***

Aerial and terrestrial arthropod biomass did not differ significantly between sampling plots within each study site (Table 1). Thus, I pooled plots within sites for all analyses.

Mean winter aerial arthropod biomass did not differ significantly between years or sites in the desert, but was significantly less in the eucalypt woodland than any of the sampling locations/years at the desert sites (Kruskal-Wallis ANOVA:  $H_5=36.14$ ,  $P<0.00001$ ; Figure 2a). Examination of the data for each month separately indicated that aerial arthropod biomass differed significantly between locations in July, August, and September ( $P<0.05$ ; Figure 2b). The biomass at the irrigated desert in 2005 was significantly greater than for the eucalypt woodland for July and September and irrigated desert biomass in 2004 was greater than the eucalypt woodland in August. The desert site and the eucalypt woodland did not differ significantly during any month. Arthropod biomass in light traps differed significantly between August and September across all sites (GLM:  $F_{2,82}=3.65$ ,  $P<0.05$ ).

The biomass of arthropods sampled by pitfall traps differed by site (years combined for desert sites; GLM:  $F_{2,1002}=12.25$ ,  $P<0.0001$ ) and month ( $F_{3,1002}=4.56$ ,  $P<0.01$ ). The terrestrial biomass at the irrigated desert site was significantly greater than for both the desert ( $T=3.95$ ,  $P<0.0005$ ) and the eucalypt woodland sites ( $T=4.35$ ,  $P<0.00001$ ). Biomass in July ( $T=3.18$ ,  $P<0.01$ ) and September ( $T=2.69$ ,  $P<0.05$ ) was significantly higher than in August. Further analysis by month for different years at the desert sites, indicated that terrestrial arthropod biomass at the irrigated desert site during both 2004 and 2005 was significantly greater than all other groups for each month tested (Kruskal-Wallis ANOVAs:  $P<0.00001$ ; Figure 3). Biomass was similar at the irrigated desert site in both years, but was significantly greater at the desert site in 2004 compared to 2005. The eucalypt woodland had a lower terrestrial arthropod biomass than all other sites with the exception of the desert in 2005. The terrestrial

arthropod biomass at the desert site did not differ from the eucalypt woodland during any month in 2005.

### ***Comparison of Arthropod Biomass between Seasons at the Eucalypt Woodland Site***

A comparison of biomass between seasons in the eucalypt woodland indicated that aerial arthropod biomass was significantly less during winter relative to summer and autumn ( $H_3=14.10$ ,  $P<0.005$ ; Figure 4a). However, even in summer, arthropod biomass was low ( $7.9 \pm 3.6$  g), exceeded by winter samples at the irrigated desert site ( $15.8 \pm 5.0$  g and  $85.5 \pm 58.0$  g) and at the desert site ( $10.9 \pm 3.5$  g and  $8.3 \pm 2.8$  g).

Likewise, terrestrial arthropod biomass at the eucalypt woodland site was generally lower than at either desert site (Figure 4b). Even in summer, mean biomass at the eucalypt woodland was lower than the irrigated desert in winter during 2004 ( $H_5=213.2$ ,  $P<0.0001$ ; Figure 3). Terrestrial biomass was significantly less in the woodland during autumn and winter compared to summer and spring ( $H_3=81.70$ ,  $P<0.0001$ ).

### ***Effect of $T_a$ on Arthropod Biomass***

Aerial and terrestrial biomass was positively correlated with  $T_a$  (ANCOVA: MIN  $T_a$ :  $F_{1,158}=58.00$ ,  $P<0.0001$ ; MAX  $T_a$ :  $F_{1,158}=90.09$ ,  $P<0.0001$ ; Figure 5). The log mean trap biomass of aerial arthropods was significantly greater than terrestrial arthropods (MIN  $T_a$ :  $F_{1,158}=92.88$ ,  $P<0.0001$ , model  $R^2=0.50$ ; MAX  $T_a$ :  $F_{1,158}=107.04$ ,  $P<0.0001$ , model  $R^2=0.56$ ). The slopes of the aerial and terrestrial biomass were similar for both  $T_a$  measures (MIN  $T_a$ :  $F_{1,158}=1.09$ ,  $P=0.30$ ; MAX  $T_a$ :  $F_{1,158}=0.26$ ,  $P=0.26$ ). A two-way ANOVA using minimum  $T_a$  and moon phase as factors showed that  $T_a$  had a significant effect on the biomass caught in aerial traps while moon phase did not ( $T_a$ :  $F_{2,117}=16.67$ ,  $P<0.00001$ ; Moon:  $F_{2,117}=0.94$ ,  $P=0.39$ ,  $R^2=0.27$ ). The ratio of aerial-to-terrestrial arthropod biomass was not different between sites (Kruskal Wallis ANOVA:  $H_5=4.57$ ,  $P=0.47$ ; Figure 6a) or seasons (ANOVA:  $F_{3,14}=1.32$ ,  $P=0.32$ ; Figure 6b).

### ***Comparison of Arthropods between Sites***

The dominant arthropod order by biomass in light trap samples was the Lepidoptera ( $77.2 \pm 3.8$  %;  $\chi^2_{0.05,6} = 20.9$ ,  $P<0.005$ ; Figure 7). Lepidopterans represented the greatest proportion of biomass for all sites except for the eucalypt woodland in summer, which was dominated by Coleoptera ( $59.7 \pm 11.8$  %). Lepidoptera biomass collected at the irrigated desert site in both years and at the desert site in 2005 was significant higher than at the desert site in 2004 and at

the eucalypt woodland site in summer (Kruskal-Wallis ANOVA:  $H_5=27.0$ ,  $P<0.0001$ ). The biomass of Coleoptera in the eucalypt woodland during summer was significantly greater than at all other sites ( $H_5=18.7$ ,  $P<0.005$ ). Blattodea biomass was also greater during summer in the eucalypt woodland than in the desert in 2005 ( $H_5=13.9$ ,  $P<0.05$ ). Trichoptera biomass represented 21% of the biomass at the desert site in 2004, significantly more than at the irrigated desert or eucalypt woodland sites ( $H_5=34.16$ ,  $P<0.0001$ ). The biomass of Diptera ( $H_5=12.7$ ,  $P<0.05$ ) was significantly greater in the eucalypt woodland in winter than at the irrigated desert in 2004, but Hemiptera biomass was less ( $H_5=11.2$ ,  $P<0.05$ ). Aerial Hymenoptera biomass did not differ between sites ( $H_5=5.8$ ,  $P=0.33$ ).

The dominant arthropod taxon by biomass in the pitfall samples was the Formicidae (Order Hymenoptera). This family had the greatest mean proportion of biomass and numbers at all sites except the eucalypt woodland in winter, which had a higher proportion of Araneae (spiders) than all other sites ( $32.6 \pm 2.3$  %;  $H_5=28.1$ ,  $P<0.0001$ ; Figure 8). Mean Formicidae biomass was significantly lower in the eucalypt woodland site in winter ( $20.4 \pm 4.3$  %) than at all other sites, and at the desert site in 2004 ( $37.1 \pm 3.3$  %) compared to the irrigated desert in both years ( $H_5=102.6$ ,  $P<0.0001$ ). Coleoptera biomass in the eucalypt woodland in summer was significantly greater than in the irrigated desert in both years and in the desert in 2005 ( $H_5=66.3$ ,  $P<0.0001$ ). In 2004 the desert site had a greater diversity of prey types than the other sites. Both Blattodea ( $H_5=14.5$ ,  $P<0.05$ ) and Orthoptera ( $H_5=54.2$ ,  $P<0.0001$ ) biomass was greatest at this site.

### ***Comparison of Arthropods among Seasons in the Eucalypt Woodland Site***

While total biomass of prey in the eucalypt woodland varied greatly throughout the year, the composition of the available prey was consistent. I found no significant seasonal differences in biomasses for any of the aerial arthropod taxa captured in light traps. Lepidoptera dominated the biomass of light traps in the eucalypt woodland in all seasons except summer, when Coleoptera was more abundant ( $61.1 \pm 18.3$  %; Figure 9a). However, there was no significant difference for Lepidoptera ( $H_3=5.8$ ,  $P=0.12$ ) or Coleoptera ( $H_3=7.7$ ,  $P=0.052$ ) among seasons.

Formicidae was the dominant taxon in pitfall traps in all seasons except winter, which consisted largely of 'other' arthropod taxa ( $43.8 \pm 6.8$  %), including centipedes and millipedes (Figure 9b). However, the low biomass collected at this site in winter (0.4 g) meant the presence of only one or two large arthropods dominated the biomass. Formicidae biomass

was significantly lower in winter and higher in summer relative to spring and autumn ( $H_3=43.5$ ,  $P<0.0001$ ). There were less Coleoptera in autumn than summer ( $H_3=36.9$ ,  $P<0.0001$ ) and Orthoptera were more abundant in spring compared to winter or summer ( $H_3=11.8$ ,  $P<0.01$ ). The biomass of Blattodea ( $H_3=4.1$ ,  $P=0.25$ ) and Araneae ( $H_3=5.7$ ,  $P=0.13$ ) did not differ significantly among seasons.

### ***Diet and Prey Selection***

The main arthropod taxa in the diet of owlet-nightjars were Formicidae ( $29.7 \pm 11.5$  %) and Coleoptera ( $27.8 \pm 9.4$  %;  $X^2_{0.05,7} = 19.5$ ,  $P<0.01$ ; Figure 10). The volume of Formicidae in the diet did not differ significantly amongst owlet-nightjars at different sites ( $H_5=6.89$ ,  $P=0.23$ ), but represented the greatest proportion of the diet at the desert site in 2004 (Table 2). All Formicidae found in the diet of owlet-nightjars were flightless workers. The major genera in faecal samples collected in the desert were *Polyrachis* and *Camponotus*. *Iridomyrmex*, *Myrmeci*, *Odontomachus*, and *Rytidoponera* were also common. At the eucalypt woodland site *Polyrachis* and *Myrmecia* were the main genera, with some samples containing *Camponotus*. Although no winged castes of Formicidae were found in the diet, other Hymenoptera, including Ichneumonidae (Ichneumon wasps) and Apoidea (bees) were found in low proportions (<2%) at the desert sites.

Coleoptera was the major prey item found in faecal samples for half of the sites and years studied, including the irrigated desert in 2005 ( $25.0 \pm 14.7$ %) and the eucalypt woodland in winter ( $47.7 \pm 12.1$  %) and summer ( $42.5 \pm 12.6$  %), but did not differ significantly between groups ( $H_5=5.97$ ,  $P=0.31$ ). Families of Coleoptera identified for the desert sites included the Chrysomelidae (leaf beetles) and the ground-dwelling Tenebrionidae.

Lepidoptera were the most abundant prey type found in the diet at the irrigated desert in 2004 ( $36.5 \pm 18.1$ %) and the desert in 2005 ( $39.6 \pm 12.5$ %), and differed significantly in abundance from the desert in 2005 and the eucalypt woodland in summer and winter ( $H_5=25.3$ ,  $P<0.0005$ ; Table 2). Lepidoptera represented 16% ( $\pm 6.6$ %) of the total diet across all groups. However, no Lepidoptera occurred in the diet of owlet-nightjars at the irrigated desert site in 2005 and at the eucalypt woodland in summer, and only one individual was found in the diet of individuals in the eucalypt woodland in winter. One individual at the irrigated desert site in 2004 site had consumed Lepidoptera larvae (caterpillars), which were present in abundance on foliage and dropping onto the ground when this individual was captured in mid-July. While handling it, the individual regurgitated 6-8 larvae.

All Hemiptera consumed were from the suborders Heteroptera and Auchenorrhyncha. Families of Heteroptera included Pentatomidae (stink bugs), which were frequently observed on the ground in the desert during 2004, and Scutelleridae. Auchenorrhyncha or plant hoppers were only found in the diet of desert birds. Less than 7% of the owlet-nightjar diets were composed of Hemiptera, and groups did not differ significantly in the proportion of Hemiptera in their diet ( $H_5=6.25$ ,  $P=0.28$ ).

Orthoptera were present in the diet of birds at all sites except for the desert in 2005 and the eucalypt woodland in winter, yet represented <6% of the owlet-nightjar diet overall. In 2004, some prey were identified as Acrididae (locusts). Birds from different sites did not differ significantly in the proportion of Orthoptera in their diet ( $H_5=9.14$ ,  $P=0.10$ ).

The final major taxon represented in owlet-nightjar diets was the Araneae, which comprised 7% of the diet across all groups. The Araneae was an especially important part of the eucalypt woodland diet during summer ( $26.5\% \pm 11.2\%$ ), but Araneae biomass did not differ significantly between groups ( $H_5=8.2$ ,  $P=0.15$ ). I included scorpions in this taxonomic group, which were found in the diet of one bird in the desert and two birds in the eucalypt woodland during winter.

Other taxonomic groups of minor importance in the diet were Blattodea, present in <3% of the diet for the desert and woodland sites, and Chilopoda (centipedes), present in the faecal sample of one desert bird. The jawbone of a small reptile, likely Scincidae (skink), occurred in the faecal pellet of a desert bird in 2005.

The number of faecal samples I collected was low in 2005 (Figure 10), thus I combined years to compare the relative importance of aerial prey to terrestrial prey in the diet. Likewise, seasons were combined at the eucalypt woodland site, as there were no significant differences in diet. A comparison of sites with aerial arthropods pooled (Lepidoptera and other Hymenoptera) resulted in a significant difference in the proportion of aerial prey in the diet ( $H_2=17.1$ ,  $P<0.0005$ ). Birds at the desert site had significantly more aerial arthropods in the diet than at the eucalypt woodland site (Table 3). When the analysis was repeated with Coleoptera and Blattodea classed as aerial prey this difference was removed ( $H_2=3.34$ ,  $P=0.19$ ). However, given the low  $T_a$ s during winter (desert mean minimum =  $7.4 \pm 0.6$  °C), especially at the eucalypt woodland site ( $2.9 \pm 1.0$  °C) it is unlikely that Coleoptera and

Blattodea were capable of flight (Taylor, 1963). I found no significant difference between sites in the grouped proportion of terrestrial arthropods (Formicidae, Araneae/Scorpiones, Hemiptera, Orthoptera) in the diet with ( $H_2=1.7$ ,  $P=0.42$ ) or without ( $H_2=5.9$ ,  $P=0.31$ ) the inclusion of Coleoptera and Blattodea as terrestrial prey.

I found no correlation between the availability of aerial arthropods in light traps compared to the diet (Lepidoptera and other Hymenoptera; Spearman rank correlation:  $p_s=0.14$ ,  $P=0.59$ ,  $N=17$ ; Figure 11a). Likewise, the availability of terrestrial arthropods in pitfall traps compared to the diet (Formicidae, Araneae/Scorpions, Hemiptera, Orthoptera) were not related ( $p_s=0.07$ ,  $P=0.78$ ,  $N=20$ ; Figure 11b). Adding Coleoptera and Blattodea to aerial arthropods ( $p_s=0.13$ ,  $P=0.63$ ,  $N=17$ ) or terrestrial arthropods ( $p_s=0.97$ ,  $P=0.97$ ,  $N=20$ ) did not improve the correlation. The biomass of Coleoptera captured in aerial traps was significantly correlated to the biomass in pitfall traps ( $p_s=0.71$ ,  $P<0.005$ ,  $N=17$ ), but the volume of Coleoptera in the diet was not correlated to captures in either trap type (light:  $p_s=0.13$ ,  $P=0.59$ ,  $N=18$ ; pitfall:  $p_s=0.09$ ,  $P=0.72$ ,  $N=19$ ).

Substantial size differences between individual arthropods within each order between the desert sites and the eucalypt woodland resulted in a difference in the energy content per arthropod (Table 4). Thus, the number of arthropods that an owlet-nightjar would be required to consume to meet its daily energy requirement varied between locations. Due to their small size in the eucalypt woodland, the number of Lepidoptera, and terrestrial Coleoptera and Blattodea that an owlet-nightjar would need to consume each day was more than double that at the desert site. However, Formicidae (aerial or terrestrial), and aerial Coleoptera, Blattodea and Hemiptera were larger in the eucalypt woodland, representing a more profitable prey choice.

An analysis of my data on the occurrence of different arthropod orders in the diet of owlet-nightjars and in the stomach contents of owlet-nightjars at various sites in eastern Australia (Barnard, 1914; White, 1917; Lea & Gray, 1935; Serventy, 1936; Gray, 1938; Rix, 1943; Webb, 1989; Rose, 1973; Rose, 1997; Jones, 2004) indicated that Coleoptera are the most common prey (Figure 12). However, Formicidae and Araneae also occurred in more than 50% of the stomachs and faecal samples. The difference that I found for Lepidoptera between the desert and woodland is apparent, with reports in the literature being intermediate.

### ***Crepuscular Foraging Behaviour***

Owlet-nightjars were consistent in the time they left their roosts to commence foraging. In the desert, owlet-nightjars exited roosts at civil twilight ( $1.05 \pm 1.82$  minutes, range -19 to +15 minutes,  $N=23$ ,  $n=10$  birds) and  $25 \pm 1.86$  minutes after sunset (range +5 to +40 minutes after sunset). All birds left the roost before the end of nautical twilight or the start of true darkness ( $-26.10 \pm 1.80$  minutes, range -13 to -46 minutes before nautical twilight). The timing was similar in the woodland habitat. Birds left the roost  $1.47 \pm 1.70$  minutes after civil twilight (-8 to +54 minutes,  $N=42$ ,  $n=15$  birds),  $23.05 \pm 2.32$  after sunset (-15 to +78 minutes), and  $-28.72 \pm 2.04$  minutes before nautical twilight (-26 to +64 minutes). Birds in the desert and the eucalypt woodland did not differ in the time they left their roosts in relation to sunset (Mann-Whitney:  $T=753$ ,  $n_1=22$ ,  $n_2=39$ ,  $P=0.29$ ). Although I only had data for two birds, owlet-nightjars waited until it was light before returning to their roosts. One desert bird returned 30 minutes after sunrise. The eucalypt woodland bird returned to its roost 18 minutes before sunrise, but 43 minutes after nautical twilight or true darkness ended.

**Table 1:** Comparison of mean aerial arthropod biomass (g) sampled by light traps and mean terrestrial arthropod biomass (g) in pitfall traps between plots within each study site for each year sampled and in years combined. Data from irrigated desert (ID) and desert (D) plots were compared using Kruskal-Wallis ANOVAs and eucalypt woodland (EW) plots were compared using a Mann-Whitney *U*-test.

	Site N	Mean ± SE Plot 1	Mean ± SE Plot 2	Mean ± SE Plot 3	<i>P</i> Value
<b>Aerial Biomass (g)</b>					
ID-2004	6	30.8±12.7	9.2±4.6	7.4±2.6	0.28
ID-2005	4	62.3±58.6	180.5±168.9	13.8±10.0	0.65
ID 2004+2005	10	43.4±23.2	77.7±67.8	10.0±4.1	0.57
D-2004	6	7.2±2.2	20.0±10.9	7.3±4.5	0.97
D-2005	12	3.7±2.3	7.5±3.7	5.0±2.4	0.53
D 2004+2005	18	5.1±1.6	11.7±4.4	5.7±2.1	0.71
EW All Seasons	15	2.0±0.7	2.7±1.1		0.90
<b>Terrestrial Biomass (g)</b>					
ID-2004	96	0.054±0.013	0.032±0.006	0.073±0.020	0.16
ID-2005	36	0.057±0.019	0.022±0.009	0.020±0.005	0.42
ID 2004+2005	132	0.055±0.011	0.029±0.004	0.058±0.015	0.06
D-2004	96	0.016±0.009	0.053±0.020	0.015±0.003	0.80
D-2005	84	0.007±0.002	0.005±0.002	0.003±0.001	0.08
D 2004+2005	180	0.012±0.005	0.030±0.011	0.010±0.002	0.20
EW All Seasons	176	0.011±0.003	0.011±0.002		0.83

**Table 2:** Mean  $\pm$  SE of the % volume of arthropod taxa found in the diet of owlet-nightjars by site. Contents of faecal samples collected in the irrigated desert (ID), desert (D) and eucalypt woodland (EW) sites were compared using Kruskal-Wallis ANOVAs.

	<b>ID-2004</b> <b>N=6</b>	<b>ID-2005</b> <b>N=4</b>	<b>D-2004</b> <b>N=5</b>	<b>D-2005</b> <b>N=5</b>	<b>EW-W</b> <b>N=11</b>	<b>EW-S</b> <b>N=10</b>	<b>P-Value</b>
<b>Lepidoptera</b>	36.5 $\pm$ 18.1	0.0	19.6 $\pm$ 8.7	39.6 $\pm$ 12.5	0.1 $\pm$ 0.1	0.0	<0.0005
<b>Coleoptera</b>	13.3 $\pm$ 15.7	25.0 $\pm$ 14.7	29.1 $\pm$ 7.6	9.0 $\pm$ 2.9	47.7 $\pm$ 12.1	42.5 $\pm$ 12.6	0.31
<b>Formicidae</b>	35.7 $\pm$ 18.5	22.5 $\pm$ 12.0	32.9 $\pm$ 8.8	31.0 $\pm$ 12.4	39.3 $\pm$ 11.5	8.5 $\pm$ 5.9	0.23
<b>Orthoptera</b>	4.2 $\pm$ 2.0	16.3 $\pm$ 13.1	0.2 $\pm$ 0.2	0.0	0.0	14.4 $\pm$ 9.9	0.10
<b>Hemiptera</b>	2.5 $\pm$ 1.7	21.0 $\pm$ 21.0	7.0 $\pm$ 7.0	5.2 $\pm$ 3.8	0.0	4.6 $\pm$ 3.2	0.28
<b>Aranea</b>	1.0 $\pm$ 0.82	1.8 $\pm$ 1.4	4.0 $\pm$ 2.8	1.0 $\pm$ 1.0	8.8 $\pm$ 5.1	26.5 $\pm$ 11.2	0.15

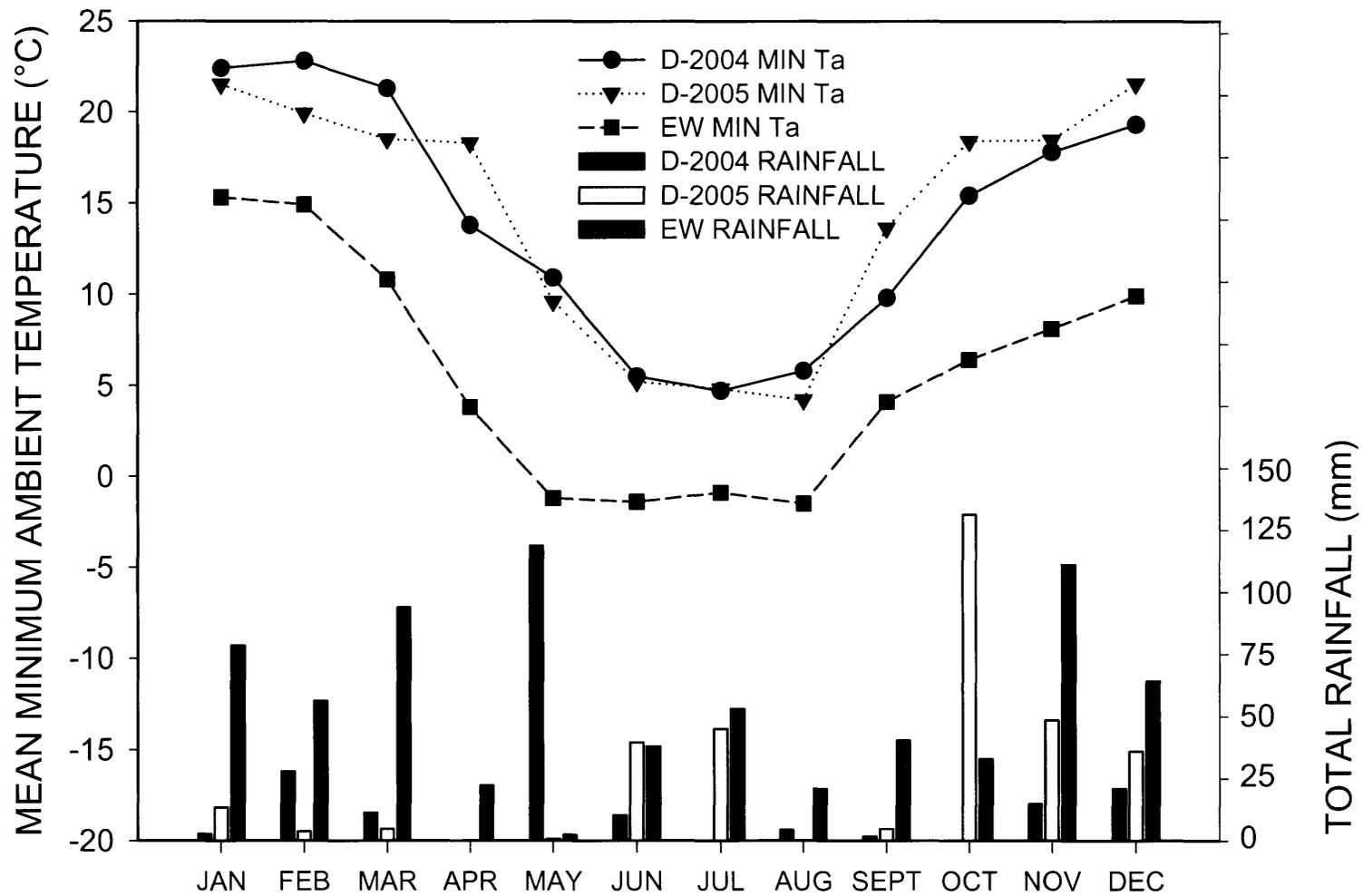
**Table 3:** Proportion (%) of the total diet volume in the desert, irrigated desert, and eucalypt woodlands that are comprised of aerial and terrestrial prey.

<b>Prey Type</b>	<b>Desert (%)</b>	<b>Irrigated Desert (%)</b>	<b>Eucalypt Woodland (%)</b>
<b>Aerial</b>	<b>31</b>	<b>22</b>	<b>0</b>
Lepidoptera	30	18	0
Other Hymenoptera	1	3	0
<b>Terrestrial</b>	<b>44</b>	<b>52</b>	<b>51</b>
Formicidae	32	24	29
Aranea/Scorpiones	2	1	18
Hemiptera	9	12	2
Orthoptera	2	10	7
<b>Both Aerial &amp; Terrestrial</b>	<b>25</b>	<b>25</b>	<b>49</b>
Coleoptera	19	19	45
Blattodea	6	0	3

**Table 4:** Water and energy content of arthropods in the diet of owlet-nightjars. Mean dry mass (g) of individual arthropods was determined for the two desert habitats combined (D) and the eucalypt woodland habitat (EW). N values are the total number of arthropods collected in samples that were weighed to determine biomass. Designations of aerial or terrestrial for the taxa indicate the type of trap (light or pitfall) in which individuals were captured. Energy content (kJ g<sup>-1</sup>) values for the two habitats are a reflection of the differences in mean mass of arthropods in a given order for the two sites. The minimum number of individual arthropods required per day to support the energy requirements of a 45 g owlet-nightjar was calculated based on the owlet-nightjar basal metabolic rate of 1.27 ml O<sub>2</sub> g<sup>-1</sup> h<sup>-1</sup> or 27.6 kJ day<sup>-1</sup>. Values in bold type indicate more than a 2-fold difference in energy content (kJ) arthropod<sup>-1</sup> and number of arthropods required per day to sustain an owlet-nightjar between the two habitat types.

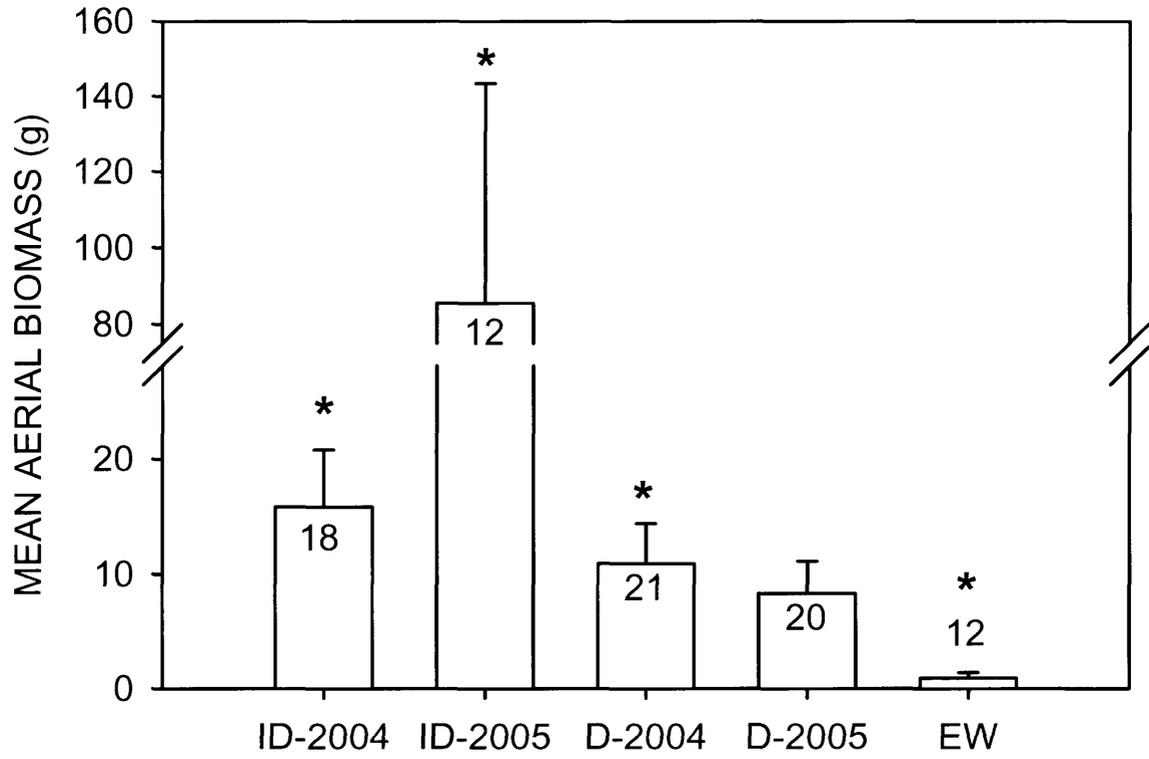
Taxa	N		Mean Dry Mass (g)		Water Content (%)	Mean Wet Mass (g)		Energy Content (kJ g <sup>-1</sup> )	Energy (kJ) Arthropod <sup>-1</sup>		Number Arthropods Day <sup>-1</sup>	
	D	EW	D	EW		D	EW		D	EW	D	EW
Lepidoptera	52 271	3248	0.0227	0.0097	73.6	0.0394	0.0168	21.25	<b>0.482</b>	<b>0.206</b>	<b>57</b>	<b>134</b>
Trichoptera	5201	211	0.0020	0.0026	81.2	0.0036	0.0046	20.92	0.042	0.054	663	515
Diptera	5323	1963	0.0005	0.0007	76.8	0.0009	0.0012	21.23	0.011	0.014	2602	1927
Orthoptera	105	10	0.0092	0.0164	73.5	0.0159	0.0284	23.95	0.220	0.392	126	70
Arachnida	190	144	0.0053	0.0042	70 <sup>1</sup>	0.0090	0.0072	22 <sup>1</sup>	0.116	0.093	237	297
Aerial Formicidae	1783	139	0.0013	0.0036	70 <sup>1</sup>	0.0022	0.0061	19.03	<b>0.025</b>	<b>0.069</b>	<b>1116</b>	<b>402</b>
Terrestrial Formicidae	19 483	1067	0.0004	0.0010	70 <sup>1</sup>	0.0007	0.0016	19.03	<b>0.007</b>	<b>0.018</b>	<b>3784</b>	<b>1504</b>
Other Hymenoptera	1072	52	0.0054	0.0053	70 <sup>1</sup>	0.0093	0.0090	20.37	0.111	0.107	249	257
Aerial Coleoptera	2578	1550	0.0033	0.0215	61.5	0.0053	0.0347	23.94	<b>0.079</b>	<b>0.514</b>	<b>349</b>	<b>54</b>
Terrestrial Coleoptera	83	94	0.0125	0.0062	61.5	0.0202	0.0101	23.94	<b>0.299</b>	<b>0.149</b>	<b>92</b>	<b>185</b>
Aerial Blattodea	112	10	0.0055	0.0749	65.8	0.0092	0.1242	22.58	<b>0.125</b>	<b>1.692</b>	<b>221</b>	<b>16</b>
Terrestrial Blattodea	56	16	0.1780	0.0312	65.8	0.2952	0.0518	22.58	<b>4.020</b>	<b>0.705</b>	<b>7</b>	<b>39</b>
Aerial Hemiptera	3034	79	0.0014	0.0044	70 <sup>1</sup>	0.0023	0.0074	23.59	<b>0.032</b>	<b>0.103</b>	<b>864</b>	<b>267</b>
Terrestrial Hemiptera	17	11	0.0024	0.0013	70 <sup>1</sup>	0.0040	0.0023	23.59	0.056	0.032	494	876

Data on arthropod water content and energy content from Bell (1990). <sup>1</sup>Taxa for which water or energy content values were not available were assigned the mean value as determined for the other orders (i.e. mean water content = 70% and mean energy content = 22 kJ g<sup>-1</sup>).

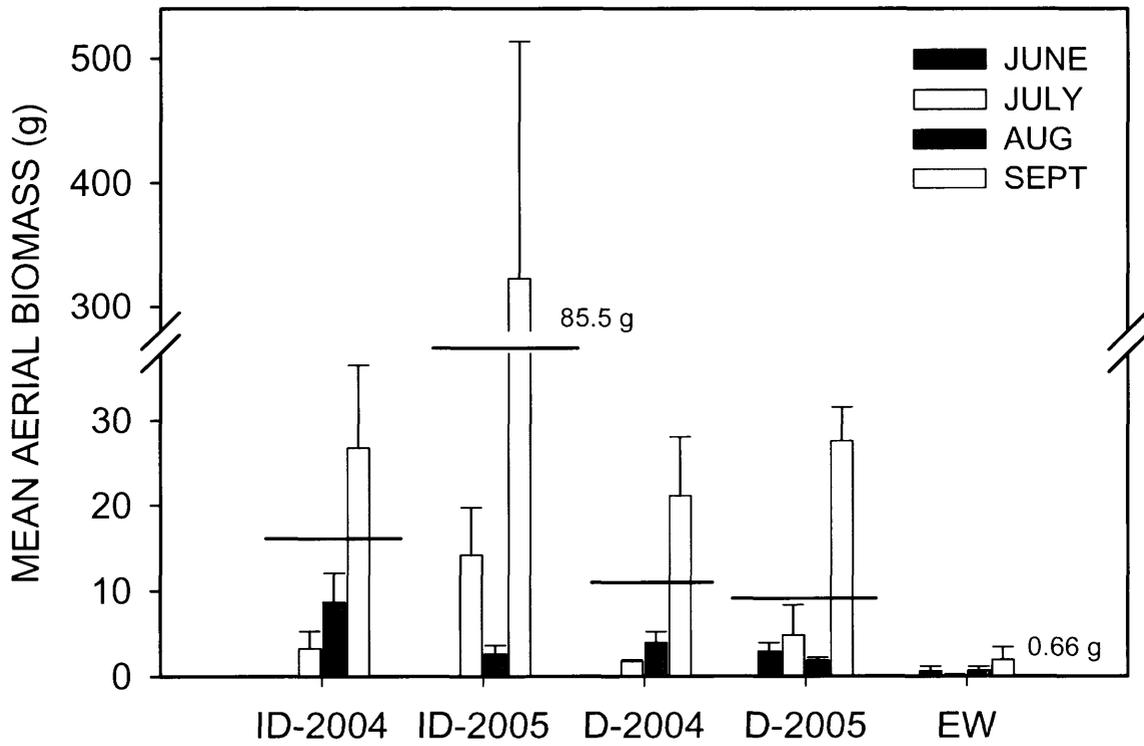


**Figure 1:** Mean monthly minimum ambient temperature (°C) and total rainfall (mm) for desert (D) sites in 2004 and 2005 and the eucalypt woodland (EW) site in 2006. Total annual desert rainfall in 2004 was 214 mm and in 2005 was 328 mm. Total annual rainfall at the EW site in 2006 was 614 mm.

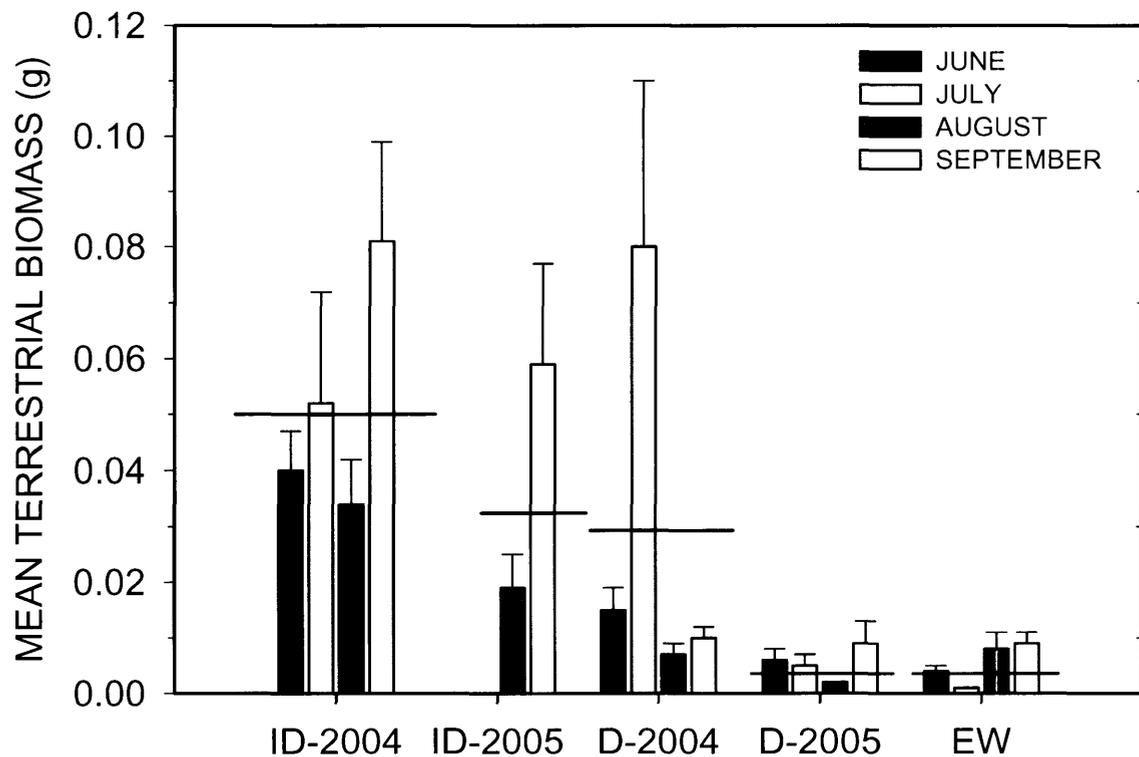
A



B

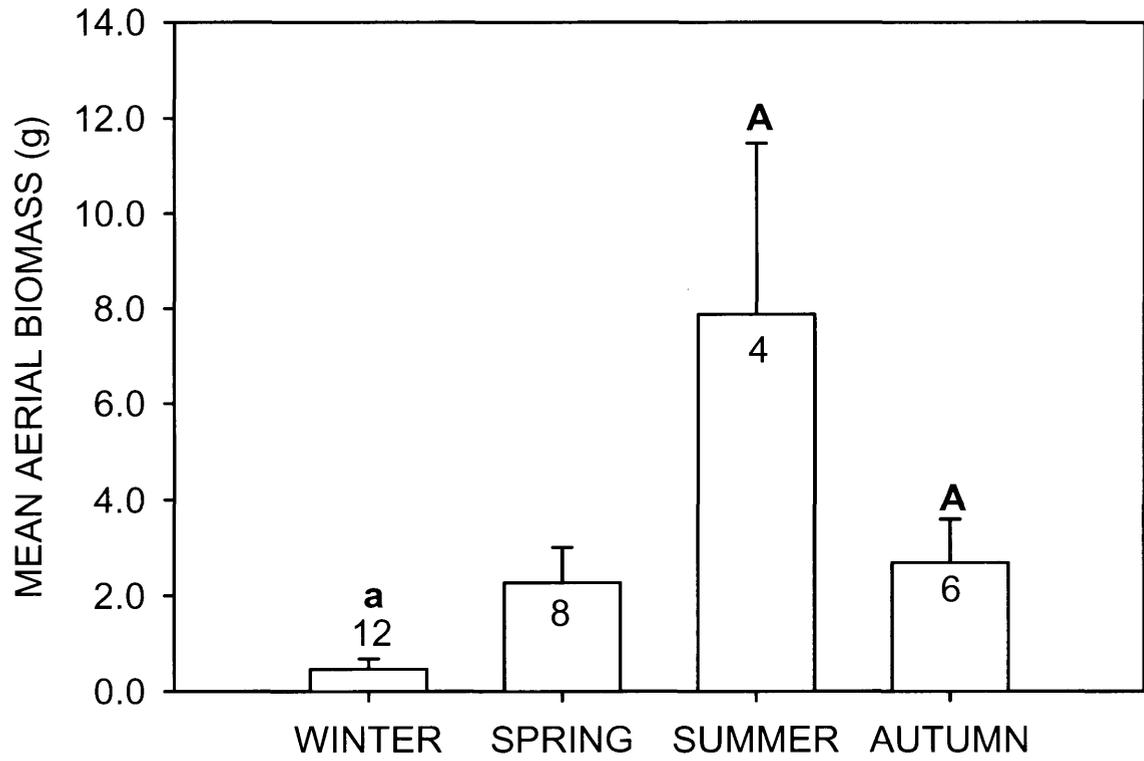


**Figure 2:** A) Mean aerial arthropod biomass (g) collected in light traps during winter (July to September) for the irrigated desert (ID) in 2004 and 2005, woodland desert (D) in 2004 and 2005 and the eucalypt woodland (EW) site. Sample sizes (N) are given on the bars. ID-2004, ID-2005 and D-2004 had biomasses significantly higher than the EW site (Kruskal-Wallis ANOVA:  $H_4=23.3$ ,  $P<0.001$ ). B) Mean aerial arthropod biomass (g) collected in light traps for winter months separately. Horizontal lines indicate the mean biomass for all months sampled at each location. Labels for ID-2005 and EW are mean winter biomass where bars could not be placed. Aerial arthropod biomass differed significantly between locations in July, August and Sept (Kruskal-Wallis ANOVAs:  $P<0.05$ ). The biomass values for ID-2005 were significantly greater than EW for July and September and ID-2004 was greater than EW in August. EW and D did not differ significantly during any month. Monthly samples sizes: ID-2004: July = 3, Aug = 7, Sept = 8; ID-2005: July & Sept = 3, Aug = 6; D-2004: July = 4, Aug = 8, Sept = 9; D-2005: June = 12, July = 9 Aug = 7, Sept = 4; EW: June-Sept = 4.

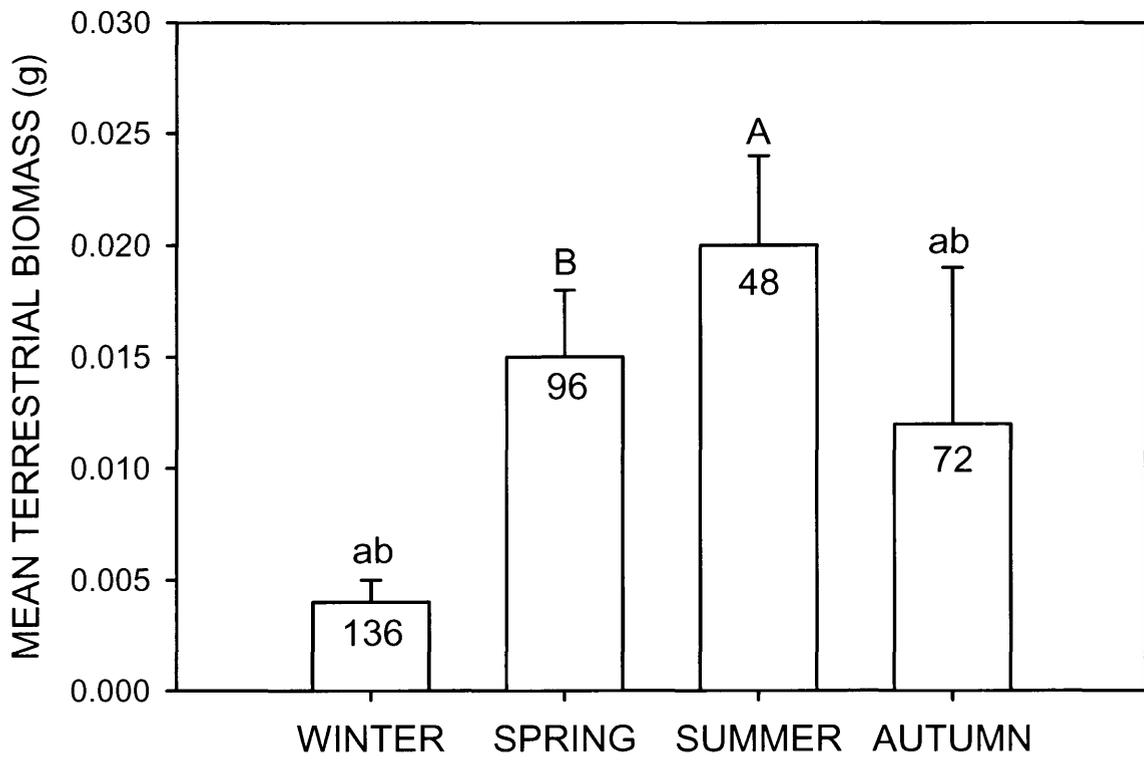


**Figure 3:** Mean terrestrial arthropod biomass (g) collected in pitfall traps from June to September of the years indicated. The x-axis labels are as in Figure 2. Horizontal lines indicate the mean biomass for all months at each location. Terrestrial arthropod biomass differed significantly between locations in each month (Kruskal-Wallis ANOVA:  $P < 0.00001$ ). The biomass values for ID-2004 and ID-2005 were significantly greater than all other groups for each month tested. D-2004 had a greater mass than EW during June and July. D-2004 had a greater biomass than D-2005 in June. EW and D-2005 did not differ significantly during any month. Monthly sample sizes: ID-2004: June = 36, July = 108, Aug-Sept = 72; ID-2005: Aug = 72, Sept = 36; D-2004: June-Sept = 72; D-2005: June-July = 72, Aug-Sept = 36; EW: June-Sept = 48.

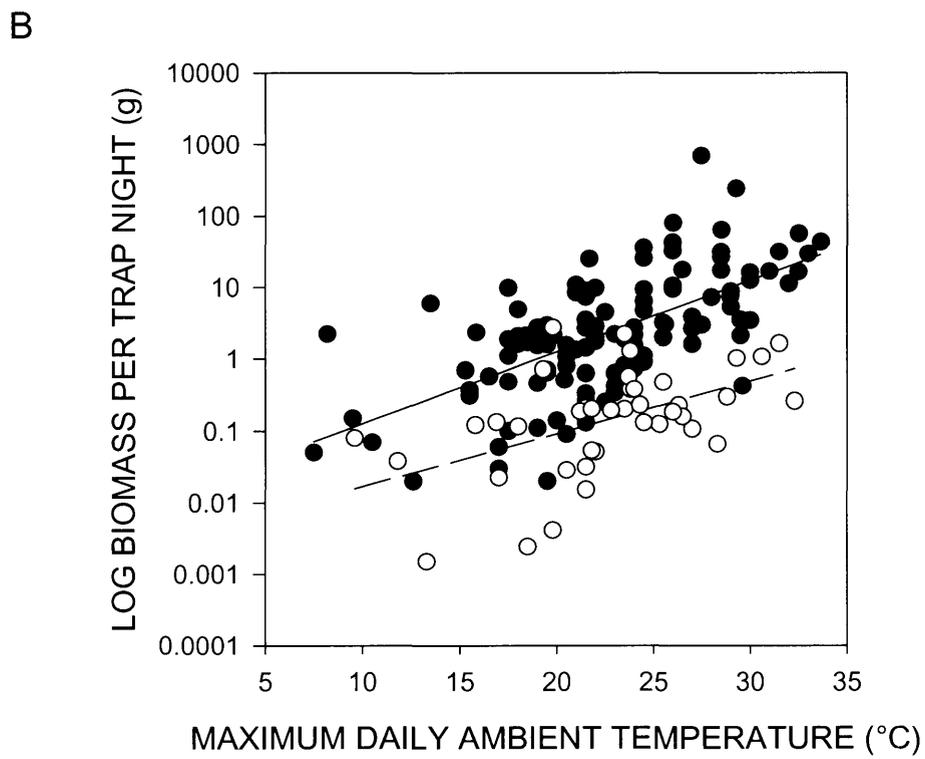
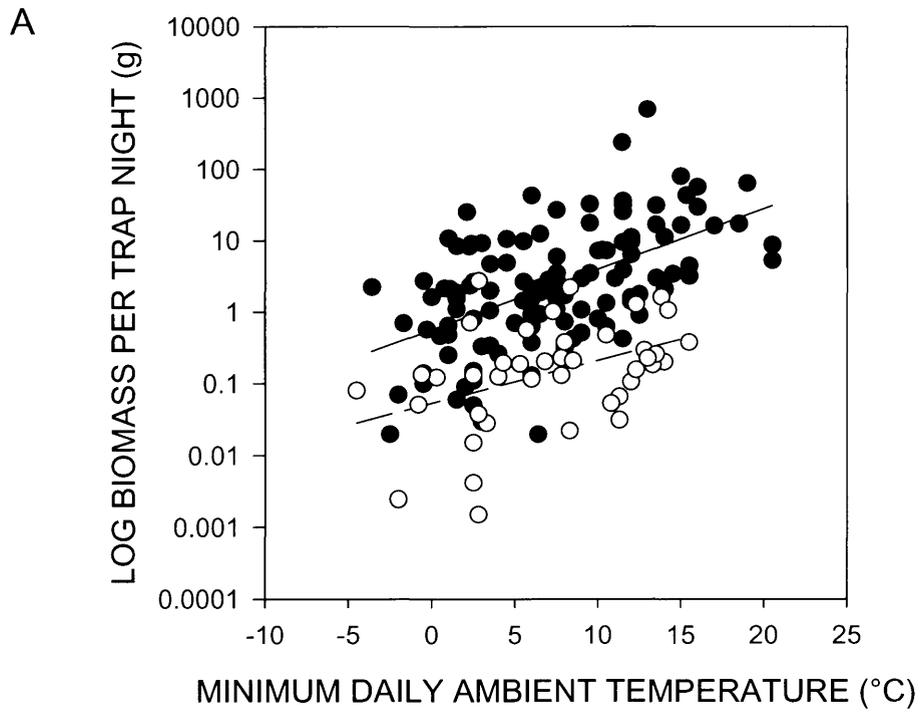
A



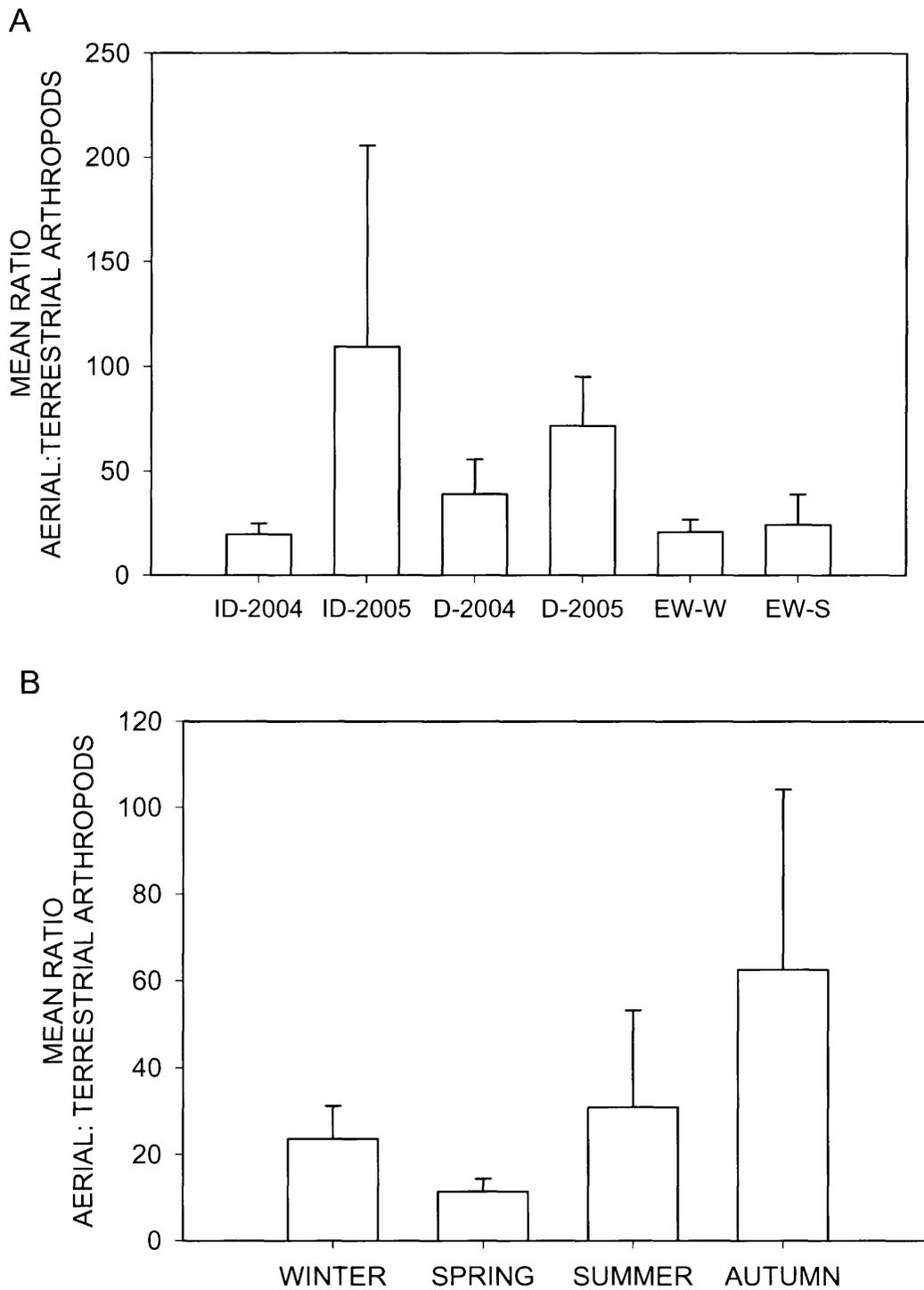
B



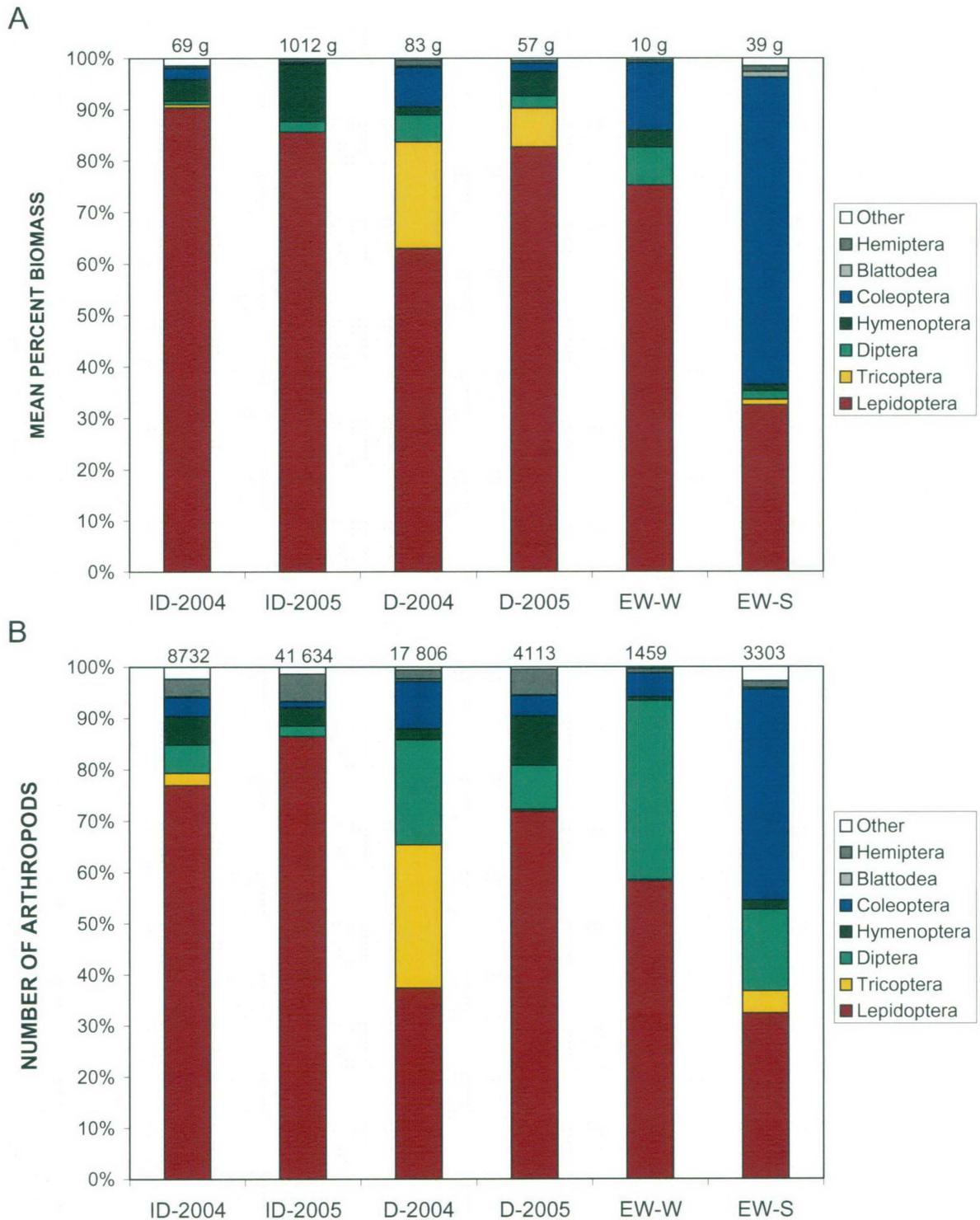
**Figure 4:** A) Mean seasonal biomass (g) of aerial arthropods collected in light traps at the eucalypt woodland (EW) site. Biomass values in summer and autumn 'A' were significantly higher than winter 'a' (Kruskal-Wallis ANOVA:  $H_3=14.1$ ,  $P<0.005$ ); B) Mean seasonal biomass (g) of terrestrial arthropods collected in pitfall traps at the eucalypt woodland (EW) site. Biomass values in spring 'B' and summer 'A' were significantly higher than winter 'ab' and autumn 'ab' (Kruskal-Wallis ANOVA:  $H_3=14.1$ ,  $P<0.00001$ ). Sample sizes (N) are given on the bars.



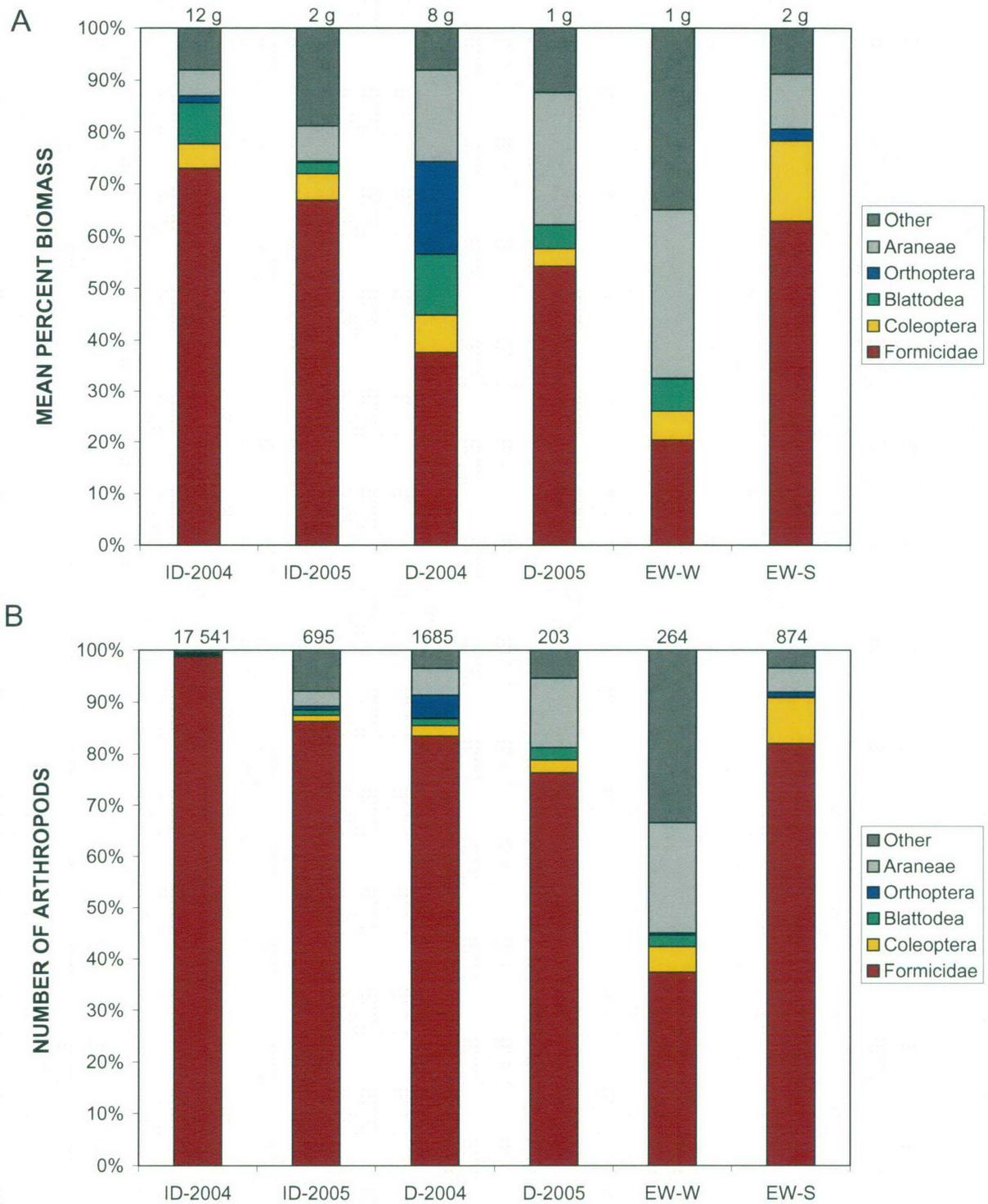
**Figure 5:** Higher minimum (A) and maximum (B) ambient temperatures ( $T_a$ ) resulted in greater arthropod log mean biomass in aerial (●; N=118 trap nights) and terrestrial (○; N=41 plot nights) traps. The log mean trap biomass of aerial arthropods was significantly greater than terrestrial arthropods for both minimum (ANCOVA:  $F_{1,158}=92.88$ ,  $P<0.0001$ , model  $R^2=0.50$ ) and maximum daily  $T_a$  ( $F_{1,158}=107.04$ ,  $P<0.0001$ , model  $R^2=0.56$ ). The slopes of the aerial and terrestrial biomass did not differ significantly for either temperature measure (MIN  $T_a$ :  $F_{1,158}=1.09$ ,  $P=0.30$ ; MAX  $T_a$ :  $F_{1,158}=0.26$ ,  $P=0.26$ ) and biomass increased significantly with increasing  $T_a$  for both aerial and terrestrial arthropods (MIN  $T_a$ :  $F_{1,158}=58.00$ ,  $P<0.0001$ ; MAX  $T_a$ :  $F_{1,158}=90.09$ ,  $P<0.0001$ ). Linear regression equations: A) Aerial Biomass =  $-0.25 + 0.08$  (MIN  $T_a$ ),  $P<0.00001$ ; Terrestrial Biomass =  $-1.27 + 0.06$  (MIN  $T_a$ ),  $P<0.01$ ; B) Aerial Biomass =  $-1.90 + 0.10$  (MIN  $T_a$ ),  $P<0.00001$ ; Terrestrial Biomass =  $-2.21 + 0.07$  (MIN  $T_a$ ),  $P<0.001$ ).



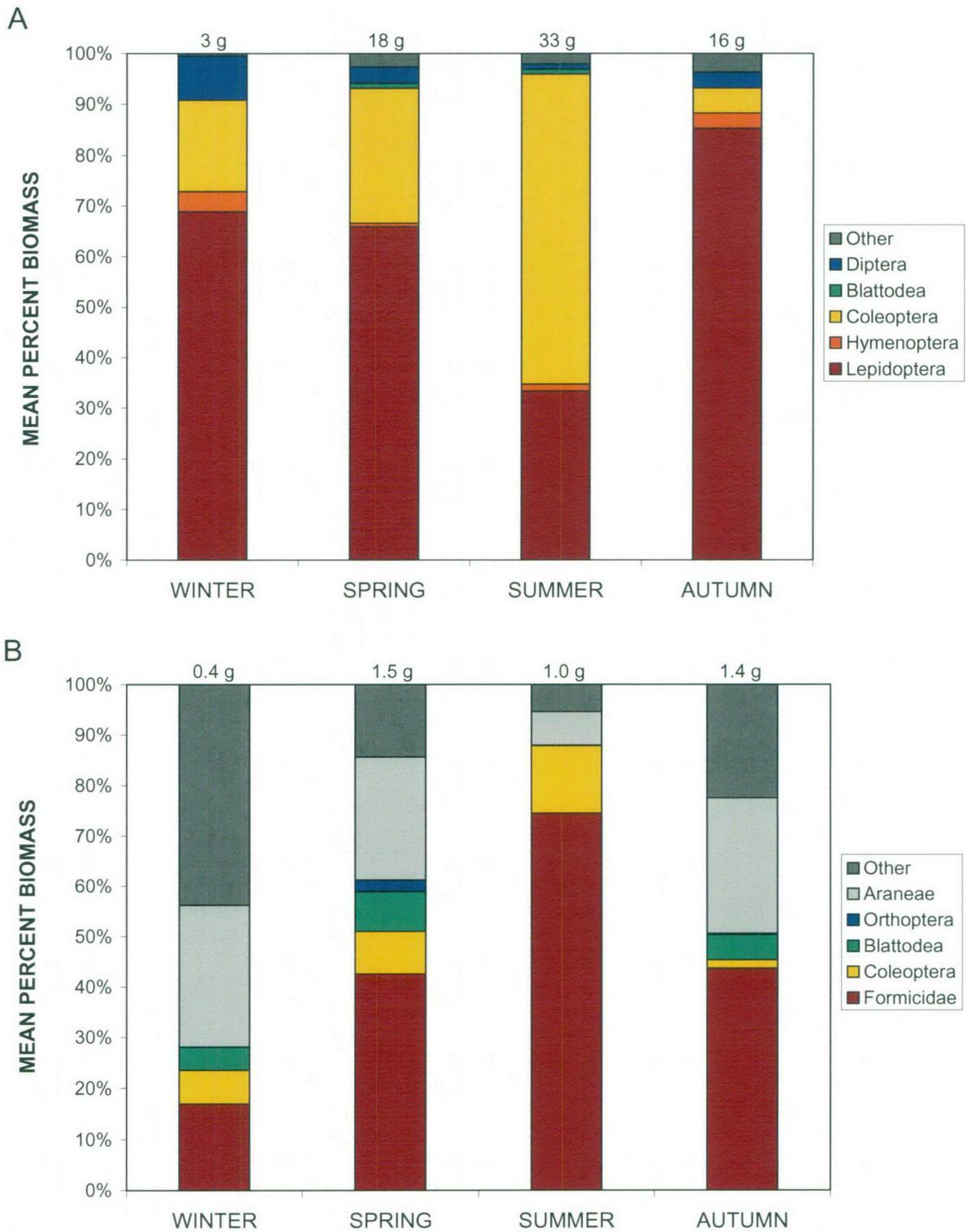
**Figure 6:** The mean ratio of aerial-to-terrestrial arthropod biomass (g) as a function of A) location and sampling year; and B) season at the eucalypt woodland (EW) site. The aerial-to-terrestrial biomass ratio did not differ significantly between locations or years sampled for the irrigated desert (ID), desert (D) and the eucalypt woodland during winter (EW-W) and summer (EW-S) (Kruskal-Wallis ANOVA:  $H_5=4.57$ ,  $P=0.47$ ) or between seasons in EW (ANOVA:  $F_{3,14}=1.32$ ,  $P=0.32$ ).



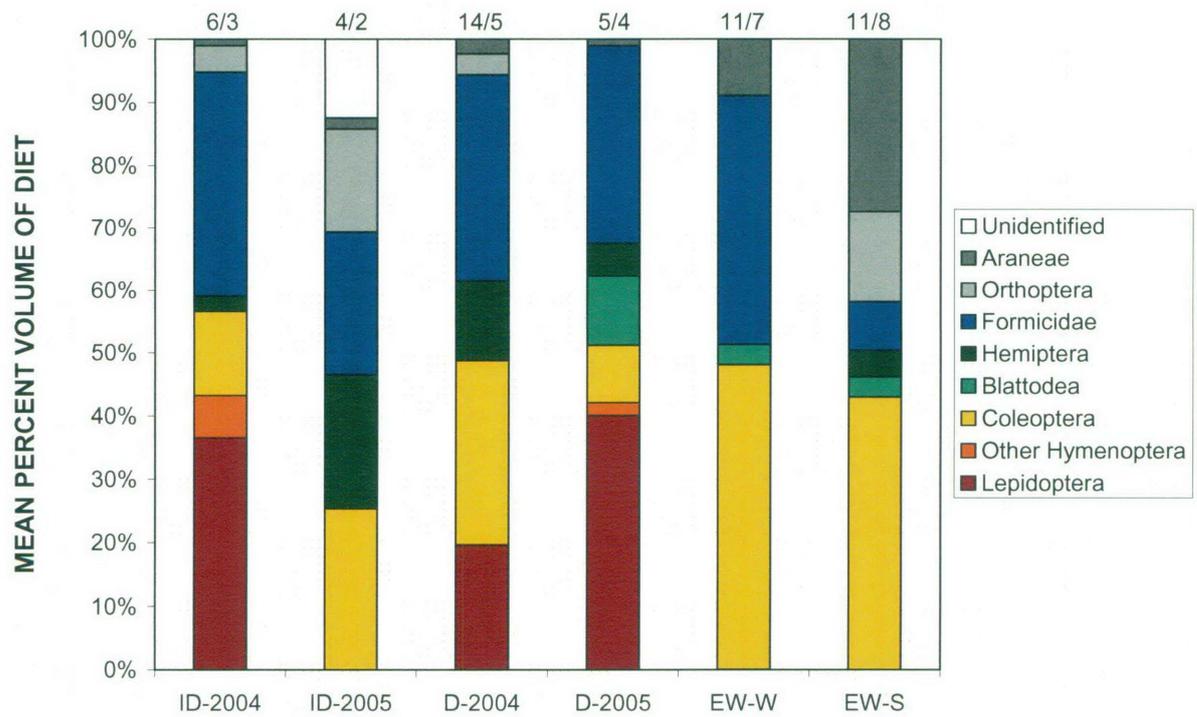
**Figure 7:** Arthropod availability in light traps based on A) the mean percent of trap biomass and B) the total number of arthropods, for the irrigated desert site (ID-2004, ID-2005), desert (D-2004, D-2005), and the eucalypt woodland in summer (EW-S) and winter (EW-W). The total biomass or total number of arthropods collected is at the top of each bar. Number of light trap nights: ID-2004 = 9, ID-2005 = 9, D-2004 = 9, D-2005 = 13, EW-W = 8, EW-S = 6. Winter is defined as June-September and summer as November-February to match the collection of diet samples.



**Figure 8:** Arthropod availability in pitfall traps based on A) the mean percent of trap biomass and B) the total number of arthropods, for the irrigated desert site (ID-2004, ID-2005), the desert site (D-2004, D-2005), and the eucalypt woodland in summer (EW-S) and winter (EW-W). The total biomass or total number of arthropods collected is at the top of each bar. Number of trap nights: ID-2004 = 576, ID-2005 = 216, D-2004 = 576, D-2005 = 504, EW-W = 336, EW-S = 144. Winter is defined as June-September and summer as November-February to match the collection of diet samples.

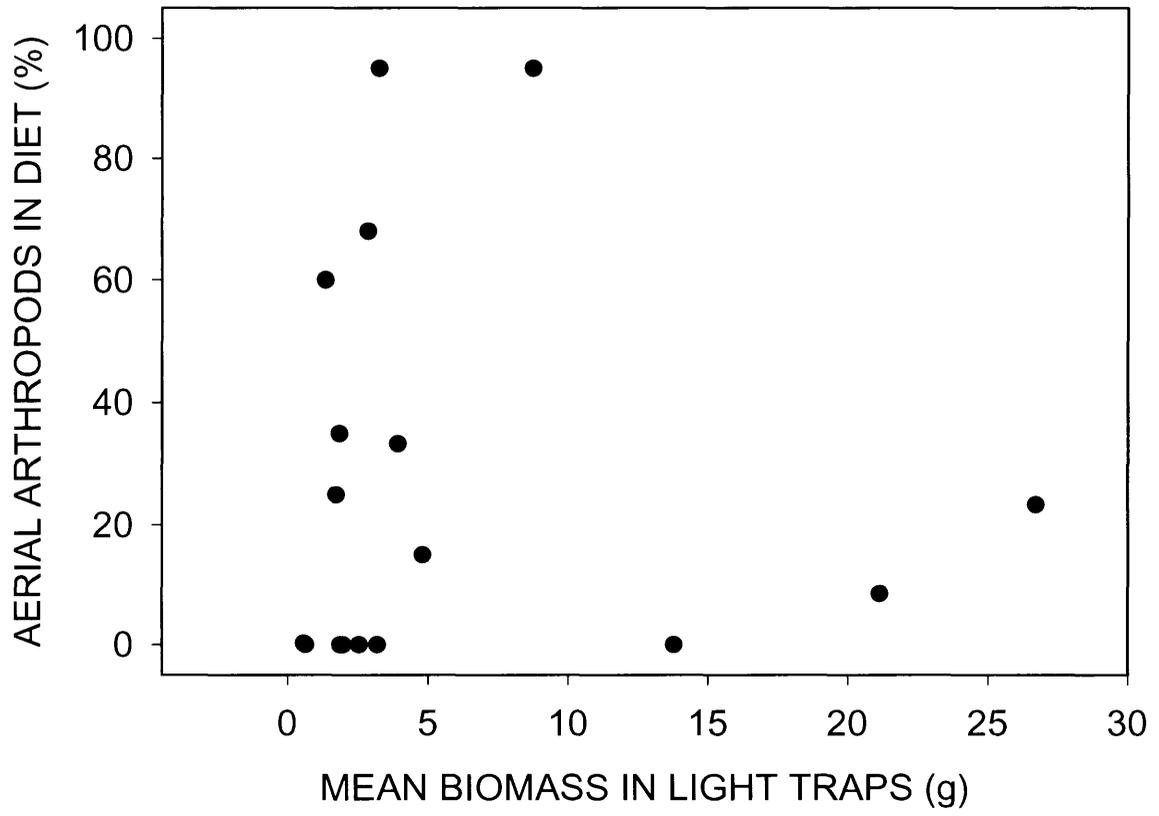


**Figure 9:** Arthropod availability based on the mean percent biomass of A) aerial arthropods in light traps and B) terrestrial arthropods in pitfall traps for each season at the eucalypt woodland (EW) site. The total biomass of arthropods collected is at the top of each bar. The ‘Other’ category includes millipedes and centipedes. Number of light trap nights: summer = 4, spring, winter, and autumn = 6; Number of pitfall trap nights: summer = 96, spring, winter, and autumn = 144. Seasons include data only for the appropriate months (i.e. winter = June-August), thus values for summer and winter may differ slightly from Figures 7 and 8.

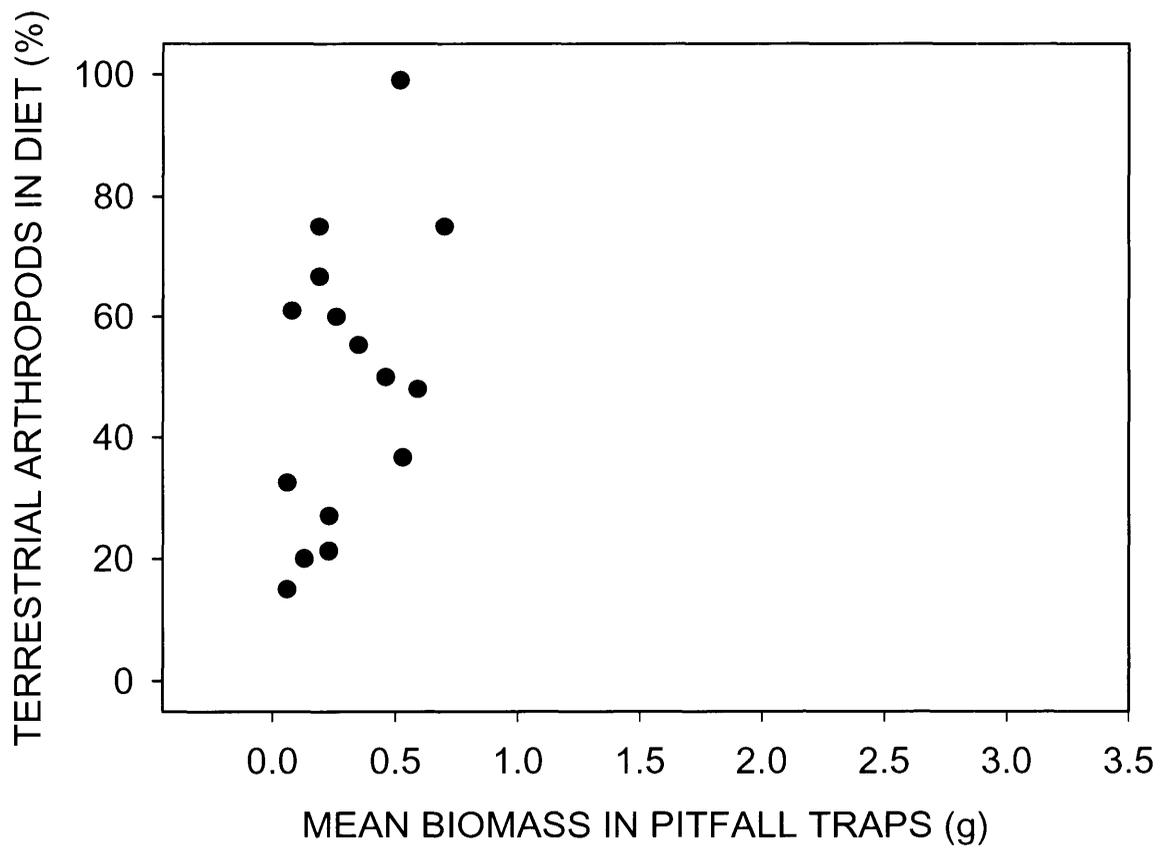


**Figure 10:** Mean percent volume of arthropod orders in owlet-nightjar faecal samples for the irrigated desert site (ID-2004, ID-2005), desert (D-2004, D-2005), and the eucalypt woodland in summer (EW-S) and winter (EW-W). The numbers of pellets / number of individual birds from which pellets were obtained for each site and sampling period are given above the bars.

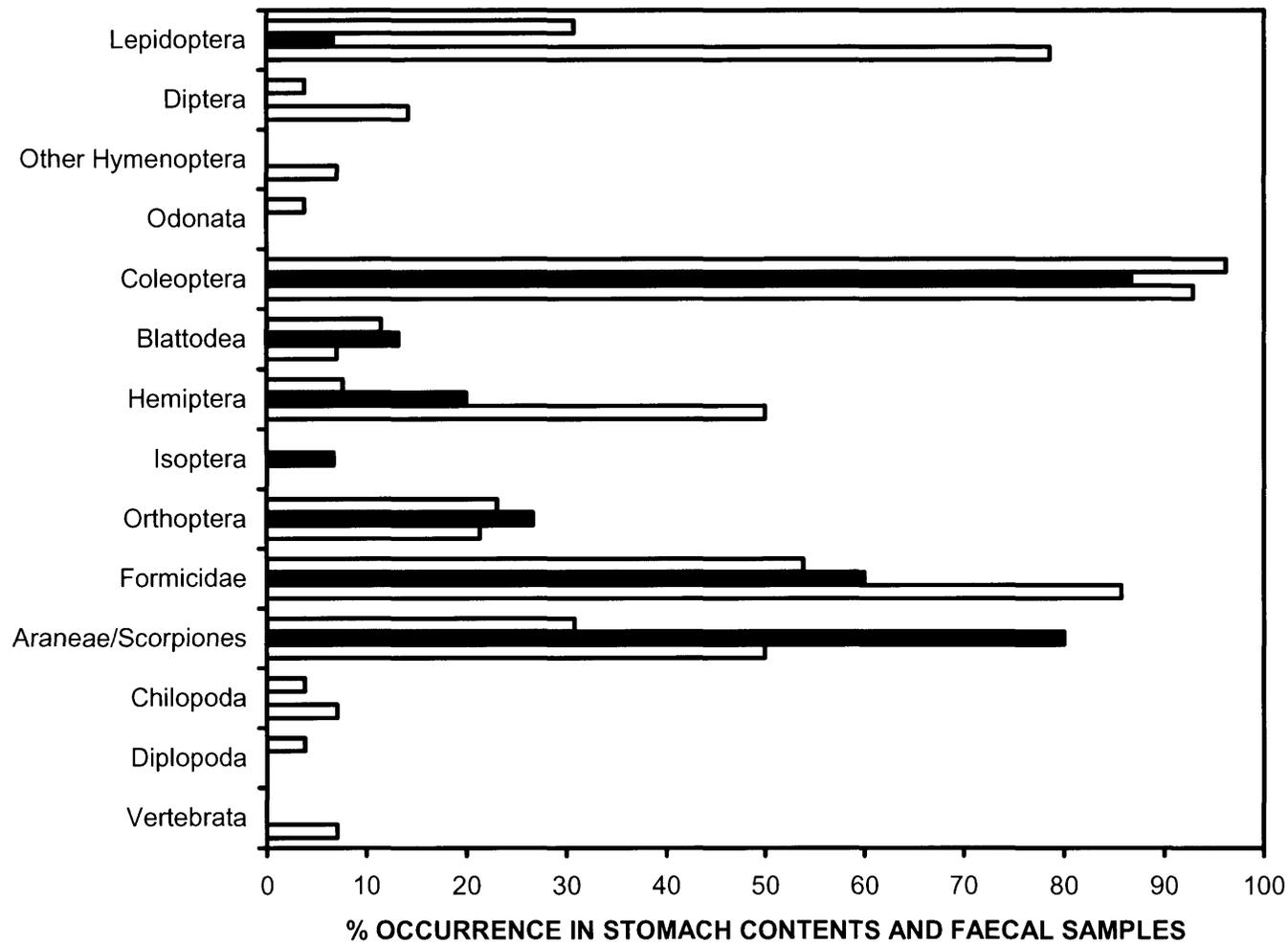
A



B



**Figure 11:** Comparison of owlet-nightjar diet (% volume) to availability for aerial (A) and terrestrial (B) arthropods. A) Spearman rank correlation indicated no significant relationship between the mean biomass in light traps (g) and volume of aerial arthropods in the diet ( $p_s=0.14$ ,  $P=0.59$ ,  $N=17$ ). Each point represents the monthly mean of light trap catches per site compared to the mean volume of the aerial content (Lepidoptera and Other Hymenoptera) in faecal samples from that site during that particular month. B) Spearman rank correlation showed no significant relationship between the mean biomass in pitfall traps (g) and the volume of terrestrial arthropods in the diet ( $p_s=0.07$ ,  $P=0.78$ ,  $N=20$ ). Each point represents the monthly mean of total pitfall biomass collected per plot at each site compared to the mean of the terrestrial content (Formicidae, Aranea/Scorpions, Hemiptera, Orthoptera) in faecal samples from that site during that particular month. Removal of mean pitfall trap biomasses  $>1.0$  g (grey circles) did not change the insignificant correlation between pitfall trap biomass and the percentage of terrestrial arthropods in the diet ( $p_s=0.39$ ,  $P=0.14$ ,  $N=15$ ). Linear regression equation: Terrestrial Arthropods in Diet (%) =  $33.57 + 52.16$  (Pitfall Biomass),  $P=0.09$ ,  $R^2=0.20$ ).



**Figure 12:** Occurrence (%) of prey items by order in owlet-nightjar stomachs based on data from the literature (grey bars, n=26) and in faecal samples from individual owlet-nightjars in the eucalypt woodland (black bars, n=15) and desert habitats (irrigated and non-irrigated combined, white bars, n=14) in the current study.

A



B



C



**Plate 1:** Three habitats where arthropods were sampled at the desert site (Ormiston Gorge). A) Plot 1: Edge of creek bed with an under-storey of mixed grasses and an upper-storey of tall river red gums (*Eucalyptus camaldulensis*); B) Plot 2: Sand area with mulga shrubs (*Acacia aneura*); and C) Plot 3: Mallee (*Eucalyptus socialis*) with an under-storey of spinifex grasses (*Triodia brizoides*, *T. longiceps*), rock substrate. Photos by L. I. Doucette.

A



B



C

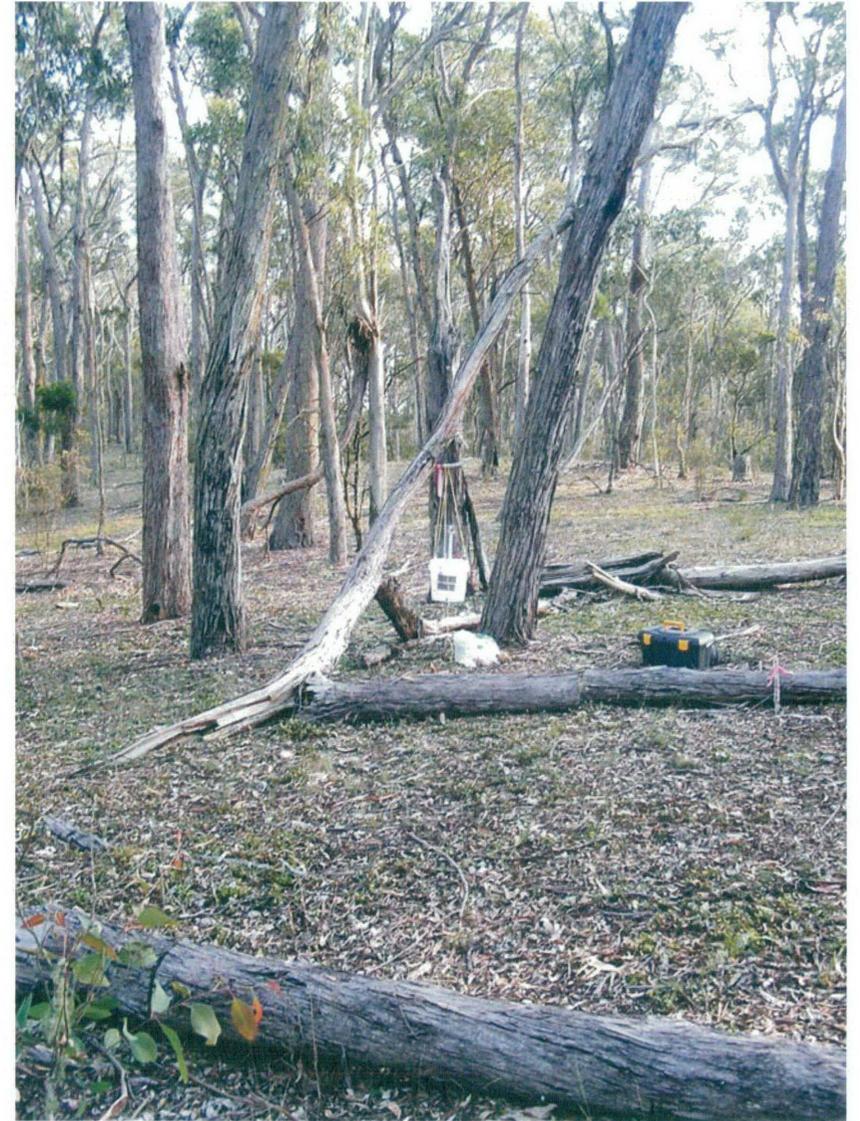


**Plate 2:** Three habitats where arthropods were sampled at the irrigated desert site (Alice Springs Desert Park). A) Plot 1: Rocky substrate with mulga shrubs (*Acacia aneura*) of different ages; B) Plot 2: Similar to Site 1, sandy and rocky substrate with mulga shrubs (*A. aneura*) but more open; and C) Plot 3: *A. aneura* upper-storey with a dense under-storey of invasive buffel grass (*Cenchrus ciliaris*). Plots 1 and 2 were irrigated once a fortnight, and plot 3 was not irrigated or weed controlled. Photos by L. I. Doucette.

A

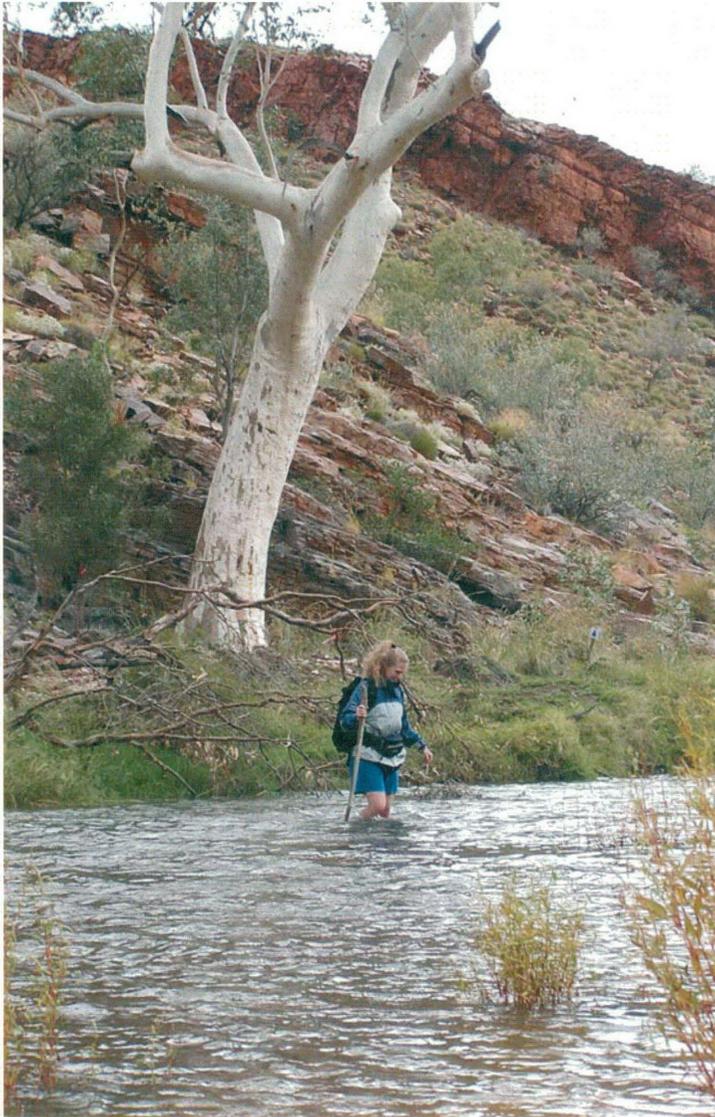


B

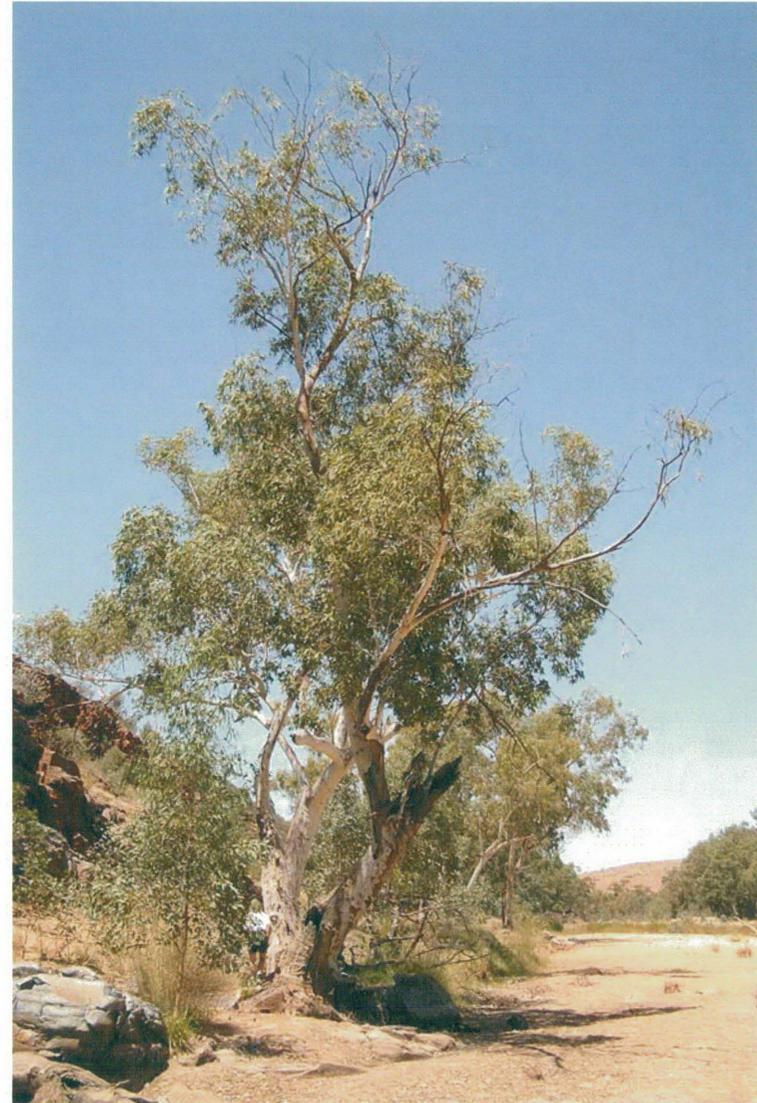


**Plate 3:** Two habitats where arthropods were sampled at the eucalypt woodland site (Imbota Nature Reserve). A) Plot 1: *Eucalyptus sp.* woodland with an open understorey and a ground cover of mixed grasses; B) Plot 2: Similar to plot 1, but on higher ground with a ground cover of leaf litter. The light trap is suspended from a tree in the centre of the photo. Photos by L. I. Doucette.

A



B



**Plate 4:** Ormiston Creek at the desert site flooded during May-June 2004 (A) but is typically dry, as it was throughout winter 2005 (B). Photos by F. Harvey.

A



B



**Plate 5:** The permanent waterhole at the desert site (Ormiston Gorge) in winter 2004 (A) and winter 2005 (B). Coloured arrows mark features for comparison in the two photos. Photos by L. I. Doucette.



**Plate 6:** Despite the aridity in central Australia, insect abundance can be high. This photo was taken in Alice Springs on 19 August 2004 (minimum  $T_a = -0.3$  °C), the beginning of several weeks of high Lepidoptera abundance. A trend for increased Lepidopteran abundance occurred in mid-August during both 2004 and 2005 irrespective of differences in rainfall between years. Photo by L. I. Doucette.



**Plate 7:** An Australian owlet-nightjar captured in a small mammal pitfall trap at Kinchega National Park, western New South Wales (32°30'S, 142°20'E). Pitfall trap catches of owlet-nightjars provides further evidence for ground foraging. Photo by L. Warnecke.

## Discussion

As I predicted, lower arthropod abundance as found at the eucalypt woodland site resulted in owlet-nightjars increasing the number of terrestrial prey items in their diet. However, understanding prey selection by owlet-nightjars is not simple. I found no relationship between diet and arthropod availability. Even when Lepidoptera represented more than 90% of the available biomass, one third of the diet of owlet-nightjars was Formicidae. In a habitat with cold winter  $T_{as}$  and a very low biomass of active nocturnal arthropods, owlet-nightjars ignored Lepidoptera altogether, despite them representing more than 70% of the available biomass. Given that diets are dominated by Formicidae and Coleoptera, owlet-nightjars forage more on terrestrial prey, irrespective of habitat or season, than previously considered. While it is likely that optimal foraging and the ease of capture of different taxa play a major role in determining the diet of owlet-nightjars, habitat structure and predation risk are also likely to be factors explaining the dominance of terrestrial prey in the diet.

### *Prey Availability*

The biomasses of both aerial and terrestrial arthropods sampled at the desert sites were much higher than expected in a semi-arid habitat during winter, in most cases even exceeding biomass at the eucalypt woodland site in summer. The mean biomass of aerial arthropods at the desert site ( $6.4 \text{ g trap night}^{-1}$ ) was five times that collected during winter in the eucalypt woodland ( $1.25 \text{ g trap night}^{-1}$ ) and values for the irrigated desert site ( $60 \text{ g trap night}^{-1}$ ) were, astoundingly, 48 times greater (Figure 3 and 7). Large biomasses of aerial arthropods in the arid zone are due to masses of Lepidopterans, which occurred in late winter at both our desert sites during 2004 and 2005 (Plate 6). Results from other studies suggest that a moth “plague” is common in arid and semi-arid regions in late winter. Gilfillan (2001) found that arthropod biomass at Ormiston Gorge (my desert site) was greatest in July and August due to the high proportion of Lepidoptera in pitfall traps. Similarly, in an arid region in south-eastern NSW (Fowler’s Gap Station,  $31^{\circ}05'S$ ,  $141^{\circ}45'E$ ), Read (1987) sampled using light traps and reported a “plague” of Noctuidae (moths) in August. Drake & Farrow (1985) report details of an early spring migration of Lepidoptera in inland New South Wales followed by a major caterpillar plague. I witnessed a similar event at the irrigated desert site in early spring 2004. This migration is apparently an almost regular feature of the population dynamics of several moth species and is attributed to the erratic rainfall in inland Australia (Drake & Farrow, 1985).

Differences in terrestrial arthropod abundance were less extreme, but biomass and abundance was still much higher at the desert sites than in the eucalypt woodland during winter. The irrigated desert site ( $0.018 \text{ g trap night}^{-1}$ ) had six times and the desert site ( $0.008 \text{ g trap night}^{-1}$ ) almost three times the biomass of the eucalypt woodland site ( $0.003 \text{ g trap night}^{-1}$ ). However, these results are consistent with other studies. Gilfillan (2001) collected pitfall trap samples at Ormiston Gorge from September 1991 to February 1993. A direct comparison between the two studies is difficult as her traps were open for 24 h while mine were closed during the day. However, it is fair to compare results by order of magnitude. The biomass in her traps in July was nearly three times my results in 2004 and 40 times that of 2005. Pitfall biomass during the other winter months (Gilfillan, 2001) were comparable to my results at the desert site in 2004 ( $\sim 0.02 \text{ g trap}^{-1} \text{ night/day}^{-1}$ ), and eight times mine in 2005 ( $0.02 \text{ vs. } 0.0025 \text{ g trap}^{-1} \text{ night/day}^{-1}$ ). Thus, a relatively high arthropod biomass in this semi-arid region during winter is a regular rather than an unusual occurrence. Similar levels of arthropod biomass occurred in the arid habitat of Fowler's Gap Station. Morton (1978) collected higher winter biomass in pitfall traps ( $\sim 0.05 \text{ g trap}^{-1} \text{ day}^{-1}$ ) than either Gilfillan (2001) or I did in central Australia. Morton's (1978)'s values are 25 times the biomass I found in the eucalypt woodland in winter ( $0.002 \text{ g trap}^{-1} \text{ day}^{-1}$ ) and 5 times the summer values ( $0.01 \text{ g trap}^{-1} \text{ day}^{-1}$ ).

While the arthropod biomass at the eucalypt woodland site was unexpectedly much lower than in the desert, especially the summer samples, the abundance values are reasonable in light of another study in the same region. Lowman (1982) used light traps to sample arthropod abundance from September 1979 to February 1981 in New England National Park on the Northern Tablelands, about 40 km south of my study site and at a similar altitude (1200 m). Mean numbers of aerial arthropods collected per trap night in Lowman's (1982) study were 245 and 300 during winter and summer, respectively. My mean arthropod numbers per light trap night were 182 for winter and 551 for summer (Figure 7b). Thus, our winter values were similar and my summer values were almost double.

Gilfillan (2001) performed multiple regression analysis using climatic variables at the desert site, including rainfall during and one month prior to the pitfall sampling dates and minimum and maximum  $T_a$  on the sampling dates. She found no significant relationships. In contrast I found that aerial and terrestrial biomass were both strongly and equally influenced by  $T_a$  (Figure 5), resulting in similar aerial-to-terrestrial ratios between sites (Figure 6). This contradicts the suggestion that aerial prey is more susceptible to low  $T_a$  than terrestrial prey (King, 1974). It is likely that moderate to high daytime  $T_a$  in the desert, resulting in warmer

evenings and consequently increased arthropod activity, further contributes to the higher biomass compared to the eucalypt woodland site. Total biomass in the eucalypt woodland site was low throughout the year. Aerial arthropod biomass varied the most seasonally, with summer abundance being 10 times higher than winter. Terrestrial arthropod biomass varied less with season.

In contrast to patterns in tropical regions which experience clearly defined wet and dry seasons (Rautenbach et al., 1988; Pouline et al., 1992), aerial arthropod abundance was unaffected by moisture levels in the desert. Higher rainfall, flowing creeks, and standing pools in 2004 were not correlated with increased biomass of aerial arthropods at the desert site, although there was an increased abundance of Trichoptera. Aerial biomass did not exhibit a substantial increase at any site for 2004 and 2005 until  $T_a$  increased in September, despite heavy rains in May 2004 and moderate rainfall in late June-early July 2005. With the exception of the peak in Lepidoptera in September 2005, there was even little difference in aerial arthropod biomass between the irrigated and non-irrigated desert habitats.

Terrestrial arthropod biomass was more strongly related to increased moisture through rainfall or irrigation. The early rainfall in May 2004 and flowing rivers at the desert site likely contributed to the peak in biomass during July 2004. Similarly, the low rainfall and absence of flowing water in 2005 was correlated with a significant decrease in biomass. This decreased abundance in 2005 was not seen at the irrigated desert, where moisture levels were more constant between years.

The lack of difference in biomass between plots within the desert sites further supports the relationship between  $T_a$  and arthropod biomass. The plot habitats at the desert site were quite different in terms of vegetation and in their proximity to the flowing creek, yet in 2004 there was no difference in either aerial or terrestrial abundance (Table 1). Likewise, despite one plot (plot 3) at the irrigated desert site being at least 200 m from an irrigated area, arthropod abundance was no lower than at the two irrigated plots. The consistency in  $T_a$  across all plots at each site, and the lack of influence of moisture on aerial arthropods, may explain the similarities.

Compared to the influence of  $T_a$  on light trap catches, the effect of the lunar cycle was insignificant. In detailed investigations of weather factors on light trap performance, Muirhead-Thomson (1991) found  $T_a$  and wind speed had a greater effect on catches than lunar

cycle (but see Bowden & Church, 1973). Light traps were ideal for catching large numbers of nocturnal arthropods to allow comparison between sites. My preliminary trials with sticky traps caught too few aerial arthropods to make useful comparisons. I used the same trap type at all sites in my study to ensure valid comparisons. Pitfall traps also appear to represent a valid way to sample terrestrial arthropods. All arthropod taxa in owlet-nightjar diet were represented in light or pitfall trap samples.

### ***Diet and Prey Selection***

There has been criticism of faecal analysis to assess diet as being biased toward hard bodied insects, suggesting that some arthropod parts are more easily recognizable, and soft-bodied prey items may not appear in the samples (Morton, 1978; Schulz, 1988). However, soft prey items, such as Lepidoptera larvae, occurred in faecal samples in the current study and Oligochaeta (earthworms) were found in the faecal samples of the mountain owlet-nightjar (*Aegotheles albertisi*; Schulz, 1988). Thus, at least some soft prey items are detectable in owlet-nightjar faeces. Another criticism of the method is that some prey are likely dismembered before being eaten, and thus legs and mouthparts may not appear in the faeces (Morton, 1978). This would not be an issue for nightjars, as all species studied to date eat prey live and whole (Holyoak, 2001; Jackson, 2003c). So while it is possible that some minor prey items or types were not detectable, this would not affect the between habitat comparison and final conclusions. There is no evidence in the literature to suggest that owlet-nightjars regurgitate undigested material as pellets (Holyoak, 2001), and I found no evidence of pellet production during my research. No pellets were found near roosts and birds held in the laboratory overnight were never found to regurgitate pellets.

Unexpectedly, I found that the major constituents of owlet-nightjar diets, irrespective of habitat, consist of terrestrial arthropods. All Formicidae, which formed the major portion of the owlet-nightjar diet overall (Table 2), were of the worker caste and incapable of flight, and from genera that primarily forage and nest on the ground (Shattuck, 1999). The two most common genera found in the diet of desert birds have relatively large body sizes (*Polyrachis* 5-10 mm; *Camponotus* 2.5 to 14 mm; Shattuck, 1999). *Myrmecia*, the dominant genus in the woodland samples, are also large ants, with the smallest species >6 mm in length. Nonetheless, the small size of ants indicates that owlet-nightjars may be actively searching the ground for prey as opposed to simply employing perch-and-pounce tactics. Owlet-nightjars would have to consume a large number (1504 to 3784) of the worker caste Formicidae, to support their daily energy requirements (Table 4). However, Formicidae are capable of

tolerating a wide range of  $T_a$ s (Andersen, 1983), and some genera, including *Polyrachis*, are primarily nocturnal in arid areas (Shattuck, 1999). Thus, they may represent the most reliable food source for owlet-nightjars throughout their range. The larger size of terrestrial Formicidae in the eucalypt woodland did not lead to an increase in their ratio in the diet.

The other terrestrial taxon that formed a major component of the eucalypt woodland diet was the Araneae (spiders). Araneae were the most available taxon in the eucalypt woodland during winter, yet spiders were consumed in greater proportion by owlet-nightjars in summer. Arachnids can tolerate a remarkably wide range of  $T_a$ s (-1 to +48 °C; Schmalhofer & Casey, 1999; Punzo et al., 2007), and thus are active throughout the winter months in cold habitats. Common house spiders (*Achaearanea tepidariorum*) can actively spin webs at 5 °C (Barghusen et al., 1997), but most species prefer  $T_a > 11$  °C for hunting (Schmalhofer & Casey, 1999). The presence of active arachnids at low  $T_a$  makes them a viable food source in winter. Furthermore, venom synthesis in some species ceases at  $T_a < 15$  °C (Vapenik & Nentwig, 2000), thus they should be more likely to be consumed by predators in colder months. Yet they figured most prominently in the summer woodland diet (27%) and comprised less than 9% of any winter owlet-nightjar diet, despite there being a large number of arachnids available during winter (Figure 8). It is possible that my sampling methods underestimated the abundance of arachnids during summer. Web building behaviour, which greatly increases in summer, and the semi-aerial existence of some species, would make them less susceptible to pitfall traps. It is also possible that owlet-nightjars capture orb spiders from their webs in summer using aerial foraging tactics.

Hemiptera and Orthoptera, although not major components of the diet, were consumed in greater proportions than their availability. This suggests that they may be a preferred, if sporadically available and patchy, food source. Hemiptera were found in such low abundance (<1%) in pitfall traps that they were combined with 'others' for analysis. Hemiptera made up to 3% of the volume of light traps at some sites. All Hemiptera found in the diet were terrestrial (Pentatomidae) or plant hoppers (Auchenorrhyncha), suggesting the possibility that owlet-nightjars may occasionally obtain prey by gleaning arthropods off foliage. Orthoptera were found in the diet at all but the driest (D-2005) and coldest (EW-W) sites, despite only being recorded in pitfalls at three sites. Orthoptera are large, with the highest energy content of any taxa I sampled (Table 4), thus relatively few individuals would be needed to fill owlet-nightjar daily energy requirements. Acrididae (locusts) typically increase in abundance in the arid zone after rainfall (Zborowski & Storey, 1995), such as in the desert in 2004.

Several orders of arthropods can be considered aerial in that they regularly use long flights for locomotion. These include the Lepidoptera, Hymenoptera (excluding worker caste Formicidae), Diptera and Coleoptera. Diptera were conspicuously absent from owlet-nightjar diets in my study, despite individuals >3 mm in length being available in large numbers (Figure 7b). Their small size may be below the threshold of detection by owlet-nightjars (see Brigham & Barclay, 1995). Lepidoptera and Coleoptera were the only potential aerial taxa that comprised major portions of the owlet-nightjar diet in my study. The extent to which owlet-nightjars catch these taxa using aerial versus terrestrial foraging techniques relies heavily on the issue of arthropod activity levels and flight capabilities at low  $T_a$ s.

The main difference in diet between habitats was the exclusion of Lepidoptera in the owlet-nightjar diet in the eucalypt woodlands, despite their representing an abundant food resource (Figure 7). While the abundance of Lepidoptera greatly increased in late winter, they were found in the desert bird's diet from May to September. The absence of Lepidoptera from the diet of the two birds in the irrigated desert in 2005 is potentially explained by the small sample size, with all four faecal samples obtained during a short period in early-August when  $T_a$  was quite low (mean minimum 1.8 °C). Brigham (1990) found that common nighthawks (*Chordeiles minor*), an obligate aerial predator, significantly avoided eating moths on several nights sampled. Generally, ectothermic arthropods require warm  $T_a$ s (>14 °C) for flight (Taylor, 1963). However, in controlled experiments investigating the effect of  $T_a$  on insect flight, Taylor (1963) found Lepidoptera in suction trap catches at 5 °C. Some species of Lepidoptera can increase body temperatures through thoracic contractions and can initiate flight at  $T_a$ s as low as 11 °C (Casey, 1981; Casey & Joos, 1983), but others require  $T_a$ >15 °C for flight initiation (Cox et al., 2007). Once flight has commenced, Lepidoptera produce their own heat through thoracic conductance allowing them to remain active as  $T_a$  drops. Thoracic temperatures and the  $T_a$  at which moths are active differs among species and are related to body size, with larger moths able to be active at lower  $T_a$ s (Casey, 1981; Casey & Joos, 1983). The Lepidoptera captured at the desert were on average twice the size as those the eucalypt woodland (Table 4). Furthermore, many species of desert moths captured in winter were heavily 'furred' on the thorax and legs, enabling them to tolerate colder  $T_a$ s (Casey, 1981). These two features suggest that desert moths are more likely to be active at low winter  $T_a$ s compared to woodland moths. Additionally, Lepidoptera would be sought after by desert birds due to their high water content (74%), which is 12% higher than the average Coleoptera (Bell, 1990), and would be an important resource in the desert. The larger size of moths in the

desert makes them the most profitable prey available, apart from the rare large Blattodea. In contrast, Coleoptera, Blattodea, and Araneae at the woodland site all provide more energy return per individual than Lepidoptera (Table 4). Aerial foraging is an energetically demanding foraging technique (Goldstein, 1990). If owlet-nightjars are able to obtain energy-rich prey items through the less energy demanding perch-and-pounce or ground foraging techniques (Goldstein, 1990; Bryant, 1997), it would be feasible to do so. This implies that owlet-nightjars obtain Coleoptera off the ground rather than by aerial foraging.

My analyses of catches of Coleoptera in light and pitfall trap samples were unable to resolve the question as to whether owlet-nightjars were catching Coleoptera on the ground or on the wing. In Taylor's (1963) experiments, Coleoptera were never caught at  $T_a < 12$  °C and no flight occurrences of beetles were observed below 13 °C. Thus, in the eucalypt woodland during winter, when daytime  $T_a$  rarely exceeded 12 °C and nighttime  $T_a$  typically dropped below 0 °C I assume that most Coleoptera are captured on the ground. However, the mean proportion of Coleoptera in light trap catches at this time was 13%, indicating that some individuals or species must be capable of some short flights, likely during early evening when  $T_a$  is higher. However, summer catches of Coleopterans at the same site represented 65% of the total biomass. Others have noted major increases in Coleoptera biomass in light traps during summer, some reporting 'plagues' of beetles (Read, 1987). Warmer daytime  $T_a$ s in the desert result in a period during early evening when Coleoptera may be caught during aerial foraging, yet they comprised <10% of the biomass in light trap at these sites, indicating they are low in abundance in the desert habitats. The proportion of Coleoptera in the diet at all desert sites was greater than what was available in light or pitfall traps (<7%), implying that they are a preferred prey item, likely due to their large size and high energy content (Table 4).

Coleoptera appear to be the primary prey of Aegothelidae and, more broadly, Caprimulgiformes. Coleoptera occurred in the stomach contents of >90% of road-killed owlet-nightjars (Barnard, 1914; White, 1917; Lea & Gray, 1935; Serventy, 1936; Gray, 1938; Rix, 1943; Webb, 1989; Rose, 1973; Rose, 1997; Jones, 2004), and in faecal samples of 85% of the birds in my study (Figure 12). The diet of the mountain owlet-nightjar (*A. albertisi*) in Papua New Guinea was dominated by Coleoptera (Schulz, 1988), and Coleoptera were recorded in the stomach contents of the feline owlet-nightjar (*A. insignis*) and Wallace's owlet-nightjar (*A. wallacii*; Holyoak, 2001). Coleoptera represented 85% of the diet of Afrotropical caprimulgids (Jackson, 2000a), and large Coleoptera and Lepidoptera dominated

the diet of common poorwills (*Phalaenoptilus nuttallii*) and common nighthawks in North America (Csada et al., 1992; Bayne & Brigham, 1995; Todd et al., 1998).

As Caprimulgiformes are one of the few orders of birds known to use torpor regularly (McKechnie & Lovegrove, 2002), these birds may show a preference for Coleoptera as they have a high proportion of linoleic acid in their fat (22.3%), an unsaturated essential fatty acid (EFA) that may facilitate the use of torpor (Schalk & Brigham, 1995; Chapter 4). EFAs cannot be synthesized by animals, and must be acquired in the diet. Thus, a diet high in EFA allows for a lower body temperature during torpor and hence longer torpor bouts (Chapter 4), as the melting point of animal fat greatly decreases as the degree of fatty acid unsaturation increases (Geiser & Kenagy, 1987; Schalk & Brigham, 1995; Falkenstein et al., 2001; Munro & Thomas, 2004). Thus, the difference in diet may enhance the ability of owlet-nightjar in the colder woodland to enter deeper, longer torpor bouts and conserve a considerable amount of energy during winter (Chapter 4).

#### ***Observations of Foraging Behaviour***

Brigham et al. (1999) light-tagged six owlet-nightjars in Imbota Nature Reserve, the same eucalypt woodland as my study, and observed no instances of birds walking or foraging on the ground. Foraging attempts were exclusively sally-type from perches. However, all observations occurred during early spring and late summer when aerial arthropods are abundant and aerial foraging should be profitable. As I did not make direct observations of foraging behaviour, I can only infer activity based on diet data. However, it would seem that due to the large proportion of the owlet-nightjar diet that is composed exclusively of ground-dwelling species, especially in the woodland, a major part of the night must be spent foraging on the ground or pouncing from a perch. Perhaps the presence of several observers caused the birds to remain in trees and avoid the ground during the Brigham et al. (1999) study. Another possibility is that owlet-nightjars use aerial foraging earlier in the evening (when observations were made) and then switch to the more energetically conservative perch or ground hunting strategies during the remainder of the night (Neuweiller et al., 1987).

Due to darkness and the cryptic nature of owlet-nightjars, I rarely observed foraging attempts during >200 hours of tracking birds to assess home range in the eucalypt woodland (Chapter 7). On one occasion I did observe a bird hopping along the ground picking up prey items. Another indication that owlet-nightjars forage by hopping on the ground is they are occasionally caught in pitfall traps intended for small mammals (Plate 7; L. Warnecke; pers.

comm.; C. Cooper, pers. comm.; Davidge, 1979) or netted on the ground (F. Geiser & G. Körtner, personal comm.). Owlet-nightjars were more frequently observed to pounce on prey items from a perch (4 occasions), and once a bird landed within 2 m of my position to capture a small centipede on the ground. On one occasion I watched an owlet-nightjar exit its roost and perform an acrobatic maneuver in flight to snatch an arthropod from the air and on another, a bird veered from its flight path to pick an arthropod from the trunk of a tree. Others have reported observations of owlet-nightjars snatching prey from the ground and tree trunks, often without landing (Higgins, 1999). Thus, owlet-nightjars apparently employ a suite of behaviours to obtain prey. No direct observations of owlet-nightjars foraging in the desert were recorded despite >300 hours of tracking (Chapter 7). However, desert birds spent longer periods of time in a single location than birds in the woodland. Records up to two hours long of a bird remaining at one location, but changing heights regularly, were indicative of a bird flying from a tree to the ground and back, or sallying for aerial prey.

### ***Optimal Foraging in Two Diverse Habitats***

Based on the proportion of Lepidoptera in the diet and the likelihood that most Coleoptera consumed in winter were terrestrial, it is reasonable to conclude that terrestrial foraging is greater in the eucalypt woodlands than in the desert. In fact, the diet of woodland owlet-nightjars in winter could be composed entirely of terrestrial-caught arthropods. The lower level of aerial foraging at the eucalypt woodland site can be explained first, by the low availability of arthropods decreasing energy intake and influencing optimal foraging conditions, and secondly, by the physical restrictions on foraging imposed by constraints on visual acuity in shaded woodlands.

Colder winters at the eucalypt woodland site may mean that aerial prey are not available and active in enough abundance to be a viable foraging option. Aerial arthropod biomass was 10 fold greater in the desert compared to the eucalypt woodland, and birds relying on aerial nocturnal prey in the woodland would have few potential targets. I hypothesize that it would be more energetically feasible to spend time on the ground picking at small prey items than to use energy in bursts trying to capture rare aerial prey (Goldstein, 1990; Bryant, 1997). For example, the trailing and nesting behaviour of Formicidae make them reliable prey throughout the year, and longer winter nights provide more search time for small terrestrial prey to compensate for the lower rate of energy intake. Similarly, it would be more likely for birds to find beetles under leaves in the woodland while ground foraging than in flight.

There were substantial size differences between arthropods within orders in the desert and the eucalypt woodland. The largest and most profitable arthropod available in the woodland are Blattodea, however, these are relatively rare. The second best choice in terms of energy intake, are the Coleoptera, which formed the greatest proportion of the woodland diet. According to my trap catches, aerial Coleoptera were larger, and thus a more profitable resource than terrestrial Coleoptera, however this depends on their activity levels and the ease owlet-nightjars would have in locating, capturing and handling the prey. On average, Coleoptera in the woodland were twice the size of desert Coleoptera, and this may partially determine the habitat difference in diet. The mean size of Lepidoptera in the woodlands was half of that in the desert, meaning birds would have to consume twice as many moths to survive. Next to Blattodea, moths were energetically the best choice in the desert. Thus, the diet differences between the two habitats could be explained by birds selecting the largest and most profitable prey item. Other species of Caprimulgiformes select prey items based primarily on size rather than order (Todd et al., 1998). Of course, energy expended on foraging must be considered, and if abundant, prey that can be obtained using a less costly mode of foraging, such as perch-and-pounce, should be preferred.

Relative to other Caprimulgiformes, owlet-nightjars appear to be better adapted for terrestrial foraging. Their legs are long, making them far more agile on the ground than any of the frogmouths or caprimulgids (Schodde & Mason, 1980), better enabling them exploit terrestrial prey. Mountain owlet-nightjars also forage terrestrially, with faecal samples from three of 32 birds studied containing the remains of *Opisthopora* (earthworms; Schulz, 1988). If terrestrial foraging proved successful in times of food scarcity, the behaviour may be retained throughout the year in habitats where overhead cover reduced the risk of predation (see below). Another advantage of terrestrial foraging is that owlet-nightjars do not have to compete with bats, and thus exploit a unique niche amongst nocturnal birds. Tawny frogmouths (*Podargus strigoides*) also capture much of their food off the ground, including small vertebrates and large arthropods, using perch-and-pounce techniques, but they do not hop on the ground in search of food (Holyoak, 2001). Moreover, the ten-fold body-size difference and corresponding difference in prey size allows for the coexistence of tawny frogmouths and Australian owlet-nightjars over much of Australia (Holyoak, 2001).

Dark conditions due to increased tree density and canopy cover in the woodland would reduce the visual acuity of birds and make aerial foraging difficult. Most Caprimulgiformes rely on visual acuity for hunting and the aerial foraging activity of the Caprimulgidae appears to be

dependent on and constrained by vision (Brigham & Barclay, 1995). With the exception of moonlit nights, crepuscular feeding dominates among Caprimulgidae (Brigham & Fenton, 1991; Aldridge & Brigham, 1991; Brigham, 1992). Common nighthawks have been observed to make two foraging bouts daily, one at dusk and another at dawn, and actively pursue or 'hawk' insects (Brigham & Fenton, 1991). Afrotropical nightjars feed intensively at dusk followed by a less intensive period of dawn foraging (Jackson, 2003c). Jetz et al. (2003) suggested that nightjar foraging is confined to dusk and dawn due to both greater prey availability and visibility. Many species also adjust their foraging behaviour to the lunar cycle, foraging throughout the night when the moon is full (Mills, 1986; Brigham, 1992; Jackson, 2003c; Jetz et al., 2003). Others take advantage of the open canopy cover above roadways, which enables them to better see and catch flying insects backlit against the sky (Jackson, 2003b; Jackson, 2003c; Jackson, 2003a).

In contrast to other species of Caprimulgiformes (Aldridge & Brigham, 1991; Brigham & Fenton, 1991; Brigham, 1992; Jetz et al., 2003), owlet-nightjars wait until almost complete darkness before leaving their roosts (also see Brigham et al., 1999). The correspondence between roost departure times of owlet-nightjars and civil twilight, a period when only large objects are discernible to human eyes, was precise in both habitat types. Likewise, activity levels of owlet-nightjars on or near full moon nights is reduced (Brigham et al., 1999). Avoiding twilight foraging and reducing activity during full moon are likely behaviours that have evolved due to high levels of predation (Brigham et al., 1999; see below). Many nocturnal predators concentrate their hunting around dusk (Fenton et al., 1994; Jetz et al., 2003). Some species of Australian bats wait until civil twilight to exit their tree roosts to avoid this increased level of predation (Campbell et al., 2005).

The requirement of foraging only in darkness has two disadvantages. First, by waiting until twilight has passed owlet-nightjars miss the daily peak in aerial arthropod activity (Racey & Swift, 1985; Rautenbach et al., 1988). Thus, their options for prey selection are less, and in winter, when  $T_a$  drops quickly after dark, may mean a total absence of aerial prey. Second, darker conditions would greatly restrict the ability of owlet-nightjars to detect, and accurately hunt, aerial prey (Brigham & Barclay, 1995), and may necessitate the need for terrestrial foraging. Owlet-nightjars may be further disadvantaged in their ability to forage at low light levels by the apparent absence of tapetum lucidum behind the retina, which increases the sensitivity of the eye in other families of Caprimulgiformes (Rojas et al., 2004). The function of the highly reflective tapetum is to increase the chance that light will be intercepted by the

photoreceptors, and thus roughly doubles the chance that any light which enters the eye will be detected (Martin, 1990). It is unknown whether frogmouths and owlet-nightjars possess a tapetum, but the lack of eye shine in owlet-nightjars suggests that they do not. However, frogmouths and owlet-nightjars may have better binocular vision than other Caprimulgiformes, due to visual Wulst structure in the brain similar to owls (Iwaniuk & Wylie, 2006). This may make them more successful at detecting terrestrial prey active on the ground, leading to similar hunting tactics as many species of owls.

### ***Influence of Predation Risk on Foraging Decisions***

Many species alter their foraging behaviours in response to the risk of predation (Lima & Dill, 1990; Doucette et al., 2004; Guillemain et al., 2007). Despite the energy saved by relying on terrestrial foraging at times of prey scarcity, ground foraging may be employed less in the desert due to the exposed nature of the habitat and potentially increased risk of predation (Ford et al., 1990). Some species of birds that forage on the ground in open grassland choose foraging locations close to trees and forest edges to decrease the risk of avian predation, flushing to nearby trees when a potential predator approaches (Elchuk & Wiebe, 2002; Whittingham et al., 2006).

As stated above, predation rates on owlet-nightjars can be high (Brigham et al., 1999). In an earlier study at the same eucalypt woodland site, Brigham & Geiser (1997) reported that 57% to 86% of their tagged owlet-nightjars were depredated during the course of the study. Most were victims of avian predators. However, during my year long study, only 11% (2 birds) were depredated, both by owls. Predation rates vary from year-to-year and between habitats. In 2004, none of my tagged desert owlet-nightjars were depredated. However, in 2005, a dry season when food resources were low and predators aggressive, 57% of the birds were depredated by owls (1 bird) and feral cats (*Felis catus*; 3 birds) within a short period. All predation events in both studies occurred when the birds were foraging at night, and when predated by cats at least, on the ground. Other potential terrestrial predators of owlet-nightjars in the desert are large snakes (*Morelia spilota bredli*), goannas (*Varanus giganteus*) and dingoes (*Canis lupus dingo*). In the eucalypt woodlands foxes (*Vulpes vulpes*) and domestic dogs (*Canis lupus*) can be added to the list. Thus, a clear disadvantage to terrestrial foraging is an increased risk of predation. Increased canopy cover in the eucalypt woodland may provide cover from aerial predators (*Ninox novaeseelandiae* and *N. connivens*) and provide a place to flee from terrestrial predators. In contrast, open desert habitats leave owlet-nightjars exposed to aerial predators, and often with no place to flee. Thus, it would be prudent for them to

avoid terrestrial foraging in favour of sallying/hawking from high perches and perch-and-pounce techniques (Ford et al., 1990). Reducing foraging time by selecting larger prey items, such as Lepidoptera, would also decrease the exposure time to desert predators.

### ***Summary***

Ground foraging for terrestrial prey was more prevalent amongst owlet-nightjars than predicted, especially in the eucalypt woodland habitat. The diet of owlet-nightjars at this site was consistent seasonally, suggesting that ground foraging is a year-round adaptation to cope with relatively low arthropod availability. Even when Lepidoptera represented more than 90% of the available biomass, one third of the diet of owlet-nightjars consisted of Formicidae. Terrestrial foraging requires less energy than aerial prey capture (Goldstein, 1990), and may be the preferred method of foraging if adequate cover offering protection from predators is present. Furthermore, darker conditions and a complex aerial habitat due to denser canopy cover in the eucalypt woodland may place visual restrictions on aerial foraging. Most types of arthropods were readily consumed and the diet of owlet-nightjars was surprisingly diverse, including a high proportion of Formicidae and Arachnids.

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## CHAPTER 7

### Home Range Size and Territoriality of Australian Owlet-Nightjars: A Comparison between Habitats and Seasons

#### Abstract

Home range size is generally determined by the resources available within a specific area, such as those needed for foraging, mating, and raising young. While undefended home ranges are common amongst mammals, most species of birds defend territories. Cavity nesting birds may be more territorial than non-cavity users, as they need to defend an often limited resource from both avian and mammalian competitors. Sedentary Australian owlet-nightjars (*Aegotheles cristatus*) are one of the few species of Australian birds that roost in cavities year-round, and are thought to mate for life and maintain stable home ranges throughout the year. These factors would lead to the prediction that they should be highly territorial, yet nothing is known about their home range requirements or level of site fidelity. I used radio-telemetry and GPS to determine home range size in the semi-arid zone of central Australian and in the eucalypt woodlands on the Northern Tablelands of NSW. Thirteen owlet-nightjars were tracked during two winters in the arid zone and 14 individuals were tracked in the eucalypt woodlands throughout one calendar year. The mean home range in the eucalypt woodland was 17.7 ha based on the minimum convex polygon (MCP) method and 17.4 ha based on the fixed kernel contour (95%). The mean home range in the desert was 23.8 ha and 24.1 ha based on the MCP and kernel methods, respectively. With the exception of mated pairs (range overlap 41.9%), there was little overlap in home range areas (<13.0%), even in the densely populated woodland. Home range size did not differ significantly between sexes, seasons, or study sites, nor did it correlate with arthropod abundance by site or season. Owlet-nightjars showed high site fidelity, using the same home range throughout the year with a 68% overlap between seasons. The low percentage of home range overlap between individuals, high site fidelity and records of aggression suggest that this species is highly territorial, yet individuals live in close proximity to conspecifics. This information on the habitat requirements of owlet-nightjars will be useful for the management and conservation of this species, which is currently listed as vulnerable and 'in decline' in two Australian states.

## Introduction

An animal's home range is defined as "that area traversed by the individual in its normal activities of food gathering, mating, and caring for young" (Burt, 1943). While most species of mammals have a home range, in general they do not defend territories with the same energy shown by many species of birds. Furthermore mammal home ranges typically have a greater degree of overlap than those of birds (Nice, 1941). Territoriality is defined as the defence of an area by an animal from which other individuals are partially or totally excluded (Howard, 1920; Begon et al., 1996). To be considered territorial, a species must defend a physical space from other animals for at least part of its annual cycle. Many territorial species defend space only during the breeding season, becoming non-territorial occupants of a home range for most of the year. Another strategy is to defend a core area but use a much larger area for foraging. For example, many species of owls defend a territory around a breeding site, but hunt over a much wider home range (Martin, 1990). Not surprisingly, food based territories are generally much larger than breeding territories (Alcock, 1993).

The defense of any area requires the expenditure of time and energy for aggression and/or display, thus, in order to justify defending a territory, survival and/or reproductive success must be enhanced (Orians, 1971). Furthermore, the increased risk of predation due to more frequent vocalizations and conspicuous behaviour often associated with territorial behaviour increases the costs of territoriality. Thus, territoriality is only advantageous when there is a limited supply of potentially exhaustible resources, such as food or roosting/nesting sites. Cavity nesting birds have been hypothesized to be more territorial than non-cavity users, as they need to defend an often limited resource from both avian and mammalian competitors (von Haartman, 1957). In contrast, when resources, such as roosts or food supply, are abundant, territoriality may not occur (Gibbons & Lindenmayer, 2002). Territorial behaviour can be flexible, reflecting the balance between cost and benefits. For example, great tits (*Parus major*) abandon defense of their winter territories on cold days to save essential energy (Hinde, 1956).

There is a strong correlation between territory size, body mass, and diet in species of birds (Schoener, 1968). Territory size should be negatively correlated with food availability (Orians, 1971; Hixon, 1980), and territoriality is more common in species whose prey are distributed uniformly, as a patchily distributed food supply is usually not defensible (Brown, 1964; Gilfillan, 2001). Resources that rapidly change invite opportunistic use, not site-specific commitment. Thus, species should defend larger territories where food resources are lower

and predictable (Cody, 1985), as animals need to occupy an area large enough to obtain adequate food to meet their energy requirements (Gilfillan, 2001). Territory size also depends on the density of competitors for the available space (Brown, 1964; Hixon, 1980), and may become smaller in years with denser populations (Pitelka, 1959). The interaction between energetics and competition should generate territories with sufficient resources to support a resident pair (Gorrell et al., 2005). Declining resources should necessitate an increase in territory size. However, pairs in densely populated areas may not be able to gain access to additional resources by expanding their territories due to the presence of interspecific neighbors in close proximity (Caccamise, 1974).

There has been considerable discussion about how to define the conditions in which the home range of a bird can be considered a territory (see Schoener, 1968). Most definitions are behavioural and define a territory as a defended area (Howard, 1920; Nobel, 1939). However, I agree with suggestions by Pitelka (1959) that territory be defined by the degree to which a home range is used exclusively by its occupant or pair of occupants. This places emphasis on the degree to which habitat is partitioned amongst the members of a population (Pitelka, 1959), and enables an objective quantification of a territory (Schoener, 1968). Relying on the intensity and duration of behaviours to define a territory is biased and makes it difficult to interpret the degree of territoriality between species (Schoener, 1968). According to Pitelka's (1959) definition, a species would be more or less territorial according to the percent overlap of the home ranges of its individuals or pairs.

Another important aspect in quantitatively defining a home range or territory is to examine site fidelity, defined as the tendency of an animal either to return to an area previously occupied, or to remain within the same area for an extended period of time (Spencer et al., 1990; White & Garrott, 1990). Non-migratory avian species tend to show greater specific site fidelity, while migratory species may show fidelity to seasonal ranges, but not specific sites (White & Garrott, 1990). It is advantageous for individuals to confine activities to a more or less permanent area because the best foraging sites and refuges become familiar. Thus, it is common for non-migratory species to vigorously defend year-long territories. For example, long-term pair bonds, often on year-long territories, are common among tropical insectivorous passerines, which have stable territory boundaries (Gorrell et al., 2005).

Virtually nothing is known about home range or territory size of owl-nightjars (Aegothelidae). Mountain owl-nightjars (*Aegotheles albertisi*) have been described as

solitary, while Moluccan owlet-nightjars (*A. crinifrons*) have been observed, singly, in pairs and occasionally in groups (Holyoak, 2001). It has been suggested that Australian owlet-nightjars (*A. cristatus*) are permanently territorial and solitary (Schodde & Mason, 1980), however, there are no quantitative evidence of territoriality or home range size for this species (Higgins, 1999). The purpose of my study was, primarily, to determine the home range size of Australian owlet-nightjars in diverse habitats and relate it to resource abundance. Owlet-nightjars are found throughout Australia, and are listed as vulnerable or in decline in at least two states, yet little is known of their habitat requirements. Secondly, I attempted to define the degree of territoriality by owlet-nightjars. If owlet-nightjars are required to defend a territory throughout the year, energetic costs will be greater, which could make a crucial difference in survival during adverse conditions. Furthermore, territoriality may restrict foraging areas by preventing owlet-nightjars from expanding their home range, exacerbating the effect of seasonal or drought induced food shortages.

## **Methods**

### ***Study Sites***

This study was conducted during two winters (May to October 2004 – 2005) at two locations in the semi-arid zone of central Australia, and for one calendar year (November 2005 to November 2006) on the Northern Tablelands of New South Wales. Ormiston Gorge (23°37'S, 132°43'E) is located in the West MacDonnell Ranges National Park at the junction of the Chewings and Heavitree Ranges, about 150 km west of Alice Springs. The Alice Springs Desert Park (23°37'S, 132°43'E) is 7 km west of Alice Springs, NT, at the base of Mt Gillen on the Heavitree Range. Both of these sites are described in detail in Chapter 2. Ormiston Gorge represents a typically desert woodland site with mulga and riverine woodland habitats. It is designated as the desert site for the current study. Areas at the Alice Springs Desert Park were irrigated. Thus, this site is designated as irrigated desert for the current study. Research on the Northern Tablelands took place in the 218 ha Imbota Nature Reserve (30° 35' S, 151°45'E, 1000 m elevation), 10 km southeast of Armidale, New South Wales. Details of this site are described in Chapter 4. This location is designated as the eucalypt woodland site. I estimated home ranges of birds tracked throughout the year at the eucalypt woodland by season: spring (September- November), summer (December-February), autumn (March-May), and winter (June-August).

The mean minimum and maximum ambient temperatures ( $T_a$ ) in Alice Springs for July are 4.0 °C and 19.9 °C and the mean annual rainfall is 282 mm (1941-2007, Australian Bureau of

Meteorology). The mean daily minimum and maximum  $T_a$  for Armidale are 13.0 °C and 26.6 °C in summer and 1.0 °C and 13.2 °C in winter (1857-1997, Australian Bureau of Meteorology). Mean annual rainfall is 790 mm and mean monthly rainfall in summer (93.8 mm) is almost double winter rainfall amounts (51.5 mm).

### ***Arthropod Sampling***

Pitfall traps and light traps were used for arthropod sampling at all study sites. Pitfalls traps (diameter = 68 mm, depth = 150 mm), each containing 50 ml of 50% ethanol, were placed in a grid pattern consisting of three rows of four traps (12 traps per plot). To focus on nocturnal arthropods only, each pitfall trap was uncovered at dusk and covered at dawn. Traps were opened for two nights fortnightly at each site. Nocturnal aerial arthropods were sampled using an ultra-violet light trap (Australian Entomological Supplies Pty. Ltd., Coorabell, NSW, Australia) for three nights every fortnight. Details of sampling plots and procedures are given in Chapter 6. All light and pitfall trap samples were weighed to assess dry biomass to 0.01 g using a Mettler AE 260 balance (Mettler Instrumente AG, Switzerland). Arthropods <3 mm in length or >11 mm diameter were excluded from analysis as these were outside the range of prey sizes normally consumed by nightjars (Jackson, 2000; Jetz et al., 2003).

### ***Radio Tracking***

Owlet-nightjars were caught by broadcasting taped owlet-nightjar calls to lure individuals into mist nets. Following capture I determined each bird's body mass and placed an alloy band (Australian Bird and Bat Banding Scheme Project 1418-8) on the right leg. Birds were generally fitted with external radio transmitters weighing 2.2-2.6 g (model PD-2T, Holohil Systems, Carp, Ontario, Canada). External transmitters were attached using a back-pack-style harness made from elastic thread (Figure 5.1E in Kenward, 1987). Two birds in central Australia in 2004 were kept overnight to allow surgical implantation of internal transmitters (Sirtrack Ltd, Havelock North, New Zealand) for the purposes of another study (Chapter 2 and 4). Details of surgery are given in Chapter 2. No external characteristics can reliably distinguish the sex of owlet-nightjars. The sex of birds caught in 2005 and 2006-2007 was determined through DNA sexing using the shaft of feathers pulled from the chest area (Genetic Science Services, Fitzroy, Victoria, Australia).

Birds were tracked using hand-held three-element Yagi antennae and Icom receivers (IC\_R10, Icom, Bellevue, WA, U.S.A.). The effective range of the transmitter signal was greater for external (up to 1 km) than internal transmitters (~ 200 m). I tracked each animal

for 4 h per night on 5 nights for a total of 20 h per bird. Birds were not tracked on consecutive nights and tracking did not commence for several days after tagging. In most instances, birds were tracked one night per week over a period of several weeks. Birds were either tracked from their roosts at dusk or located later in the evening. As owlet-nightjars are active throughout the night, I attempted to gather data throughout the entire night period for each individual. For example, on night one an individual may be tracked from dusk until 10:00 h, on the second night from 10:00 h to 2:00 h, and on the third from 2:00 h until dawn. Due to logistical reasons, it was not always possible to obtain a full night sequence for each owlet-nightjar. Occasionally, inclement weather meant that birds could not be tracked for the full 4 h on a given night, in which case an extra night(s) of tracking were added to compensate for the lost time. Some birds were not tracked for the full 5 nights due to loss of transmitters or predation events. The battery life of transmitters was 16 weeks; however, due to loss of transmitters or depredation the average duration birds carried transmitters was 40 days (range 2-78). Intermittently, on nights when birds were not being tracked, spot checks were performed at random times and the position of the bird recorded. Owlet-nightjars were also located at their diurnal cavity roosts daily.

I used a homing-in, non-triangulation technique for obtaining positional data by following the transmitted signal's increasing strength until the tagged bird was within 10-20 m. The relationship between signal strength and distance was calibrated experimentally in the field at standardized gain settings. The accuracy of a bird's position could regularly be verified using the calls of the owlet-nightjar being tracked. Depending on the landscape, I sometimes circled within a small area to confirm the location, or sandwiched the bird between myself and a physical barrier, such as a cliff face (White & Garrott, 1990). When more than one observer was available, and depending on the landscape, the bird could be tracked between two observers to verify the position. Due to the topography of my study sites in central Australia, homing-in was more accurate than triangulation (White & Garrott, 1990), due to reflected signals from steep cliff faces of gorges (Garrott et al., 1986). Headlamps were kept on the dimmest LED setting and angled downward so that while tracking I was easily able to approach within 10-20 m of birds without causing disturbance. Birds regularly remained in one location for over 30 minutes and I observed no signs that I was affecting normal movements. I waited until birds moved to a new location before marking the birds' previous position with a GPS (Garmin GPS 12, Garmin International, Olathe, Kansas, USA), and then resumed tracking. Based on visual and audio confirmations, fixes were accurate to within ~10 m. The duration for which a bird was at each location was recorded.

### ***Vocalizations***

During tracking sessions and while mist-netting, I recorded the number and type of owlet-nightjar vocalizations and the number of birds responding. During mist-netting I played a series of 6-10 calls every 15 minutes. I modified call descriptions in Higgins (1999) to match the types of calls I heard regularly and placed calls into one of four categories: 1) a single syllable lower pitched mild churr; 2) a single syllable clear, shrill cry; 3) a triple syllable multi-pitched shrill call; 4) a soft chirp or a mew. I have designated the shrill calls in categories two and three as aggressive, as they are always loud and in response to either playback or a conspecifics call. The soft chirps or mews are communications between birds in close proximity, typically mates.

### ***Home Range Analysis***

My method of continuous tracking occasionally produced clustering of sampling, where clusters of observations are closely spaced in time, but are separated from other samples by a long time interval (Anderson & Rongstad, 1989; De Solla et al., 1999; Otis & White, 1999). Thus, it was necessary to standardize the data by subsampling using constant time intervals. In the past, the general rule was that two positions can be considered statistically independent if sufficient time had elapsed between fixes for the animal to move from one end of its home range to the other (White & Garrott, 1990). Fixes taken at shorter intervals than this arbitrarily chosen time are considered to be dependant and autocorrelated. Several researchers have proposed procedures for determining the minimum time interval at which successive observations are independent and cease to be significantly correlated (Schoener, 1981; Swihart & Slade, 1985; Swihart & Slade, 1986; Swihart & Slade, 1997). However, this index of statistical independence is not biologically relevant for many species which move in a non-independent manner (De Solla et al., 1999), such as sit-and-wait predators that do not traverse their home range in a predictable time period. Clearly, owlet-nightjars, and most avian species, could traverse their entire home range in a matter of minutes, but they usually do not. Furthermore, increasing the time interval between observations will inevitably decrease sample size, and often the size of the home range estimate, and still not achieve statistical independence of fixes (Hansteen et al., 1997; Rooney et al., 1998; De Solla et al., 1999). The degree of autocorrelation is also increased for animals that periodically return to a previously used portion of their home range (Hansteen et al., 1997), which owlet-nightjars do regularly while foraging. Thus, I followed the recommendations of Rooney et al. (1998) and De Solla et al. (1999) and selected a constant time interval of 10-minutes to maximize the

number of observations and thereby increase the accuracy of my home range estimates while minimizing sample clustering. A 10-minute time interval is conservative for owlet-nightjars. They can easily transverse their home range in less time, but this interval was close to the mean interval ( $11.08 \pm 0.32$  minutes) between fixes measured during tracking and was deemed appropriate.

I estimated two different ranges for each individual: a home range (incorporating both cavity roost and active nocturnal fixes) and a diurnal roost home range. In both instances, I included the location of each roost used by an individual as one data point in the complete dataset for analysis, irrespective of the number of times the individual was recorded using that roost. This avoided a bias towards roost locations, which were located daily, as opposed to nocturnal fixes which were recorded less frequently. I excluded the locations where birds were caught, as it was possible that individuals moved out of their home ranges in response to playback calls. I also excluded locations where transmitters were found, as it was difficult to assess whether birds had been depredated and the transmitter dropped outside of the regular home range.

I calculated home range size using the minimum convex polygon (MCP) and fixed kernel methods (Worton, 1989) using the Animal Movements extension in Arcview 3.2 (Hooge et al., 1999). Two home range estimates were calculated to enable comparison with other studies. While the MCP method simply calculates the areas bounded by the outer fixes, kernel analysis provides a statistical estimate of the likelihood of an animal being present within an area. I used 100% estimates for MCP analysis and 95% and 50% home range areas for kernel analysis. Least-squares cross-validation (LSCV) methods were used to determine the amount of smoothing for kernel analysis. The number of fixes required for a complete home range estimate was determined by plotting sample size against mean area (ha) using the MCP sample size bootstrapping function of the Animal Movements extension, which indicates the asymptote of mean area increase (examples in Figure 1). The mean number of fixes required for a complete home range was  $40 \pm 3$ , thus, I usually acquired sufficient fixes for birds tracked for two or more nights. This is within the sample size of 30 to 50 recommended by Seaman et al. (1999) for a complete home range estimate using kernel analysis (also see Otis & White, 1999). Home range area estimates based on an insufficient number of fixes were excluded from analyses, with the exception of overlap determination.

The degree of overlap between home ranges of two neighbouring individuals was analyzed by intersecting the two home range MCP polygons and calculating the percentage overlap. As this percentage is based on home range size, which typically differs between the two individuals in the pair analyzed, the following index was used (Atwood & Weeks, 2006):

$$[(\text{area}_{\alpha\beta}/\text{home range}_{\alpha}) \times (\text{area}_{\alpha\beta}/\text{home range}_{\beta})]^{0.5}$$

where  $\text{area}_{\alpha\beta}$  is the overlapping area and  $\text{home range}_{\alpha}$  and  $\text{home range}_{\beta}$  are the home ranges of individuals  $\alpha$  and  $\beta$ , respectively. Owllet-nightjars with ranges separated by less than 50 m were considered to be neighbours. Data for home range polygons at the eucalypt woodland site were divided into seasons for analysis, to ensure that birds were present during the same time period. Likewise, overlapping ranges were excluded for birds that were depredated prior to the capture of a neighbouring bird. Owllet-nightjars were deemed to be a mated pair based on behaviour, including aggressive reaction to playback calls resulting in birds being captured simultaneously (2 pairs), two individuals sharing the same roost cavities (2 pairs), and two individuals nesting together (1 pair). To assess the existence of a permanent home range, I examined the degree of site fidelity by determining the overlap in the 100% MCP area used by three individuals captured in two different seasons.

Home ranges of birds at each location during each season/year were compared to the respective values of aerial and terrestrial arthropod biomass collected for each site and season/year (Chapter 6) using Spearman rank correlation. Home range sizes were compared between sexes, years, and sites using analysis of variance (ANOVA) or t-tests. All statistical tests were performed using either Minitab Statistical Software (version 13.1) or SigmaStat (version 2.0) software. Numerical values are presented as means  $\pm$  SE for  $n$  = number of individual birds or number of home range size estimates, and  $N$  = number of home range fixes. An alpha value of 0.05 was used for all tests.

## Results

The density of birds at the eucalypt woodland site was high, with 19 individuals captured in the 218 ha reserve during the one-year study. Fourteen individual owllet-nightjars carried radio-transmitters for periods ranging from 19 to 84 days. Mean body mass was  $52.2 \pm 2.2$  g, and there was no difference between masses of birds captured in summer versus winter ( $t$ -test:  $t_{19}=0.58$ ,  $P=0.57$ ,  $n=12$ ). Based on MCP bootstrapping, the number of fixes acquired for one individual (ONJ 30), which was only tracked for one night ( $N=27$ ) before the premature

failure of the transmitter battery, were insufficient for a complete home range determination. The number of fixes obtained for the other 13 birds ranged from 45 to 160 (Table 1), which was deemed adequate for MCP and 95% kernel estimates of home range area. The mean home range in the eucalypt woodland was  $17.7 \pm 1.7$  ha based on the MCP method (Figure 2) and  $17.4 \pm 2.1$  ha based on the fixed kernel contour (95%). Mean maximum range length was  $478.1 \pm 47.8$  m. Mean core use area (50% kernel contour) was  $2.3 \pm 0.5$  ha. Roosting home range (MCP method) was  $2.8 \pm 0.7$  ha ( $n=13$ ; Figure 3), occupying on average 21.3% of the total home range. Core use foraging areas and roosting areas represented two separate areas in most home ranges with no overlap between neighbouring birds.

At the desert site, eight owlet-nightjars were captured with seven individuals monitored for periods ranging from 51 to 101 days (Table 2; Figure 4). At the irrigated desert site, seven owlet-nightjars were captured and five were monitored for 11 to 64 days (Table 2; Figure 5). The body mass of owlet-nightjars captured at the two desert sites in 2005 ( $40.4 \pm 0.6$  g,  $n=5$ ) was significantly lower than in 2004 ( $47.3 \pm 1.5$  g,  $n=10$ ;  $t$ -test:  $t_{13}=3.18$ ,  $P<0.01$ ). Due to the difficulty in capturing birds, which occurred in lower densities at these sites, fewer nights were available for tracking and, thus, I obtained an insufficient number of fixes for several birds (Table 2). Complete home range estimates were determined for seven individuals and mean home range size for the desert sites combined was  $23.8 \pm 5.3$  ha and  $24.1 \pm 6.0$  ha based on the MCP and kernel methods, respectively. Mean core foraging area was  $3.2 \pm 1.0$  ha. Mean maximum range length was  $574.3 \pm 84.6$  m. Roosting home range was  $2.6 \pm 1.5$  ha ( $n=5$ ), which occupied on average 5.3% of the total home range (Table 2).

Home range size estimates were not correlated with the number of fixes obtained (Spearman rank correlation: MCP:  $r_s=0.32$ ,  $P=0.12$ ,  $n=24$ ; 95% kernel:  $r_s=0.28$ ,  $P=0.19$ ,  $n=24$ ). Home range size did not differ significantly between sexes, study sites, seasons, or years. Mean home range size was slightly larger for males (Tables 1 and 2), but did not differ significantly between sexes ( $t$ -test: MCP:  $t_{16}=2.04$ ,  $P=0.06$ ; 95% kernel:  $t_{16}=0.91$ ,  $P=0.38$ ). Despite slightly larger home ranges in the desert, range size did not differ significantly between sites (MCP: Kruskal-Wallis ANOVA:  $H_2=0.29$ ,  $P=0.86$ ; 95% kernel: ANOVA:  $F_{2,23}=1.23$ ,  $P=0.31$ ). Likewise, neither the core foraging area (50% kernel:  $H_2=1.77$ ,  $P=0.41$ ) or maximum range length ( $H_2=1.98$ ,  $P=0.37$ ) differed between sites. The 50% use kernel contour area was consistent across sites, averaging 13.2% of the mean eucalypt woodland home range size and 12.9% of the desert range. Home range size did not differ significantly across seasons for the eucalypt woodland site (MCP:  $F_{3,15}=0.27$ ,  $P=0.85$ ; 95% kernel:  $F_{3,15}=0.07$ ,  $P=0.98$ ).

Differences in rainfall and arthropod abundance between years in the desert were great (Chapter 6), and home range size in 2004 ( $32.3 \pm 16.6$ ,  $n = 4$ ) was double the size of estimates in 2005 ( $15.2 \pm 7.3$ ,  $n = 4$ ), however, due to the variation among individuals, home range size did not differ significantly between years (MCP:  $t_{16}=1.89$ ,  $P=0.11$ ).

The mean overlap in home range (MCP) of non-mated neighbouring owlet-nightjars was  $12.4 \pm 4.2\%$  (Table 3). This includes the overlapping home ranges of ONJ 9 and 11 at the desert site (40.7%), which may have been a mated pair, although there was no direct evidence of this during the winter they were tracked. The sex of these birds was unknown. The overlap of known male-male ( $3.0 \pm 1.0\%$ ) and female-female (0.47%) home ranges was low, and the overlap of male-female ranges was still only  $9.2 \pm 3.2\%$ . The mean home range overlap of paired mates was high irrespective of season ( $41.9 \pm 13.1\%$ ), but was greatest for one pair during spring (72.3%). Several home ranges, especially at the desert site, were exclusive, and no neighbouring birds were captured despite intensive mist-netting efforts.

There was no overlap of roost MCP for non-mated neighbours. Roost MCPs overlapped for two mated pairs, one in the eucalypt woodland (ONJ 29 & 37) and one in the irrigated desert (ONJ 8 & 14). Both of these pairs shared common roosts at the start of or during the breeding season. The 50% kernel core contour area of the home range was exclusive to all individuals, with the exception of a shared core area by ONJ 29 & 37 during spring. It is likely they were nesting at this time, as they shared one roost for at least two days, however, the position of the roost hollow (at the top of a narrow 5 m high decayed stump) made confirmation impossible.

Site fidelity between seasons was high for all three owlet-nightjars recaptured and tracked during two separate periods. Mean overlap of home range MCPs was  $67.6 \pm 9.3\%$  and ranged from 49.0 to 77.2% (Figure 1). ONJ 31 exhibited the greatest shift of home range area as he maintained a similar roost range, but foraged in a more densely wooded area during winter. However, in general territories seemed to be stable, and defended, year-round. For example, ONJ 31 was captured at the exact same location, ~100 m north of his roost range, on three separate occasions during 2006 (February, June, and September). Prior to each capture, the bird responded aggressively to playback and flew at the human 'intruder' several times before striking a net.

### ***Vocalizations and Territorial Behaviour***

My study was designed to examine home ranges and vocalizations were recorded opportunistically. Thus, call playback was not carried out in a systematic method, and calls were played at only one location each night. The proximity of playback to a home range/territory, roost area or core foraging area likely impacted the responses and resulted in great variation in calls amongst nights (e.g. 95% confidence intervals of means = 2.6 calls hour<sup>-1</sup> in the winter and 11.2 calls hour<sup>-1</sup> in summer). Weather conditions and moon phase also affected responses, which I will examine elsewhere. The number of calls per hour in response to call playback is presented here to give an indication of calling patterns observed throughout the year. There was no correlation between the number of hours birds were monitored (or number of calls played) per month and the number of calls recorded in response to playback (Pearson product moment:  $r_p=0.60$ ,  $P=0.09$ ,  $N=9$  months) or between conspecific owlet-nightjars without playback ( $r_p=0.35$ ,  $P=0.29$ ,  $N=11$  months).

Owlet-nightjars were not heard to vocalize in the eucalypt woodland during winter unless in response to playback (Figure 6). Calls increased during the breeding and egg laying period in October/November (Brigham & Geiser, 1997), and call frequency was significantly greater in spring and summer relative to autumn or winter (Kruskal-Wallis ANOVA:  $H_3=21.52$ ,  $P<0.0001$ ). Although it was sometimes difficult to identify the bird calling, both males and females called regularly, and the females called more frequently than males during the breeding season. Soft chirping calls between mates were more pronounced in September and October (Figure 6a). Owlet-nightjars responded to call playback regularly throughout the year ( $H_3=1.33$ ,  $P=0.72$ ). However aggressive responses to playback were more common during the spring and summer ( $H_3=10.92$ ,  $P<0.05$ , Figure 6b). It was not uncommon for three to four birds to call simultaneously or in succession in the spring; however, this was rarer during the rest of the year. The greatest number of calls recorded in one evening was in October 2006, when I noted the occurrence of 840 unelicited calls from four different owlet-nightjars over a 4 h period. The longest consecutive string of calls was in November 2006 when I recorded the occurrence of 370 successive calls amongst three owlet-nightjars, including a mated pair.

Owlet-nightjars called spontaneously, without playback, throughout the winter in the desert, but call frequency was low ( $3.3 \pm 2.9$  calls hour<sup>-1</sup>; Figure 7a). Total call frequency did not differ amongst months (Kruskal-Wallis ANOVA:  $H_5=7.17$ ,  $P=0.21$ ), but aggressive type calls (shrill cries + triple calls) were more frequent in October at the start of the egg-laying season ( $H_5=21.90$ ,  $P<0.001$ ). Response to call playback was much greater in the desert ( $17.8 \pm 5.2$

calls hour<sup>-1</sup>) than at the eucalypt woodland site ( $5.5 \pm 1.1$  calls hour<sup>-1</sup>; Mann-Whitney *U*-test:  $T=2121.0$ ,  $P<0.0001$ ). Total call responses to playback did not differ amongst months ( $H_5=2.73$ ,  $P=0.44$ ) in the desert. Despite differences in capture rates for owlet-nightjars between years in the desert (below), there was no difference in calling frequency between years in response to playback ( $T=1148.5$ ,  $P=0.16$ ) or between unelicited calls of conspecifics ( $T=2478.5$ ,  $P=0.68$ ). As in the eucalypt woodland, several birds (up to five) could be heard exchanging calls during late winter-early spring in the desert.

Irrespective of sex or season, 83% of the 41 birds ( $n = 9$  females, 12 males, 13 unknown sex) I captured were caught in response to playback calls. Fifty-one percent ( $n = 6$  females, 9 males, 6 unknown) of the birds captured responded with loud aggressive calls and often repeated flights towards the ‘intruder’ playing the tape. During the breeding season (September-February) owlet-nightjars responded more aggressively to playback. In February, I capture six individuals during only five nights of mist-netting, and all flew aggressively towards me soon after I played the first calls. Capture rates, and responses to playback are less during winter, with one bird being captured every 4.7 nights of mist-netting (900 m<sup>2</sup> of nets erected for ~4 hrs each night) in the desert in 2004 ( $n = 11$  birds, 52 nights), and every 10.3 nights during the drier winter of 2005 ( $n = 6$  birds, 62 nights). In the eucalypt woodland, I captured a bird on average every 5.6 nights during winter ( $n = 5$  birds, 28 nights), yet birds were captured every 2 and 1.5 nights in spring ( $n = 4$  birds, 8 nights) and summer ( $n = 10$  birds, 15 nights), respectively ( $\chi^2_2=10.61$ ,  $P<0.01$ ).

Aggression between individuals can be intense, presumably generated by territorial disputes. During one moonlit evening at the irrigated desert site in June 2004, three individual owlet-nightjars approached my nets in response to playback, one skimming the top of my head in his ‘attack’, and later two of the birds engaged in a tussle of snapping beaks and beating wings on the ground nearby.

### ***Arthropod Abundance and Home Range Size***

Aerial and terrestrial arthropod biomass was significantly lower at the eucalypt woodland site compared to the sites in central Australia, except for the desert site in 2005 (Kruskal-Wallis ANOVA: Aerial:  $H_4=23.3$ ,  $P<0.001$ ; Terrestrial:  $H_4=330.36$ ,  $P<0.00001$ ). Terrestrial arthropod biomass in the desert in 2005 was significantly lower than the irrigated desert site and both sites 2004. Details of arthropod biomass and abundance at these sites are discussed in Chapter 6.

Terrestrial arthropod biomass obtained through pitfall trapping at all sites was not correlated significantly with MCP, 95% kernel, or 50% kernel estimates (Spearman rank correlation:  $P < 0.05$ ,  $n = 24$ ). Aerial arthropod biomass collected using light traps was not correlated with MCP ( $r_s = 0.36$ ,  $P = 0.08$ ) or 50% kernel ( $r_s = 0.26$ ,  $P = 0.21$ ) estimates, but was positively correlated with 95% kernel estimates ( $r_s = 0.42$ ,  $P < 0.05$ ). However, linear regression analysis indicated there was no significant difference between logarithmically transformed aerial arthropod biomass and 95% kernel estimates ( $F_{1,23} = 3.14$ ,  $P < 0.09$ ).

**Table 1:** Home range estimates for radio-tagged Australian owlet-nightjars (ONJ) at the eucalypt woodland site from November 2005 to December 2006. Three of the birds were captured twice and data are presented for different seasons as indicated (SP = spring, S = summer, W = winter, A = autumn). Roost area (%) represents the percentage of the total home range the roost minimum convex polygon (MCP) occupies. The number of core areas is based on analysis of multimodality of 50% kernel areas. Mean  $\pm$  SE are given at the bottom of the respective columns.

ONJ	Sex	Year	Season	# Days Tagged	# Nights Tracked	# Fixes	# Roosts	Roost MCP (ha)	Roost Area (%)	Max. Range Length (m)	MCP (ha)	95% Kernel (ha)	50% Kernel (ha)	# Core Areas
27SP	M	2006	Spring	63	6	137	4	0.49	2.8	326	17.60	15.65	0.82	2
37	M	2006	Spring	78	7	160	7	2.67	12.8	404	20.84	21.94	1.94	3
39	F	2006	Spring	38	6	129	4	0.49	5.0	349	9.74	9.55	0.83	1
21	F	2005	Summer	36	5	46	2			572	17.91	28.69	5.10	3
22S	F	2005	Summer	48	9	125	10	6.21	50.0	389	12.42	8.05	0.53	1
23	F	2005	Summer	70	4	98	6	1.91	9.7	511	19.60	23.97	3.46	2
26	M	2006	Summer	26	3	64	4	2.80	10.2	644	27.47	19.05	1.60	1
28	M	2006	Summer	74	5	128	1			358	17.60	13.60	1.88	2
22A	F	2006	Autumn	75	4	45	4	4.18	35.8	369	11.68	13.03	1.96	2
27A	M	2006	Autumn	76	9	123	2			388	16.23	15.73	1.11	1
29	F	2006	Autumn	66	6	126	5	1.82	16.7	305	10.86	16.11	3.72	3
30	F	2006	Autumn	24	1	27	3	0.76		365 <sup>1</sup>	3.72 <sup>1</sup>			
31A	M	2006	Autumn	84	6	130	3	0.05	0.2	509	24.04	22.93	3.39	2
31W	M	2006	Winter	19	2	56	3	1.55	6.6	805	23.31	11.23	1.74	1
32	F	2006	Winter	23	2	45	7	7.83	71.4	387	10.97	8.01	0.58	1
33	M	2006	Winter	20	2	54	5	5.52	53.2	346	10.37	11.33	1.07	2
35		2006	Winter	53	6	132	3	0.72	2.2	988	32.41	40.00	7.13	2
<b>Mean</b>				<b>43<math>\pm</math>7</b>				<b>2.8<math>\pm</math>0.7</b>	<b>21.3<math>\pm</math>6.5</b>	<b>478<math>\pm</math>48</b>	<b>17.7<math>\pm</math>1.7</b>	<b>17.4<math>\pm</math>2.1</b>	<b>2.3<math>\pm</math>0.5</b>	

<sup>1</sup> Data for ONJ 30 was excluded from further analysis as (MCP) bootstrapping indicated the number of fixes was insufficient to represent a complete home range.

**Table 2:** Home range estimates for radio-tagged Australian owlet-nightjars (ONJ) at the desert site (D) and irrigated desert site (ID) during winter (May-September) 2004 and 2005. Roost area (%) represents the percentage of the total home range the roost minimum convex polygon (MCP) occupies. The number of core areas is based on analysis of multimodality of 50% kernel areas. Mean  $\pm$  SE are given at the bottom of the respective columns.

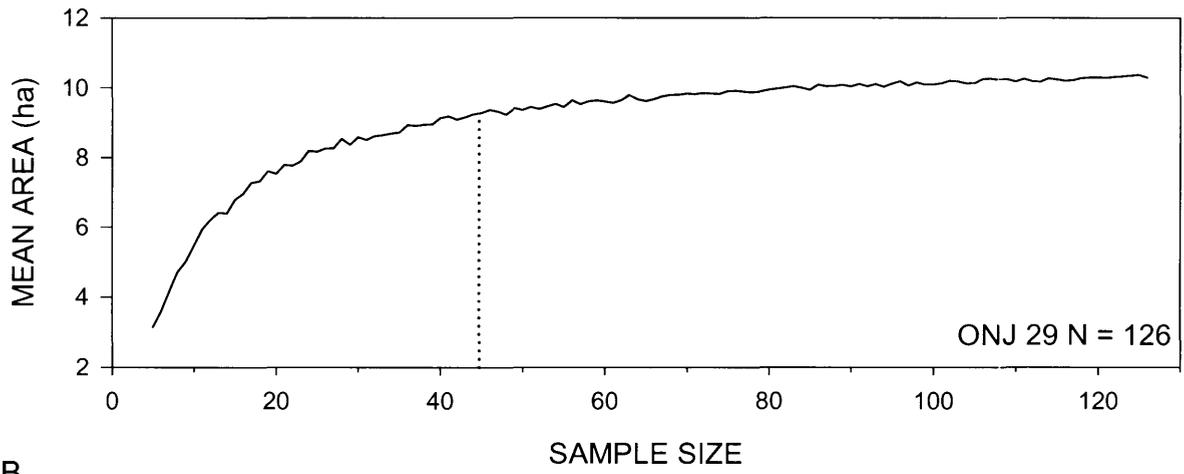
ONJ	Sex	Site	Year	# Days Tagged	# Nights Tracked	# Fixes	# Roosts	Roost MCP (ha)	Roost Area (%)	Max. Range Length (m)	MCP (ha)	95% Kernel (ha)	50% Kernel (ha)	# Core Areas
4		D	2004	101	2	51	1			313	8.95	7.38	1.02	3
9		D	2004	71	5	80	7	3.41	7.8	1042	43.87	60.79	9.77	3
11		D	2004	23	2	37	3	0.39		561 <sup>1</sup>	12.26 <sup>1</sup>			
13		D	2004	57	10	133	2			628	32.03	26.88	4.66	2
16	F	D	2005	43	3	57	5	1.70	11.0	420	15.50	17.02	2.12	1
17	M	D	2005	37	3	60	3	0.77	4.9	401	15.65	21.01	1.77	2
20	M	D	2005	23	4	73	4	0.32	1.3	643	23.75	24.73	2.89	3
6		ID	2004	64	0	8	3	0.02						
7		ID	2004	11	0	8	1							
8		ID	2004	64	2	24	4	13.85		588 <sup>1</sup>	20.47 <sup>1</sup>			
14		ID	2004	30	6	98	3	0.77	1.7	735	44.32	29.08	2.26	1
18	M	ID	2005	15	1	21	3	1.85		507 <sup>1</sup>	20.24 <sup>1</sup>			
19		ID	2005	22	5	88	1			412	5.99	6.16	0.72	2
<b>Mean</b>				<b>51<math>\pm</math>6</b>				<b>2.6<math>\pm</math>1.5</b>	<b>5.3<math>\pm</math>1.8</b>	<b>574<math>\pm</math>85</b>	<b>23.8<math>\pm</math>5.3</b>	<b>24.1<math>\pm</math>6.0</b>	<b>3.1<math>\pm</math>1.0</b>	

<sup>1</sup> Data for ONJ 8, 11, and 18 were excluded from further analysis as MCP bootstrapping indicated the number of fixes was insufficient to represent a complete home range.

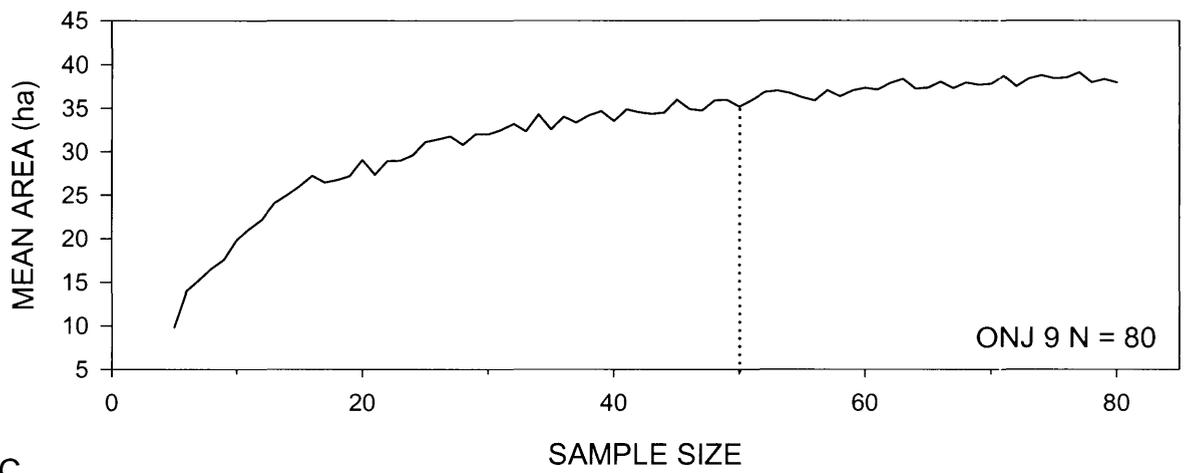
**Table 3:** Determination of percentage overlap of home ranges (100% MCP) for neighbouring owl-*nightjars* at the eucalypt woodland and the desert sites. M = male, F = female. n = number of individuals or pairs compared in each category.

<b>Pair Category</b>	<b>n</b>	<b>Mean <math>\pm</math> SE (%)</b>	<b>Range (%)</b>
Paired Mates	5	41.9 $\pm$ 13.1	0.1 – 72.3
All Non-mated Individuals	11	12.4 $\pm$ 4.2	0.5 – 40.7
M x M	3	3.0 $\pm$ 1.0	1.2 – 4.5
F x F	1	0.5	
F x M	3	9.2 $\pm$ 3.2	2.9 – 13.6

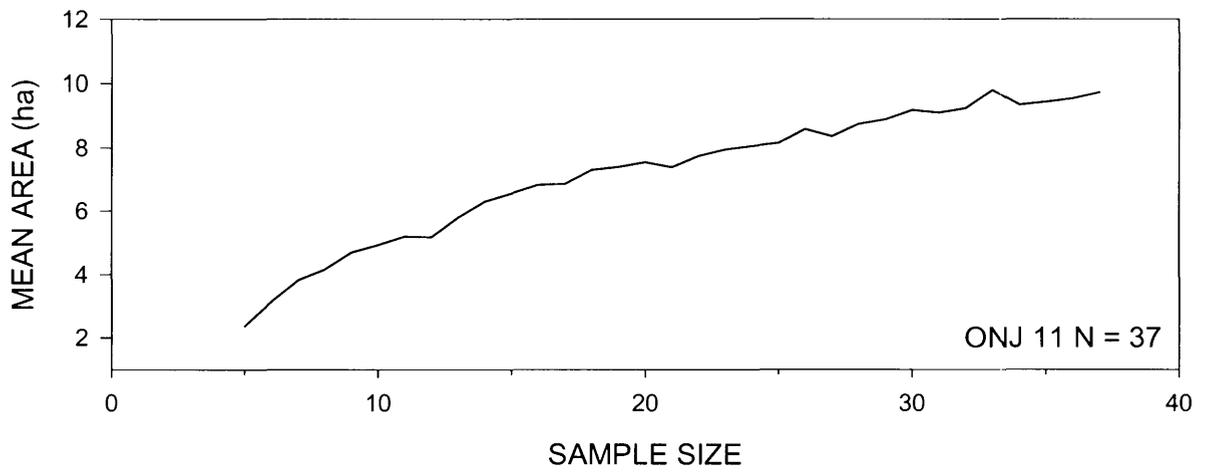
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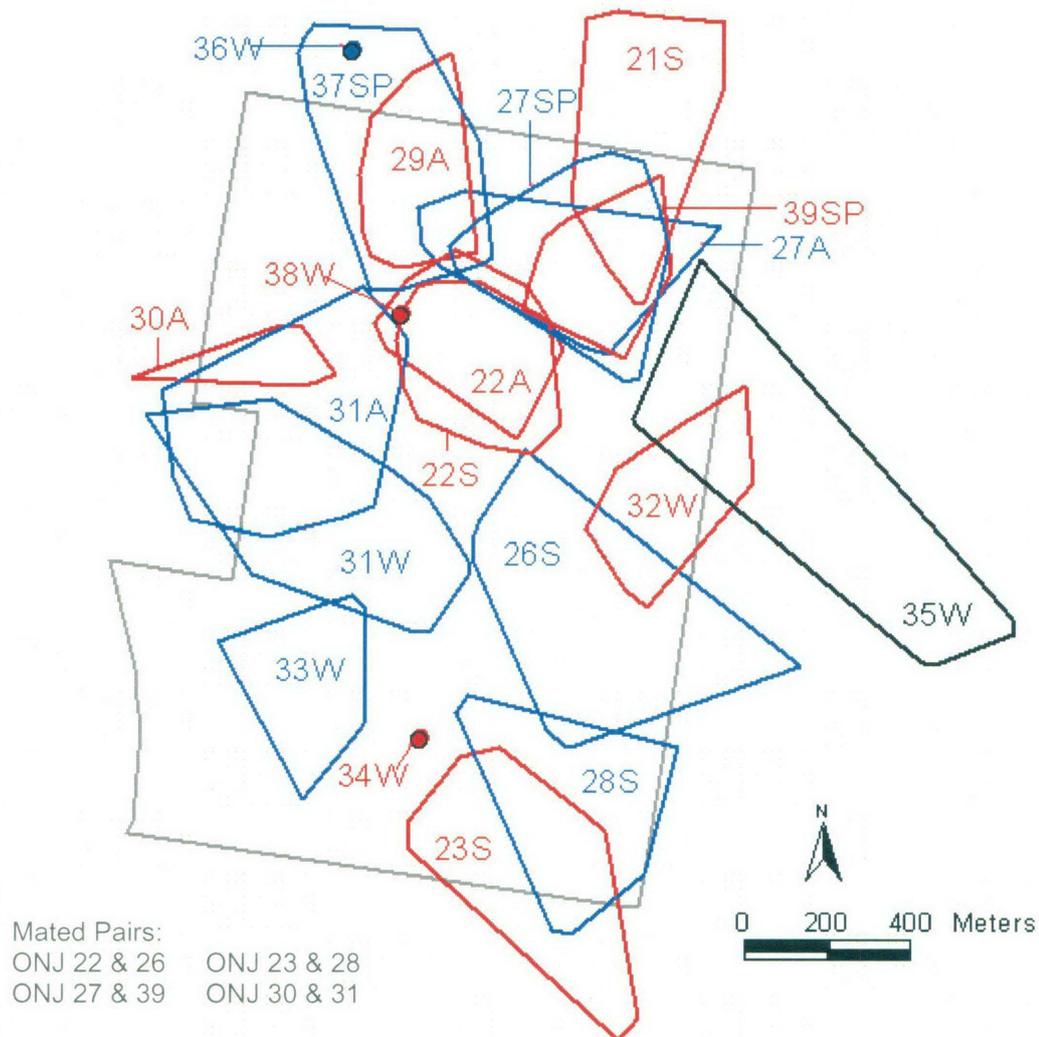
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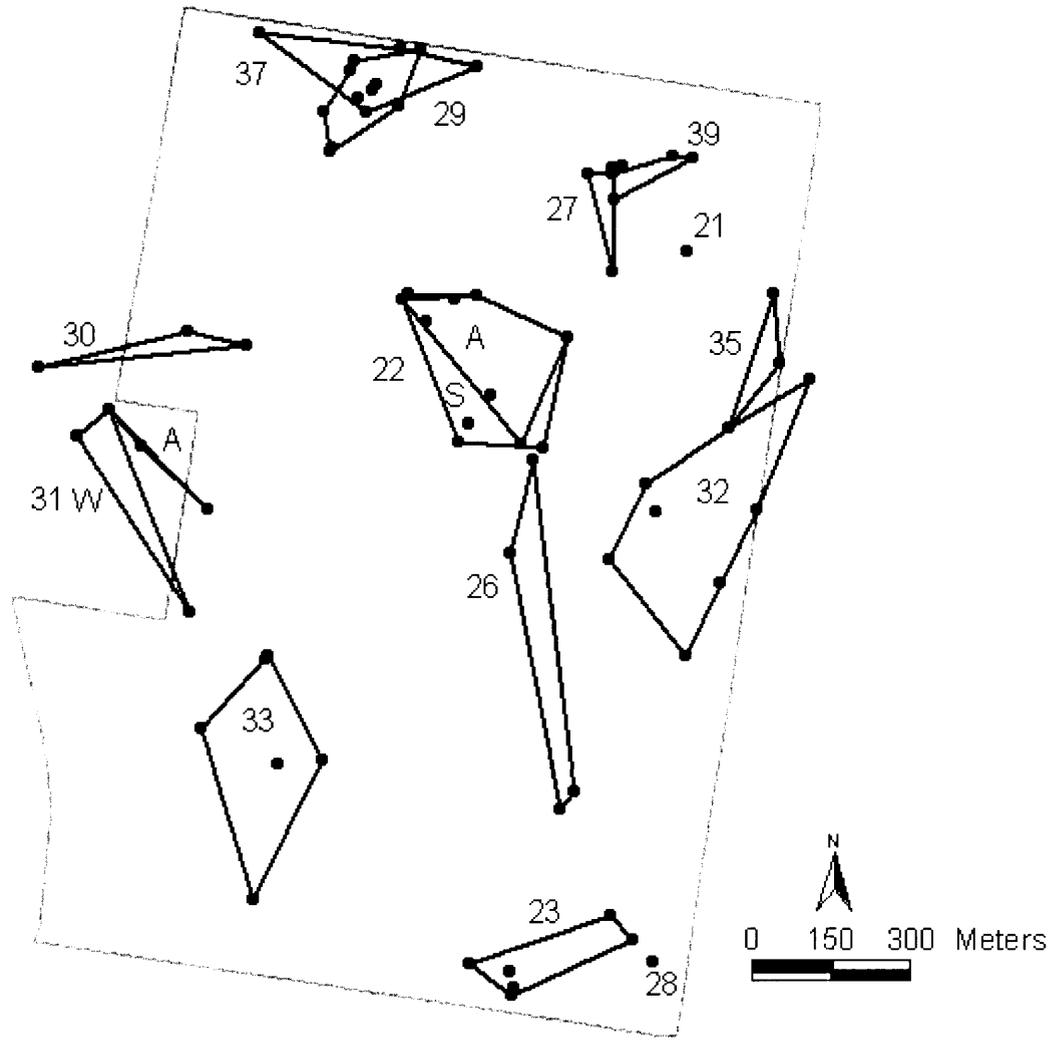
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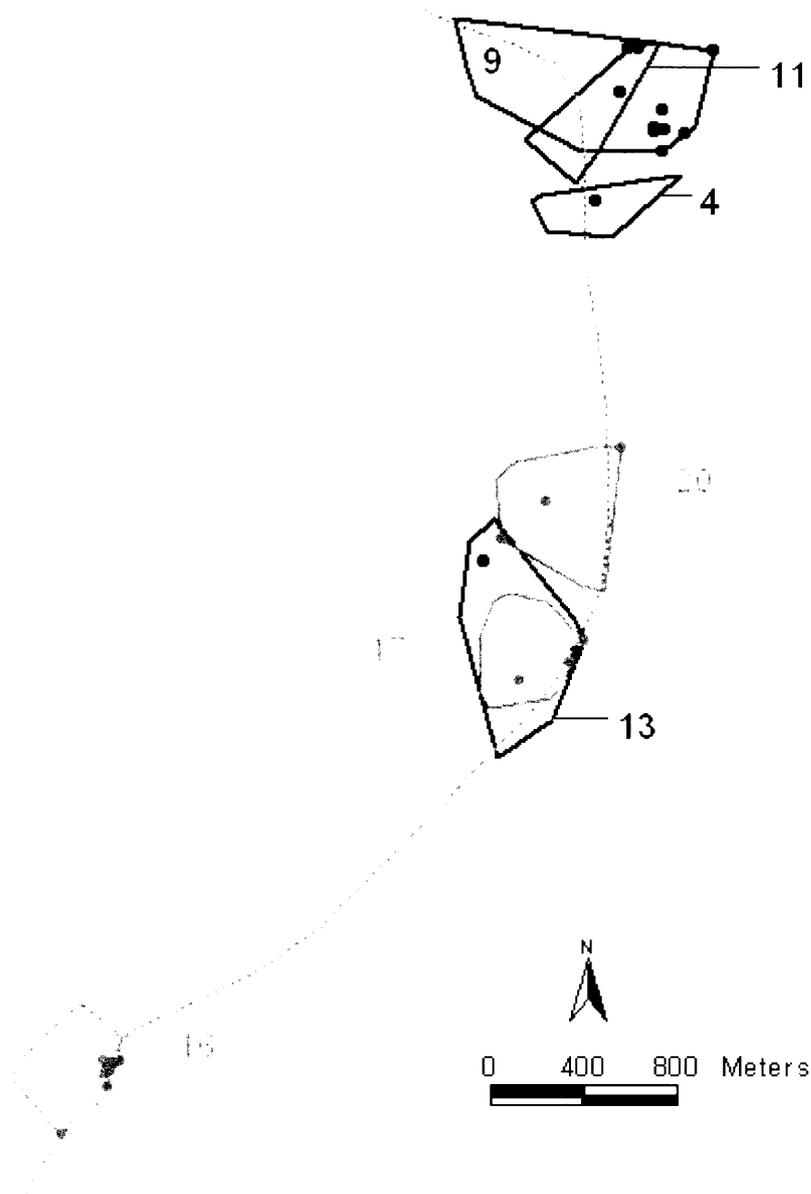
**Figure 1:** Three examples of minimum convex polygon (MCP) sample size bootstrapping to determine if sufficient fixes were collected for each owlet-nightjar. The mean asymptote for required sample size was 40. A) A large number of fixes ( $N = 126$ ) was obtained for owlet nightjar #29 (ONJ 29), which had a small home range area (10.86 ha, asymptote  $N = 45$ ). B) ONJ 9 had one of the largest home ranges (43.87 ha) yet 80 fixes were more than adequate to achieve an asymptote at  $N = 50$ . C) The sample size ( $N = 37$ ) was not sufficient to achieve an asymptote, and the home range area for ONJ 11 was excluded from statistical analysis.



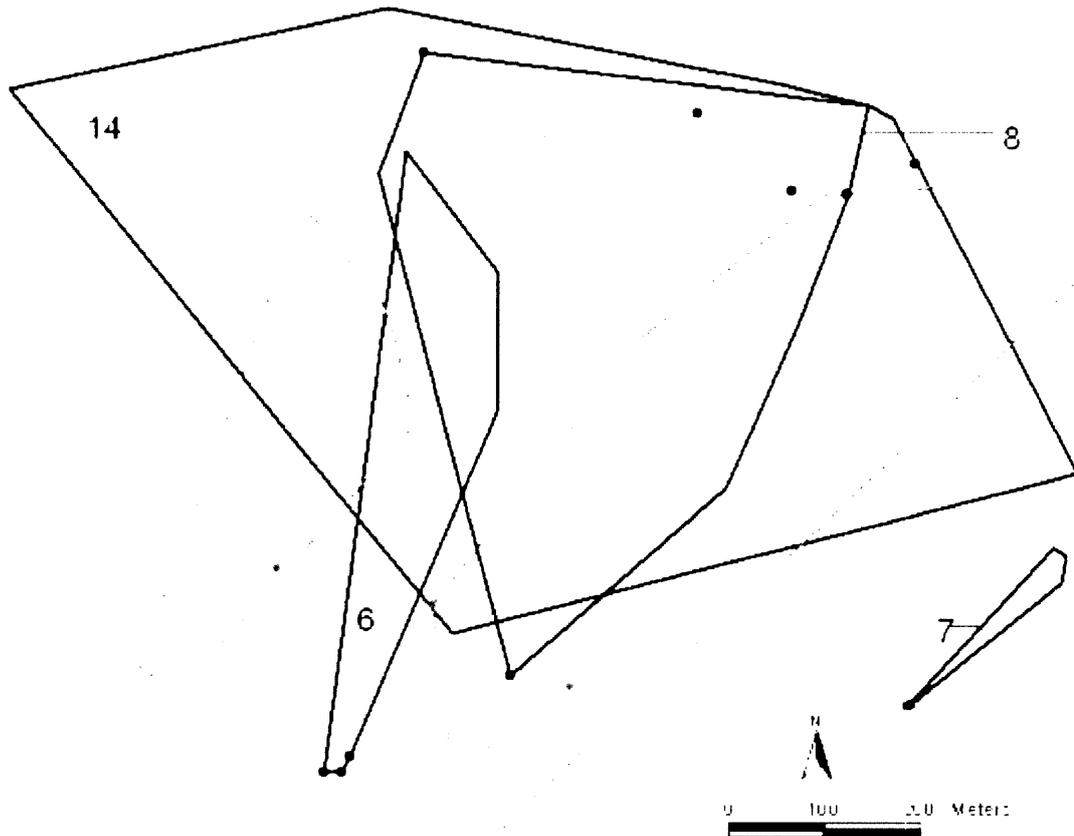
**Figure 2:** Home range estimates (100% MCP) for all owlet-nightjars, including males (blue outline), females (red outline) and one individual of unknown sex (black outline) at the eucalypt woodland site. Filled circles indicate the location of the first roost site of three owlet-nightjars (34W, 36W, 38W) that were not tracked for home range estimates as they lost transmitters within days of attachment. Labels for each polygon indicate the owl-nightjar (ONJ) identification number and the season during which it was tracked (SP = spring, S = summer, A = autumn, W = winter). Three individuals were captured and tracked in two different seasons each (ONJs 22, 27 & 31). Mated or breeding pairs are as indicated. The home range estimate for ONJ 30 was incomplete and was not use for statistical analysis. ONJs 21 and 32 were depredated during the tracking period and their home ranges were later partially occupied by other birds. The boundary of Imbota Nature Reserve is shown in grey.



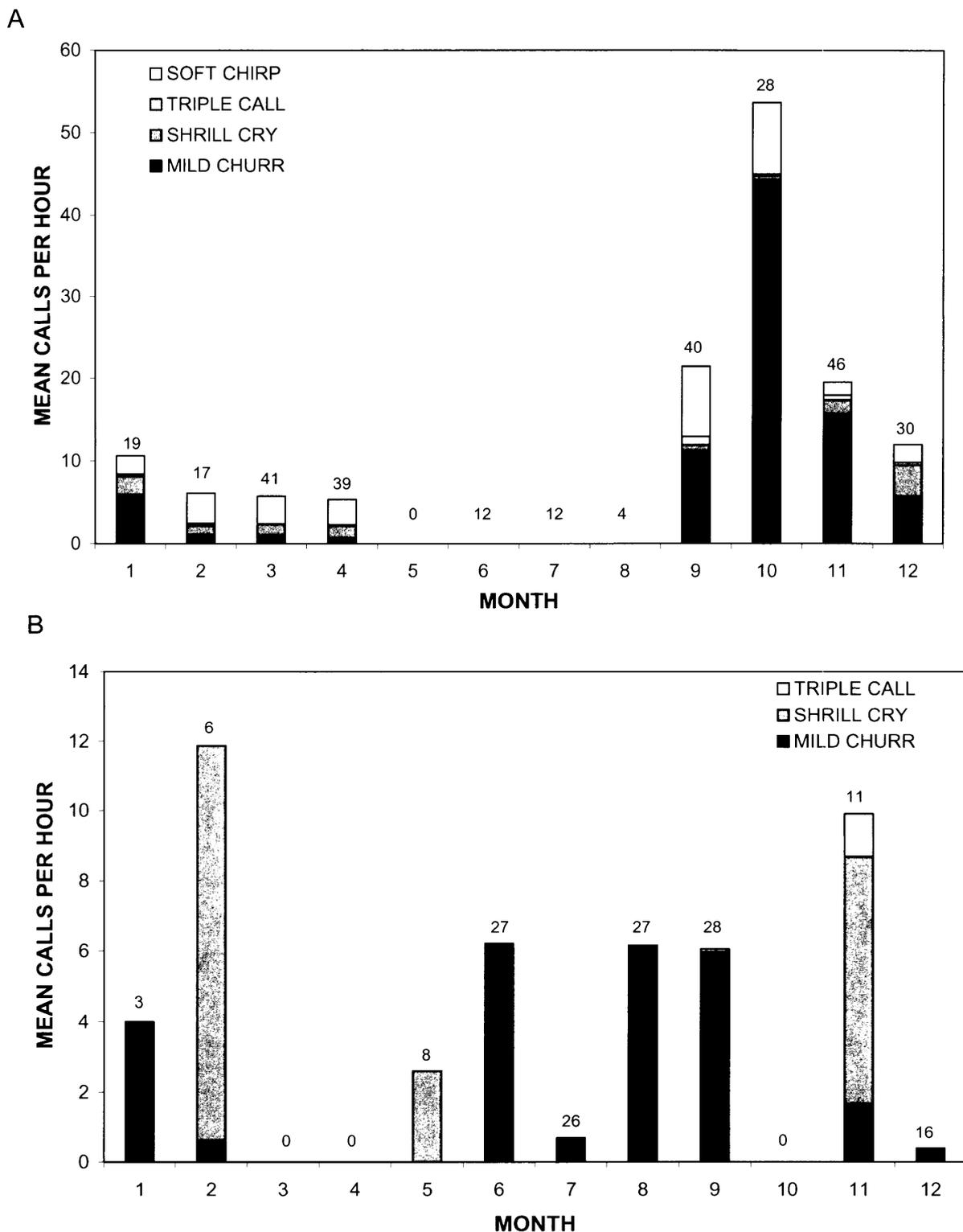
**Figure 3:** Portion of home range estimates (100% MCP) defined by roost locations for all owl-nightjars at the eucalypt woodland site. Labels for each polygon indicate the owl-nightjar (ONJ) identification number, and for two individuals captured twice with seasonal differences in roosts, the season for which the roosts were used (S = summer, A = autumn, W = winter). The apparent overlap of roosts areas for ONJ 32 & 35 and ONJ 29 & 37 is not real as both ONJ 32 & 29 were depredated prior to capturing ONJ 35 and 37. Thus, all roost areas were exclusive with the exception of breeding pair ONJ 27 & 39. The boundary of Imbota Nature Reserve is shown in grey.



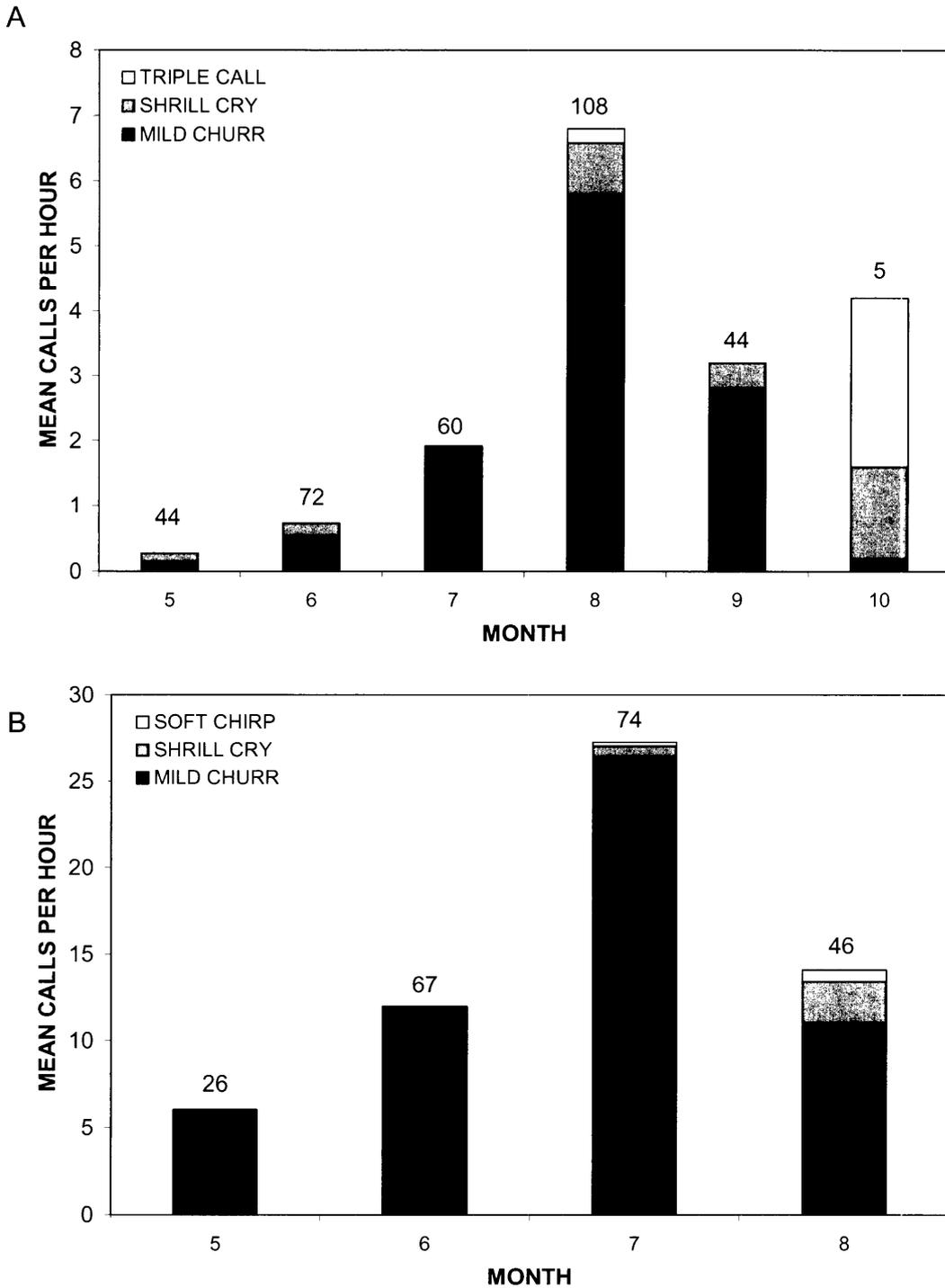
**Figure 4:** Home range estimates (100% MCP) for all owlet-nightjars tracked at the desert site (Ormiston Gorge) in 2004 (black outline) and 2005 (males solid grey outline, female, dashed grey outline). Labels for each polygon indicate the owlet-nightjar (ONJ) identification number. The dashed grey line indicates the river channel, which is typically dry, but contains the majority of large trees (river red gums, *Eucalyptus camaldulensis*), in which five of the seven individuals roosted. Birds were not sexed in 2004. The home range estimate for ONJ 11 is incomplete and was not used in statistical analysis.



**Figure 5:** Home range estimates (100% MCP) for all owlet-nightjars tracked at the irrigated desert site (Alice Springs Desert Park) in 2004 (black outline) and 2005 (grey outline). Labels for each polygon indicate the owlet-nightjar (ONJ) identification number. ONJ 8 and 14 shared roosts and were thought to be a breeding pair, which explains the large overlap in home range area. ONJ 18 is a male. The sex for all other birds is unknown. The number of fixes obtained for the home range areas for ONJ 6, 7, 8 and 18 were not sufficient for a complete home range determination and were not used in statistical analysis (see Table 2).



**Figure 6:** Vocalization rates by Australian owlet-nightjars at the eucalypt woodland site. The labels above the bars represent the number of hours birds were monitored. A) The mean number of calls hour<sup>-1</sup> between conspecifics with no playback. Calling rates were more frequent in the spring and summer (Kruskal-Wallis ANOVA:  $H_3=21.52$ ,  $P<0.0001$ ). B) The mean number of calls hour<sup>-1</sup> in response to playback of owlet-nightjar calls every 15 minutes. There was no difference in overall call rates amongst seasons ( $H_3=1.33$ ,  $P=0.72$ ), but the frequency of aggressive calls (shrill cries + triple calls) were greater in summer than in winter ( $H_3=10.92$ ,  $P<0.05$ ).



**Figure 7:** Vocalization rates by Australian owlet-nightjars in the desert during winter. The labels above the bars represent the number of hours birds were monitored. A) The mean number of calls hour<sup>-1</sup> between conspecifics with no playback. Total call frequency did not differ amongst months (Kruskal-Wallis ANOVA:  $H_5=7.17$ ,  $P=0.21$ ), but aggressive type calls (shrill cries + triple calls) were more frequent in October ( $H_5=21.90$ ,  $P<0.001$ ). B) The mean number of calls hour<sup>-1</sup> in response to playback of owlet-nightjar calls every 15 minutes. Total call frequency did not differ amongst months ( $H_5=2.73$ ,  $P=0.44$ ).

## Discussion

### *Home Range*

The average home range size estimates for Australian owlet-nightjars were remarkably consistent amongst sexes, sites, years, and seasons, although there was substantial variation amongst individuals. Home range size of owlet-nightjars averaged 19.7 ha overall, using either MCP or 95% kernel methods. Based on roosting records, Schodde & Mason (1980) predicted that home range of this species should 'rarely be larger than 80 ha', and Schodde & Tideman (1990) estimated a territory size of 50-100 ha for this species. These estimates are four times the actual home range size and 30 times the average size of the roost ranges I recorded (2.7 ha). This is perhaps indicative of the elusiveness of this species. These authors likely found only a minor portion of the actual owlet-nightjars roosting in an area, and perhaps assumed that roosts of different individuals belonged to the same bird. An estimate of a territory size of 10 ha by Blakers et al. (1984), based on bird density in a eucalypt woodland in Victoria, was close to my findings.

Few home range estimates are available for other species of Caprimulgiformes. A study of two plumed frogmouths (*Podargus ocellatus plumiferus*, 145 g), a subspecies of the marbled frogmouth, estimated that the home range of the male was 10.6 ha and the female 8.1 ha (Smith et al., 1993). These two birds were from different pairs and the area of overlap of their adjacent home ranges was 0.05 ha. No territorial behaviours were observed for either sex; however, the study was conducted outside of the breeding season within rainforest. Although these results must be treated cautiously due to the small sample size, a ~10 ha home range seems plausible for a tropical non-predatory species in an area with an abundant and stable food supply. A study based on roost locations of the much larger tawny frogmouths (*Podargus strigoides*, 500g), estimated a home range size of 20 ha (Körtner & Geiser, 1999b). These authors suggested that the reason for the small territory size was the ample foraging opportunities provided by the open woodland plus surrounding grassland. Körtner & Geiser's (1999b) study was conducted in the same eucalypt woodland as my study. Although it does seem that frogmouths have small home ranges for their large size (Schoener, 1968), they are mainly perch-and-pounce sedentary predators and can be expected to have a smaller home range than more mobile aerial foraging birds. However, it is possible the tawny frogmouth home range size was underestimated by only using daytime roost locations. Schodde & Mason (1980) estimated the roost territory of the tropical Papuan frogmouth (*Podargus papuensis*) to be 5-7 ha, but the foraging range to be 20-30 ha.

For owlet-nightjars, calculation of home range size using diurnal roosts alone would predict a home-range only 5 to 21% of the actual home range size, illustrating the importance of calculating home-range estimates using both foraging and roosting locations for some species (also see Martin, 2006). The restriction of roost areas to a small portion of the total home range area indicates that the location of roosts was not a determining factor of home range size. In the desert, owlet-nightjars usually roosted in trees within creek beds or rock crevices on cliff faces in close proximity to each other, in one portion of the home range, and roost MCPs were small (5% of home range). Birds at the eucalypt woodland site had an abundance of tree hollows to select from and roosts were usually spread over a larger area (21% of home range).

Contrary to my prediction, prey availability had little effect on home range size of owlet-nightjars. Terrestrial arthropod availability was not correlated with any measure of home range size. The 95% kernel estimate of home range size correlated positively with aerial arthropod abundance, in contrast to the negative correlation predicted by home range theories (Brown, 1964). However, the MCP method revealed no correlation between these two factors, and log transforming aerial biomass data for regression analysis indicated no relationship between arthropod biomass and 95% kernel estimates. Thus, the positive correlation may have been a product of high monthly variability in arthropod biomass at the desert sites.

The larger home ranges at the desert sites compared to the woodland may be explained by preferred habitat distribution and/or competition (Pitelka, 1959; Brown, 1964; Schoener, 1968). Schoener (1968) proposed that certain avian species will inhabit larger territories if their preferred habitats are sparsely distributed. For example, the shrike (*Lanius ludovicianus*) maintains territories on sand dunes or areas of bare ground that are two to three times larger than in wooded areas (Miller, 1931, cited in Schoener, 1968), and the chickadee (*Parus atricapillus*) holds considerably larger territories in more open or sparsely wooded territory (Odum, 1941). The same principle appears to apply to owlet-nightjars in the exposed, non-wooded desert sites. A greater number of conspecifics within an area have also been found to reduce territory size (Schoener, 1968). Thus, the larger range size may be a reflection of decreased competition in the desert as owlet-nightjar densities were lower (Pitelka, 1959; Brown, 1964; Hixon, 1980).

The overall consistency of home range size estimates amongst seasons, sites and years is a reflection of the adaptive ecology of owlet-nightjars. Owlet-nightjars forage on both terrestrial and aerial arthropods. Their diet includes a wide variety of arthropods, including taxa that would normally be ignored by other nocturnal avian insectivores, such as ants and spiders (Chapter 6). Thus, during times of adverse conditions and food shortages, owlet-nightjars are able to exploit an alternative prey rather than expand their home ranges in search of food. This is an advantage in a small fragmented area, such as the eucalypt woodland site, where a large number of conspecifics would prevent the expansion of territories in times of low prey abundance. Hence, the seasonal changes in home range size exhibited by other avian species, with size decreasing during the breeding season when food is abundant and increasing during the winter when food is sparse (Brown, 1964; Orians, 1971), do not occur in owlet-nightjars. Even dry years with lower arthropod abundance in the desert did not require an increase in range size, in fact the range size actually decreased (Table 2). Desert-dwelling common nighthawks (*Chordeiles minor*) also compensated for low food resources by using less preferred food resources, rather than expanding territory size (Caccamise, 1974). As insect abundance is uniformly distributed across a landscape, in comparison to other avian food sources such as nectar, seeds or fruit (Schoener, 1968), and the distribution of arthropods was relatively uniform throughout the my study sites (Chapter 6), increasing range size in search of more abundant food resources may be pointless. Birds that are able to use local resources are at an advantage over those that must travel far in search of food. For example, barns owls (*Tyto alba*) that ranged up to 5 km from their nest in search of prey during winter in Scotland experienced high mortalities (Taylor, 2000).

As core use areas (50%) were distinct from roost areas they likely indicate the area(s) of the home range with the most dependable food sources (Burt, 1943; Samuel et al., 1985). Core use areas were small, averaging only 13% of the total home range size, but were exclusive to individuals. While it is not uncommon for home ranges to overlap for many species, the overlap of core areas usually do not (Samuel et al., 1985). I found that home range overlap was low, but overlap of core areas of non-mated neighbours did not occur. Boundaries of core areas were distantly separated, yet it was not uncommon for owlet-nightjars to have up to three main core foraging areas within their home range (Tables 1 and 2). Habitats in both the desert and the eucalypt woodland were mostly uniform and it was often not clear why owlet-nightjars preferred some foraging areas over others. However, in some instances core areas did surround an obvious resource. For example, the core area of ONJ 9's home range at the desert site focused around a permanent water hole and was separated from the roost 'cluster'

by a distance of 1 km. A permanent waterhole hole in the desert would likely offer superior food resources and this individual defended the site aggressively. Analysis of home range core areas may also identify areas that are being used for purposes other than foraging. At the desert site, the core areas of several birds (ONJ 4, 11 and 20) were within gorges.

Temperatures in the gorges were typically lower, thus, it was unlikely these birds were selecting these areas due to arthropod availability. It is more likely that the steep walls and shadows in the gorges offered increased protection from predators compared to foraging in the open (see Habitat Use). However, for most birds, especially those in the eucalypt woodland, it is unknown why one area was selected over another and further investigation is warranted.

### ***Territoriality***

The exclusion of other birds from home ranges through aggressive defence, the low percentage of overlap between same sex neighbours, and site fidelity throughout the year are indicative of a high degree of territoriality in owlet-nightjars. While it is not clear whether owlet-nightjars defend the entire home range or only part of the range, such as core or roost areas, the aggressive response to playback distant from roosts, and the lack of overlap between ranges (Table 3), suggests that the entire range may be considered a territory (Burt, 1943; Pitelka, 1959). Several researchers have emphasized the importance of examining home range overlap to determine territoriality, as opposed to relying on defensive behaviour which differs greatly between species and may be misconstrued by the observer (Pitelka, 1959; Schoener, 1968). The maximum percentage overlap between same sex neighbours in the present study was 4.5%, fitting the criteria of Schoener (1968) of only marginally overlapping, and illustrate a distinct separation between owlet-nightjar territories.

The high percentage of home range overlap between mated pairs (42%) indicates that pairs defend territories jointly, rather than maintaining separate adjoining territories. Both sexes vigorously defend territories and cavity roosts from intruders, including other bird species and cavity using mammals (Doucette, 2007). The low degree of overlap of home ranges during winter in the eucalypt woodland (1.2%) suggests that owlet-nightjars maintain stable home ranges year-round, but the defence of territories appears to be predominately in spring and summer during the breeding and nesting season. Overlap of home ranges in the desert during winter was greater (29.1%). It is unknown whether this is a year-round trend at the desert locations, and the result may be partially explained by the presence of breeding pairs that were not identified. The situation at the irrigated site is unique in that it is productive area, in

a typically dry landscape. Thus, it was not unexpected to have a high concentration of birds in this area, with a larger than average overlap in home ranges.

Both sexes of owlet-nightjar appear to share the defence of territories, roosts, and fledglings equally (Doucette, 2007), and males and females are equally likely to be caught using playback. Territorial and nest defence by both sexes during the breeding season is not uncommon for many non-passerine species which share responsibilities in feeding young, including most species of raptors (Stokes & Stokes, 1989). I found that both sexes of owlet-nightjar share incubating and brooding duties at night, while the male attends the nest during the day once all the eggs are laid. The same pattern of nest attendance has been found for tawny frogmouths (Körtner & Geiser, 1999a). Thus, the increase in vocalizations, especially soft chirping calls, during the breeding season (Figure 6a) was likely for communication between members of the pair (Ritchison et al., 1988). Debus (1997) also found that owlet-nightjar calls were most frequent between October and February in response to playback of owl calls. The high rate of aggressive calls recorded in February may be a result of adults defending fledglings that have recently left the nest and are learning to forage and fend for themselves (Doucette, 2007). Another possibility is that resident adults are defending their territories from roaming juveniles that are searching for territories as they disperse (Lundberg, 1980; Ritchison et al., 1988).

While the low rate of calls during autumn and winter is doubtlessly due to a relaxation in territory defence after the young have fledged, it could also be that owlet-nightjars devote more energy to finding enough food during the colder nights. Lower ambient temperatures results in less arthropod activity and availability (Chapter 6), thus, owlet-nightjars must increase foraging time to obtain adequate prey. Additionally, owlet-nightjars regularly enter torpor during the nocturnal active phase (up to 25% of bird-nights; Chapter 4), making them unresponsive to playback or conspecific calls. It is probable that with low ambient temperatures and low prey availability taxing the energy reserves of owlet-nightjars, vigorous territory defence is not energetically feasible during winter (see Hinde, 1956). The greater calling frequency in the desert during winter is likely due to warmer ambient temperatures, and the greater distance calls travel in an open landscape with few large trees. Playback calls would also travel further, resulting in more numerous responses from distant birds, and it is more likely that I would have heard distant response calls and unelicited calls between conspecifics.

Typically, competition for cavity roosts should increase territoriality in avian species (von Haartman, 1957). At the eucalypt woodland site tree hollows were abundant, as were hollow stumps used for nesting (Brigham et al., 1997; Brigham et al., 1998), due to previous logging activities (Ford et al., 1985). Thus, while competition for these roosts with parrots and small mammals was evident and sometimes intense (Doucette, 2007), the fact that individual birds used up to 10 different hollows (Table 1), suggests they were not a limited resource. Tree hollows were also abundant at the desert sites, but mostly restricted to specific areas along the dry river channels. Thus, these birds used alternative resources, roosting in rock crevices throughout the gorges. The supply of available rock crevice roosts was plentiful, and it was unlikely that birds competed for this resource. Nonetheless, the use of cavity roosts is an important aspect of owlet-nightjar ecology and may make the defence of home ranges or territories throughout the year more energetically feasible. The moderate microclimate inside thermally insulated cavity roosts results in substantial energy savings for birds (Walsberg, 1985; Walsberg, 1986). The use of cavities for nesting would also save owlet-nightjars the energy costs associated with nest building. Additionally, cavity roosts provide protection from predators, allowing birds to enter torpor regularly, further increasing energy conservation (Chapter 2). These energy savings may be translated into more energy available for territorial defence and the ability for these birds to maintain stable home ranges despite adverse winter conditions.

Comparisons of territorial behaviour with other species of Caprimulgiformes are difficult because of a paucity of data. A study examining territorial behaviour between two species of nighthawk in North America with overlapping ranges found distinct differences (Caccamise, 1974). Lesser nighthawks (*Chordeiles acutipennis*) did not actively patrol a well-defined territory, but roamed over large distances in search of food and water. In contrast, common nighthawks (*C. minor*) were strongly territorial, spending the majority of their time within territorial boundaries and defending territories with flight displays and vocalizations. Tawny frogmouths exhibited variable degrees of defensive behaviours, including flying away, bill clapping, and hissing, towards a human intruder inspecting nests (Körtner & Geiser, 1999a). However, while tawny frogmouths appear to have well established territories (Körtner & Geiser, 1999a), no observations have been made for territorial defence amongst conspecifics. Several species of nightjar can be captured using playback techniques (Bub, 1995), which does indicate a degree of territoriality, depending on the level of aggression exhibited. For example, whip-poor-wills (*Caprimulgus vociferous*) respond aggressively to playback (Lane, 2002), suggesting they may defend breeding territories.

### ***Habitat Use***

Foraging home ranges at the desert sites encompassed large expanses of relatively open ground, sparsely vegetated with mallee (*Eucalyptus socialis*) and spinifex grasses (*Triodia brizoides*, *T. longiceps*). While the majority of birds at the desert site roosted diurnally in river red gums (*Eucalyptus camaldulensis*) in the creek channel, they never foraged over these areas. This is likely because they are easily visible from above against the light coloured sand in the creekbeds. Instead, owlet-nightjars often used gorges and gullies to traverse from one area to another, flying close to the ground, and as suggested previously, likely relied on these areas for concealment from predators. Birds did not require the use of large trees while foraging, and typically perched in small mallee shrubs or on the edge of rocky outcrops.

Owlet-nightjars at the eucalypt woodland site usually roosted within the woodlands, however, several birds roosting near the border foraged throughout surrounding open paddocks, spending the majority of their activity phase in open landscape with few large trees. One individual (ONJ 35) travelled >1 km outside of the woodland each night (Figure 2), regularly crossing >100 m of open paddock between small patches of trees. As I was unable to see owlet-nightjars when they crossed through exposed areas, it is likely they were flying very close to the ground in order to prevent their silhouette from being backlit against the sky. The reason some birds travelled these large distances is unknown. In the case of ONJ 35, there were two waterholes within his home range and near his roost cluster (Figure 2), on the border the nature reserve boundary, where prey availability would have been greater than in the paddocks. In contrast to the sheltered woodland, paddocks were often covered in frost at night during August and September and likely would have had offered lower food resources. Furthermore, this bird often communicated using soft chirps with another untagged bird in his roost area, which I presumed to be his mate, before dispersing across the paddocks. During his nightly trip through the paddocks I never heard him vocalize.

My study in the eucalypt woodland indicates that owlet-nightjars are able to live in high densities in relatively small fragments of woodlands. Davey & Pech (2000) also found that owlet-nightjars were 'surprisingly common' in fragments of woodland <200 ha in south eastern New South Wales. I found that owlet-nightjars readily crossed open areas and would not be restricted to corridor use to move between fragments. This suggests that when there are adequate roost cavities available, owlet-nightjars are at moderately low risk due to landscape fragmentation in comparison to many other species. Owlet-nightjars readily inhabit manmade

structures and have been found roosting in rain gutters, building cavities, and nest boxes (Menkhorst, 1984; Higgins, 1999; Lindenmayer et al., 2003; F. Geiser, personal communication). In the irrigated desert site based in a popular wildlife park, owlet-nightjars readily roosted in stumps beside busy footpaths. Their nocturnal habits, cryptic nature and camouflage allows them to live in close proximity to humans without being detected, a factor which may secure their survival in the future as human populations expand into bush areas.

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## CHAPTER 8

### General Discussion

The Australian owlet-nightjar (*Aegothelidae cristatus*), a member of the Caprimulgiformes, has distinct behavioural, ecological and physiological features that enable them to adapt and live successfully in a variety of diverse habitats throughout Australia. My study examined the biological qualities that allow this species to survive and thrive and in two of these habitats, the hot, arid desert of central Australia and the comparatively cold, mesic, eucalypt woodlands atop the Northern Tablelands of NSW. Energetically, both habitats should be taxing for a small, nocturnal bird, yet owlet-nightjars are successful and abundant at both sites, as they are throughout most of Australia. Flexible energy saving behaviour, including selecting roosts with specific thermal microclimates and obtaining prey by ground foraging, and physiological features, such as having a low BMR and employing torpor regularly during winter, allow this species to live in and exploit these habitats.

Cavity roosts are typically buffered against extremes in ambient temperature ( $T_a$ ) and offer birds and mammals that inhabit them substantial energy savings (Walsberg, 1985; 1986). In the semi-arid zone of central Australia, owlet nightjars use both rock crevices and tree hollows as roosts. Rock crevices are better insulated and, hence, thermally more stable than tree roosts. These are advantageous to owlet-nightjars on cold nights and mornings, apparently requiring torpor use less often than when roosting in a tree hollow. Nonetheless, owlet-nightjars use tree roosts more often than rock crevices (65% versus 35% of bird-days). Tree roosts may be preferred on days when individuals have had a poor night of foraging, or when ambient temperatures are low enough to be challenging their energy reserves, and torpor is beneficial. Tree hollows are cooler than rock crevices, facilitating torpor use, yet warm quickly on sunny days allowing birds to passively rewarm with minimal energy expenditure (Lovegrove et al., 1999; Mzilikazi et al., 2002; Geiser et al., 2004; Turbill, 2006). The use of torpor and the ability to passively rewarm should result in substantial energy savings for a small bird, enabling owlet-nightjars to live in habitats with cold nocturnal ambient temperatures and comparably low insect activity during winter.

Cavity roosts also offer owlet-nightjars protection from predators, especially while in torpor. However, based on the lack of diurnal predation, it seems any cavity offers adequate protection from predators, and thus, birds likely select roosts based on thermal buffering characteristics. Tree hollows were chosen based on the exposure of the roost entrance to solar radiation, and

birds preferred roosts with reduced canopy cover, greater cavity height and north-facing. Rock crevices were selected for their thermal stability. Owllet-nightjars choose deep rock crevices, with narrow entrances, located on northern-facing steep slopes. The use of cavities also serves to offset the energy required for cooling during the hot summer  $T_{as}$  at the desert site, and rock crevices remained cooler on hot days. Owllet-nightjars exhibited low roost fidelity, changing roosts every 17 days on average. Roost switching may reflect attempts of birds to find roosts with a better or more suitable microclimate on a given day. I hypothesize that owllet-nightjars specialize in finding roosts that maximize their energy savings.

Previously, most studies of torpor use by Caprimulgiformes and other avian species in the laboratory have relied on restricted diets or a period of fasting to induce birds to enter torpor (Marshall, 1955; Lasiewski & Dawson, 1964; Peiponen, 1965; Dawson & Fisher, 1969; Hohtola et al., 1991). This led to the hypothesis that energetic emergencies were necessary for torpor use by free-ranging birds. However, recent studies have found that energy deficits are not necessary for torpor induction (Reinertsen, 1983; Brigham, 1992; Körtner et al., 2001; Turbill et al., 2003; Schleucher, 2004), yet it was not clear how reduced food availability affected free-ranging birds. Owllet-nightjars used torpor regularly during winter at low  $T_a$ , but torpor bouts was more frequent, deeper, and longer in habitats with reduced prey availability. My results suggest that torpor use is a physiological adaptation by owllet-nightjars to conserve energy reserves throughout winter, even in the moderate climate of the desert. Birds using torpor frequently during winter maintained high body mass (BM), indicating that a state of pronounced energetic emergencies did not occur. My study provides one of the very few examples of a field based study that addresses the use of torpor by birds in the absence of an energetic emergency.

BM and basal metabolic rate (BMR) of owllet-nightjars did not vary seasonally. However, decreased conductance and lower resting metabolic rates at low  $T_{as}$  in winter-acclimatized birds suggests that an increase in insulative plumage enhances the ability to tolerate low winter  $T_{as}$ . The lack of variation in BMR between seasons may be due to the relatively large size of owllet-nightjars and their use of cavity roosts during their rest phase, which negates the need to respond physiologically to changing seasons in a region with a moderate winter climate in comparison to that experienced by North American birds.

Ground foraging for terrestrial prey was more prevalent amongst owllet-nightjars than predicted, especially in the eucalypt woodland habitat. The diet of owllet-nightjars at this site

was consistent seasonally, suggesting that ground foraging is a year-round adaptation to cope with relatively low arthropod availability. Terrestrial foraging requires less energy than aerial prey capture (Goldstein, 1990), and may be the preferred method of foraging if adequate cover offering protection from predators is present. Owlet-nightjars used a variety of foraging tactics including sallying, perch-and-pounce, seizing prey items from the ground and occasionally tree trunks, and hopping along the ground picking up small arthropods. Most types of arthropods were readily consumed and the diet of owlet-nightjars was surprisingly diverse, including a high proportion of Formicidae and Arachnids. This flexible foraging behaviour, combined with the physiological adaptations and the use of cavity roosts, precludes the need for owlet-nightjars to migrate in order to survive cold winter conditions, unlike most other species of Caprimulgiformes (Holyoak, 2001).

Home range size was consistent between the desert and eucalypt woodland habitats and did not vary with season. It may not be necessary for owlet-nightjars to adjust range size with fluctuating food availability given that they switch foraging tactics from aerial to terrestrial prey items and maintain BM throughout the winter by foraging on widely available prey such as Formicidae. Owlet-nightjars were highly territorial, exhibiting aggressive vocalizations, low range overlap and high site fidelity (Pitelka, 1959; Schoener, 1968). The maintenance of a permanent home range throughout the year is advantageous because the best foraging sites and refuges, such as cavity roosts become familiar (White & Garrott, 1990). This familiarity with an area would offset the energy expended by territorial defence, especially when resources are scarce.

The high degree of flexibility in ecological requirements, including the use of vastly different roost types and a variety of foraging tactics, at least partially explains the success of owlet-nightjars in diverse habitats throughout Australia. Cavity roosts seem to be a key factor in energy conservation, and in some habitats it may be this resource that promotes the high level of territorial behaviour. A low BMR reduces energy expenditure for owlet-nightjars year-round, and torpor use greatly enhances energy savings during winter, allowing birds to exploit cold habitats and those with highly fluctuating daily  $T_a$  and food availability. Moreover, cavity roosts combined with a cryptic, nocturnal nature allows owlet-nightjars to live in close proximity to humans, further increasing the range of potential habitats they can occupy.

Previously, little was known about the cryptic Aegothelidae and my research has answered many questions, but obviously there is still much to learn. Almost nothing is known about the

seven species of owlet-nightjar found in Papua New Guinea (Holyoak, 2001), which generally inhabit rainforest environments and their ecology and physiology may differ extensively from the Australian owlet-nightjar. The New Caledonian owlet-nightjar (*A. savesi*) was only rediscovered in 2002, having been thought extinct for several decades, and may yet vanish before we have the opportunity to learn about it (Ekstrom et al., 2002). It would be fascinating to learn more about unique family of birds that so differ from the other Caprimugliformes, and hopefully this thesis represents a good starting point in our knowledge of the behaviour ecology, energetics and physiology of the elusive Aegothelidae.

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## Appendix I

### Abstracts from Scientific Conferences

Doucette, L.I., Pavey, C.R., Burwell, C. and Geiser, F. 2007. Aerial versus Terrestrial Prey: Diet and Foraging Tactics of Owllet-Nightjars Differ in Desert and Woodland Habitats, 4<sup>th</sup> Biennial Australasian Ornithological Conference, Perth, Western Australia, 3-5 December 2007. Oral presentation.

Doucette, L.I., Brigham, R.M., Pavey, C.R. and Geiser, R. 2007. Roost Type Influences Thermoregulatory Behaviour of Australian Owllet-Nightjars (*Aegotheles cristatus*) in the Arid Zone. 24<sup>th</sup> Annual Meeting of the Australia and New Zealand Society for Comparative Physiology and Biochemistry, Perth, Western Australia, 1-2 December, 2007. Oral presentation.

Doucette, L.I. 2007. Dark Cavities and Sunny Canopies: Winter Roost Selection by Australian Owllet-Nightjars. 32<sup>nd</sup> Annual Conference of the Ecological Society of Australia, 25-30 November 2007, Perth, Western Australia. Oral presentation.

Doucette, L.I., Harvey, F.J., Brigham, R.M. and Geiser, F. 2006. Roost Selection by Australian Owllet-Nightjars (*Aegotheles cristatus*) in the Arid Zone of Central Australia: Behavioural and Ecophysiological Aspects. 11<sup>th</sup> Congress of the International Society for Behavioural Ecology, Tours, France, 23-29 July 2006. Oral presentation.

Doucette, L.I., Harvey, F.J., Brigham, R.M. and Geiser, F. 2006. Roost Selection by Australian Owllet-Nightjars (*Aegotheles cristatus*) in the Arid Zone of Central Australia: Behavioural and Ecophysiological Aspects. School of Environmental Sciences & Natural Resource Management Postgraduate Conference, University of New England. 27-28 June 2006. Won "Best Presentation". Oral presentation

Doucette, L.I., Brigham, R.M., Pavey, C.R. and Geiser, R. 2006. Thermal Biology and Torpor of Australian Owllet-Nightjars (*Aegotheles cristatus*) in the Arid Zone. Australian Bird Study Association Science Day, Canberra, Australia, 25 March 2006. Oral presentation.

### Publication

Doucette, L.I. 2007. Aggressive Behaviour by Australian Owllet-Nightjars Defending Fledglings. *Australian Field Ornithology*. **24**(2): 60-63 + cover.