Thermal biology of two burrowing arid zone species: The Great desert skink (*Liopholis kintorei*) and the Brush-tailed mulgara (*Dasycerus blythi*)

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Abstract

More than two thirds of Australia is arid or semi-arid. These areas are predominately in the centre of the continent and despite the low rainfall and extreme thermal conditions they are inhabited by many and highly diverse animals. The groups that are among the most successful in the arid zone are the ectothermic reptilian skinks (Family Scincidae) and the endothermic carnivorous marsupial mammals (Family Dasyuridae). The aim of my study was to examine behavioural and functional traits that make life in the arid zone possible despite a substantially different thermal biology and energy expenditure. Two locally sympatric burrowing species, the vulnerable great desert skink (*Liopholis kintorei*, Scincidae) and the brush tailed mulgara (*Dasycercus blythi*, Dasyuridae) were examined using radio telemetry and behavioural observations. Daily activity patterns and body temperature fluctuations in relation to environmental temperatures were investigated to determine seasonal use of dormancy and burrow use by desert skinks over a 12-month period. Similarly, activity patterns and torpor use, which is characterised by reductions in body temperature and results in a substantial reduction in energy expenditure, and differences between torpor use and home range between summer and winter by mulgaras were investigated.

Great desert skinks spent the majority of their time during their active months at their main burrow (65.8 ± 2.0% of days tracked), but all individuals made regular forays to other burrows (4.1 ± 2.2% of days tracked; (*N* = 16 (burrows), *n* = 3), particularly during the spring breeding season. Average *L. kintorei* T_b during summer was 32.5 ± 1.6°C, during autumn 28.4 ± 2.9°C, during winter 18.4 ± 3.2°C and during spring was 27.7 ± 3.1°C. *Liopholis kintorei* T_b was significantly different between all seasons ($P < 0.005$). They were more active than previously thought, displaying predominantly unimodal activity, particularly during autumn and the beginning of winter. In spring skinks were predominantly active after dawn, during the day and ceased activity after dusk. Movement between burrows increased 7-fold between spring and summer ($P < 0.001$) with females moving within a much smaller home range than males. During spring, skink activity was predominantly unimodal (62.5%) however, showed increased crepuscular and bimodal daily activity patterns (49.4%) during summer. They regularly switched to diurnal and highly unimodal (81.2%) activity in autumn and early winter (99.9%) when ambient temperatures were low. All skinks displayed some level of activity in the cool autumn months but there was no movement between burrows. When daily maximum temperature dropped below ~20°C, all four skinks moved to winter hibernacula 72 – 226 m from their main burrows, where they remained dormant for about three months with body temperatures falling to a minimum of 7.8°C (mean = 14.2 ± 3.5°C). Migration to separate inconspicuous hibernacula during winter may be an anti-predator strategy. Some individuals also estivated from late in summer in chambers at a depth of ~22 cm (mean body temperatures = 32.3 ± 1.8°C; mean soil temperatures at 20 cm = 32.8°C) with one female skink remaining dormant for 50 days from February to April. Because winter brumation occurred at shallow depths (~11 cm) below the surface we suggest this may provide a reproductive advantage by allowing desert skinks to be aroused as early as possible from brumation in spring by being exposed to daily fluctuating cycles of increasing ambient temperatures.

In contrast to skinks, mulgaras were active all year round, but displayed daily torpor mainly during the cold season when the combined effects of cold winter temperatures with reduced food availability also requires regular use of torpor as means to conserve energy. Mulgaras were largely nocturnal in summer but showed some diurnal activity in winter. Activity appeared to be highest during the first half of the night during both winter and summer. During the winter mating season males were more active for longer than females irrespective of ambient temperature ($P = 0.015$), whilst female mulgaras appeared to increase activity with higher night-time temperatures. Duration of activity for both sexes was significantly shorter in winter compared to summer ($P < 0.001$). Home ranges were larger in winter, particularly for males which were almost four-fold greater than in summer. Ambient temperature and season were found to be significant predictors of mulgaras using daily torpor and there was a statistically significant difference in use of torpor between at summer (8 days/320; 2.5 ± 1.1%) and winter (264 days/301 days; 86.9 ± 8.1%, $P < 0.001$). In winter, body temperatures in torpid mulgaras fell as low as 11.7°C (mean = 21.8 ± 5.8°C) and the duration of torpor bouts was on average 9 hours. Infrequent, shallow use of torpor occurred during the latter part of summer but with average burrow temperatures of 31.4°C, the ability to reduce body temperatures below the torpor threshold (32°C) appears to have been restricted. Sex had no effect on torpor use during summer, but differences in torpor expression occurred between sexes during winter due to different selective pressures on reproduction (torpor frequency of males = 88.0 ± 10.6%, 150 days tracked, $n = 3$; females = 85.4 ± 5.8%, 151 days tracked, $n = 2$). Female mulgaras used deeper and more prolonged torpor than males during winter, however, they ceased using torpor from early spring, presumably once parturition and lactation began. The number of burrows used in summer for both sexes was considerably less than burrows used during winter and overall, females used more burrows than males despite smaller home ranges in winter. Burrow fidelity appeared to be higher in summer than winter for both sexes.

Similarities between the two sympatric species included home range of males being larger than females during their distinct breeding seasons, along with increased burrow use. Males of both species presumably traversed larger areas to increase opportunities to reproduce. Activity for both species was shorter in winter than in summer and inactivity, whether displayed as daily torpor, estivation or brumation is clearly a significant survival trait to conserve energy and water through periods of low food availability and predator avoidance. My study shows that a combination of functional and behavioural traits permit both species to persist in the arid centre of Australia.

Certification

I certify that the ideas, experimental work, results, analyses, software and conclusions reported in this thesis are entirely my own effort, except where otherwise acknowledged. I also certify that the work is original and has not been previously submitted for any other award, except where otherwise acknowledged.

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Candidate Name	Date

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Chapter One

Introduction

Thermal biology, and activity in Australian arid-zone vertebrates

The Australian vertebrate fauna is highly unusual because the continent was separated from other land masses for millions of years. Many endemic species inhabit the continent and because Australia became more arid as it drifted north towards Asia in the Pleistocene, animals had to adapt to life with limited water and food and extreme temperatures (Pough & Janis, 2019). Over half of Australia is now desert, receiving less than 300 mm/year (Colls & Whitaker, 2012) and although one might assume that these areas are lacking in animal life, this is not the case at all. Many organisms live in the arid zone of central Australia and these have evolved to survive in very dry conditions with extreme ambient temperatures (T_as) ranging from below 0^oC to well over 40^oC with highly variable and unpredictable rainfall events. Many desert species have therefore adapted to harsh conditions by living a semi-fossorial existence (Kinlaw, 1999). Boom-bust rainfall events produce a temporary abundance of food resources allowing such species to survive during years of resource poor drought conditions (Körtner et al., 2016). Ongoing survival through harsh periods is further impacted by direct and indirect ecological pressures such as habitat fragmentation, introduced herbivores and predators, diseases, and climate change (Lindenmayer & Fischer, 2006), which particularly impact species already under pressure to survive on available resources and within intact refugia.

Ectotherms

Perhaps somewhat unsurprising is the fact that ectothermic reptiles with their low metabolic rate and thick skins that minimise water loss are one of the dominant arid-zone groups (Cogger, 2014). Since ectotherms absorb heat from outside of their body (Geiser, 2021), have low metabolic rates and lack insulation in the form of feathers or fur, their body temperature (T_b) rises and falls with T_a (Bogert, 1959; Tattersall et al., 2012). However, many free-living terrestrial reptiles maintain T_bs via behavioural thermoregulation often involving the uptake of radiant heat from the sun and can often display T_bs that are higher than those of sympatric endotherms (Bogert, 1959; Heatwole & Taylor, 1987). As such ectothermic reptiles can be considered low-energy, variable-temperature systems able to control their own T_bs behaviourally over a wide range of T_as (Shine, 2005; Pough & Janis, 2019).

Since ectotherms are unable to produce substantial internal heat for thermoregulation, primarily absorb warmth from the environment (Tattersall et al., 2012) and do not metabolise food for physiological thermoregulation, they achieve optimal temperature thresholds by balancing behavioural and physiological processes to gather and digest food, reproduce, and avoid predators (Huey, 1982). As such thermoregulatory behaviour of reptiles is dictated by complex relationship between costs and benefits (Huey & Slatkin, 1976). Many reptiles thermoregulate by basking to increase T_b, angling their bodies to the sun, moving to warmer surfaces, or flattening their bodies to absorb warmth (Bogert, 1959; Shine, 2005). Similarly, cooling may be achieved by realigning their bodies relative to the sun or moving to shade or burrows (Bogert, 1949). This has led to morphological and physiological characteristics such as body elongation, length/diameter ratios and ability to reduce T_b that enable them to exploit niches often unavailable to endotherms and has enhanced their survival through long periods of reduced access to resources (Pough, 1980). When annual temperatures decrease below optimal activity thresholds, most reptiles enter a state of dormancy known as brumation by not only lowering their T_b but also their metabolism and heart rate, and thus energy requirements (Seymour, 1973; Nordberg & Cobb, 2016; Holden et al., 2021). Thus, reptilian low energy and water use and their behavioural adaptions make them most suitable for life in deserts.

All ectotherms are constrained by thermal limits which affects their ability to function within their environments and must avoid critical maximum (CT_{Max}) and minimum (CT_{Min}) temperatures before temperatures beyond these limits cause death. CT_{Max} and CT_{Min} temperatures for reptiles are defined as the T_b at which locomotory ability is disorganised and the animal losses its ability to escape from conditions that may lead to its death (Cowles and Bogert, 1944), and therefore is the temperature at which a specimen loses its ability to right itself (Spellerberg & Spellerberg, 1972). High temperatures can kill animals very quickly, but they can quite often recover from hypothermia. For ecological purposes however, CT_{Max} and CT_{Min} closely represent lethal temperatures (Cowles and Bogert, 1944).

CT_{Min} was previously considered more ecologically significant than CT_{Max} in regard to species distribution (Spellerberg & Spellerberg, 1972). However, research using mechanistic modelling indicated that although mild global warming could increase dispersal in some species, increased warming would likely affect egg development, activity time and evaporative water loss (Kearney & Porter, 2004). Mean summer CT_{Min} in a laboratory study on a variety of southeastern Australian reptile species from warmer arid zones and cooler Bassian zones ranged between 2.2 and 9.8°C (Spellerberg and Spellerberg, 1972). Species from hotter zones always had higher CT_{Min} values than those in cooler zones. Although most species had CT_{Min} values between 2 and 4°C, summer CT_{Min} values were always found to be higher than winter CT_{Min} values. Mean CT_{Max} of all species studied ranged between 37.0 and 44.8°C whilst the CT_{Max} of species surviving in warmer temperate zones ranged between 40.6 and 42.8°C, and surprisingly not necessarily higher than CT_{Max} values of some cooler zone species. The difference between the CT_{Max} of small and large specimens of the same species was however found not to be significant (Spellerberg and Spellerberg, 1972).

Ectothermic reptiles are not the only vertebrates living in the arid-zone of Australia. These deserts are also inhabited by diverse small carnivorous/insectivorous marsupials of the family Dasyuridae, among others. Although dasyurids are endothermic and therefore have much higher energy requirements than ectotherms (Withers et al., 2016), the number of especially small species found in the arid zone are actually higher than those living in mesic areas (Dickman, 2003). Unlike ectotherms, endotherms burn metabolic fuels to generate heat for physiological thermoregulation and, aided by fur insulation, have the ability to maintain a high and more or less constant T_b even when exposed to low T_as (Tattersall et al., 2012; Withers et al., 2016).

Endotherms

The ability for endotherms to maintain high T_bs, especially in cold climates is made possible by an increased aerobic capacity, which allows them to sustain higher levels of activity compared to ectotherms (Hillenius & Ruben, 2004). Metabolic rates of birds and mammals are generally 20 to 30-fold higher than reptilian rates (Hillenius & Ruben, 2004), but can be 100-fold higher in small species exposed to low T_as (Withers et al., 2016; Geiser, 2021). To maintain a high and constant internal T_b, which enables increased stamina and speed as well as fast growth, endotherms need to be more active and consume much more food than ectotherms (Shine, 2005). Despite this, the evolutionary success of endotherms is exemplified by their wide-spread distribution across terrestrial, aerial, and aquatic environments (Pough & Janis, 2019).

The increase in heat production in endotherms is achieved by rapid muscle contractions (shivering), or non-shivering thermogenesis (Pough & Janis, 2019). Both are sustained by oxidation of chemical energy, which is energetically costly and requires the above-mentioned high food intake. In cold or resource-poor environments this has significant disadvantages (Körtner et al., 2008a) and this is especially the case for small species, which have a relative greater surface area than large species and therefore lose more heat per gram of body mass to the environment. As heat loss is a function of both size and the difference between T_b and T_a, small endothermic species such as dasyurids, which rely on ephemeral insects as food source are faced with an energetic conundrum (Geiser, 2021).

Many small endothermic mammals and birds deal with this challenge by lowering their metabolic rate (MR) and T_b and entering a state of torpor to conserve energy and water. In contrast to homeothermic endotherms, which always maintain a high and more or less constant T_b, the species entering torpor are referred to as 'heterothermic' endotherms (Geiser, 2021). Torpor is often defined as a drop of T_b below 30 °C, in which metabolism, respiratory rate and heart rate are depressed. And although it is widely believed that torpor is accompanied by reduced responses to external stimuli and inability to move (Thain et al., 2000), this is actually not entirely the case since, as for example dasyurids, can move while torpid from crevices or burrows to basking sites to rewarm passively in the sun from torpor and further reduce energy expenditure (Rojas et al., 2012; Warnecke et al., 2008).

Two patterns of torpor, daily torpor and multiday torpor (hibernation) are common (Ruf & Geiser, 2015). Daily torpor is the pattern observed in species that reduce T_b from over 35ºC during periods of activity, and below the 'normothermic' rest phase (33 to 35 ºC), to between 10 to 25ºC during periods of torpor. Daily torpor typically lasts between 5 and 10 hours and the torpor MR (TMR) is about 30% of the basal metabolic rate (BMR) (Geiser & Körtner, 2010). Species that use daily torpor exclusively under all thermal and trophic conditions are referred to as daily heterotherms (Ruf & Geiser, 2015). By using daily torpor, these species are able to conserve energy and reduce food and water requirements during cold periods, assisting them to survive adverse conditions such as wildfires, droughts and floods, and also permits reproduction to begin in winter or when resources are low (Geiser & Masters, 1994; Geiser & Körtner, 2010; Stawski et al., 2015).

Heterothermic mammals typically use daily torpor while resting and arouse between torpor bouts to forage (Geiser & Körtner, 2010). Studies have shown that free-ranging Australian arid zone dasyurids will enter torpor up to 20 hrs daily during winter, which can reduce energy costs and therefore food requirements by up to 80%, avoiding excessive exposure to introduced predators (Geiser & Körtner, 2010). In Australia, many small homeothermic mammals such as bandicoots, rodents and small macropods have experienced severe population declines and extinctions since colonisation by European settlers and the introduction of domestic and feral animals. In contrast all of the small (< 1kg) heterothermic mammals have survived (Geiser & Stawski, 2011; Geiser & Turbill, 2009). Torpor use however did not prevent the regional extinction of larger dasyurids such as the western quoll (*Dasyurus geoffroii* ~1300 g; Cooper & Withers, 2010), which has suffered enormous population losses and range reductions. It appears the survival success of small heterothermic mammals could be due to a combination of body size, ability to burrow or find refuges from predators and extreme climatic conditions as well as the ability to use torpor.

The other common pattern of torpor, multiday torpor in the hibernators is the pattern that is much better known by the public and is much deeper and longer than daily torpor and can occur in species distributed anywhere from the arctic to the tropics (Dausmann et al., 2004). On average, the T_b of torpid mammalian hibernators is 6°C, several species lower T_b to below 0°C and the MR is reduced to only 5% of BMR (Ruf & Geiser 2015; Geiser, 2021). Hibernation is typically characterised by torpor bouts that last between 2 and 3 weeks that are however interrupted by periodic arousals to normothermic T_bs throughout the hibernation season, usually lasting from autumn to spring. Although these arousals are energetically costly, and in many hibernators are not used to forage, their function remains obscure. Hibernation in Australian deserts has been observed in echidnas, pygmy-possums and bats, but not in any dasyurid, all of which seem to be daily heterotherms (Geiser, 2004).

Arid zone study species

Two specialist and often sympatric native burrowing species which occur at locations across the arid zone are the ectothermic great desert skink or tjakur̲a (*Liopholis kintorei*) and the heterothermic brush-tailed mulgara or murtja (*Dasycercus blythi*; McAlpin, 2001). Both species are significant in their environment because they are the dominant predator amongst smaller localised groups of native mammals (Körtner et al., 2007; McAlpin, 2011). *Liopholis kintorei* is classified as ‘Vulnerable’ under the Environment Protection and Biodiversity Conservation Act 1999 (EPBC) due to combined detrimental effects of wildfires, fragmented populations, predators (both native and feral), increased roadkill, ground water extraction and reduced traditional land management practices (Cadenhead et al., 2016; McAlpin 2001; Moore et al., 2018a). This species is of particular interest to science due to its patchy distribution, population declines, localised extinctions, and kin-based sociality (Dennison et al., 2015; McAlpin et al., 2011).

Both species of mulgara are not currently listed as vulnerable under the EPBC Act, however, *D. cristicauda* is listed as ‘Vulnerable’ under the Territory Parks and Wildlife Conservation Act 2000, and *D. blythi* has been previously classed as ‘Vulnerable’ under the same Act. With the loss of *D. geoffroii*, the largest remaining dasyurids in the arid zone, are the crest-tailed mulgara (*Dasycercus cristicauda*; 65–185 g; Burwell et al., 2018), *kowari (Dasyuroides byrnei*; 135-180 g; Van Dyck & Strahan, 2007) and brush-tailed mulgara *(Dasycercus blythi*; 44-123 g; Masters & Dickman, 2012). The persistence of *D. blythi* is therefore of interest to science and the broader community (Department of Climate Change, Energy, the Environment and Water, 2022). Importantly, both species hold cultural significance for Aboriginal people in central Australia, feature in tjukurpa (law, dreaming stories, ceremonies) and were/are considered important food sources (Gibson & Rive, personal communication, 2018; McAlpin, 2011).

Burrow use of two sympatric species

Semi-fossorial animals world-wide create and occupy burrows for a wide variety of reasons. These include protection from predators, fire and extreme temperatures, to give birth and rear young, to store or obtain food and to utilise torpor and hibernation (Shipley & Reading, 2006; White et al., 2006; Körtner et al., 2008). Species, from small rodents, lizards, arachnids and some birds, to larger species such as aardvarks surviving in arid zones globally are especially reliant on burrows to escape extreme temperatures and high rates of evaporation and will utilise both freshly made and abandoned burrows from the same or different species (Whittington-Jones et al., 2011; Williams et al., 1999).

In arid environments where ambient temperatures can range greatly, studies show that burrows can be 15-20°C cooler than surface temperatures, they maintain relatively stable temperatures and can increase humidity thereby reducing evaporative water loss (Williams et al., 1999; Whittington-Jones et al., 2011). The creation of burrows may also create favourable microhabitats for other species with some burrowing species being classified as ecosystem engineers and keystone species (Shipley & Reading, 2006). In addition to the creation of underground refugia that may be used by a variety of taxa, burrowing activity can enhance ecosystem function, structure and composition through the mixing and aeration of soils, increasing water infiltration and accumulation of nutrients (Magle et al., 2012; Shipley & Reading, 2006; Kotliar, 1999).

Burrowing habits of L. kintorei

Burrowing species either create burrows (primary excavators), transform existing burrows for their own use (secondary modifiers), or simply occupy burrows created by other species (Kinlaw, 1999). For example, in arid zones of central Australia, the burrows of one primary excavator, the greater bilby *(Macrotis lagotis)* are used with various degrees of regularity by at least 20 other animal species including mammals, birds, reptiles, amphibians and invertebrates (Hofstede & Dziminski, 2017). Mammals are generally considered primary burrowers however other species such as spiders, scorpions and reptiles may also fulfil that role in certain arid environments (Kinlaw, 1999; Polis et al., 1986). One such excavator is *L. kintorei* which digs large elaborate burrow systems (McAlpin, 2001). These burrows can be co-occupied by a variety of other vertebrate species such as *D. blythi* and other dasyurids such as dunnarts (*Sminthopsis* spp) and *Ningaui ridei* (McAlpin, 2011). Observations from expert Aboriginal trackers and hunters inform us that *L. kintorei* can tolerate the presence of goannas (*Varanus gouldii*) and *D. blythi* in their burrow (M. Gibson & M. Teamay, personal communication, 2018). McAlpin (2011) however states that *L. kintorei* burrows may eventually be appropriated by species that are known to prey on *L. kintorei* such as woma pythons (*Aspidites ramsayii),* elapid snakes (*Pseudonaja mengdeni* and *Pseudechis australis)*, monitor lizards (*V. gouldii*) and even *D. blythi*, (McAlpin, 2011). *L. kintorei* likely play an important role in creating and providing ecological niches within arid environments.

The burrow systems of *L. Kintorei* are extensive with two to over 10 entrances and interconnecting tunnels up to 1m deep offering an excellent buffer against extreme temperatures (McAlpin 2001; Moore et al., 2018b). While *L. kintorei* create large burrows systems, they also modify the burrows of other species such as *D. blythi*, sand goanna (*V. gouldii)*, spinifex hopping mouse (*N. alexis*) and the night skink (*Egernia striata*) (McAlpin, 2001). Research has shown that *L. kintorei* burrow entrance temperatures during hot summer days can be as high as 49°C while internal temperatures can drop to 34°C (Moore et al., 2018a). *Liopholis kintorei* burrows also maintain high levels of relative humidity (RH) ranging from 62% to 97% throughout the year (Moore et al., 2018a) in contrast to arid external environments where the median RH can be 23% during the day and 38% at night (Bureau of Meteorology, Yulara, 2018).

For the majority of time *L. kintorei* behavioural thermoregulation may be achieved by selecting different depths within the burrow which is important in avoiding predators, especially for gravid females and newborns (Dennison, 2015). Specific data on CT_{Min} of *L. kintorei* do not exist however, it is known that temperatures deep within *L. kintorei* burrows throughout winter months are stable ranging from 13°C at mid-depth to 14°C at the lowest depth (Moore et al. 2018a). These temperatures would support McAlpin's (1997) suggestion that *L. kintorei* may hibernate at a depth of 1 m during winter however, he later noted that *L. kintorei* spend several months sequestered in small, backfilled tunnels off the main tunnel (McAlpin, 2011). As there is little information on burrow depth of brumating *L. kintorei* during winter months it would be interesting and useful to confirm.

Burrowing habits of D. blythi

In addition to *D. blythi* constructing their own burrow systems, research based on observations, radio-tracking and spooling technique have shown that they use and modify burrows originally constructed by varanids, *Liopholis sp*., rodents, rabbits and *L. kintorei*. (Hofstede & Dziminski, 2017*;* Masters 2003; Molyneux et al., 2018; Thompson & Thompson, 2014). Typical burrows normally have a one to three entrances, however, burrow systems may be more elaborate consisting of up to nine entrances (Körtner et. al., 2007; Thompson & Thompson, 2007). *Dasycercus blythi* burrows are generally between 25-50cm deep, although can be as deep as 65 cm and 60-220 cm long (Körtner et al., 2008; Thompson & Thompson, 2007). Burrow entrances can drop steeply or descend at shallow angles (Körtner et al., 2008) and be slightly wider and higher than the inside tunnels which are 50-70 mm wide (Thompson & Thompson, 2007). *Dasycercus blythi* use a number of burrows within their home range and display low burrow use fidelity (Körtner et al., 2007).

In arid environments, with sandy soils, Körtner et al. (2008) found that where winter ambient temperature ranged from below 0°C to above 20°C, surface temperatures can be considerably warmer ranging from just above 0 to over 34°C. When informed by soil temperature records, burrow temperatures of *D. blythi* at depths of ~35-50 cm averaged 15.5°C with daily fluctuations of just 0.8°C, while shallower burrows at depths of ~17 cm displayed greater temperature fluctuations ranging from approximately 11°C to 17°C (Körtner et al., 2008). Relative humidity (RH) for all burrows during that study was close to 100% with fluctuations depending on depth and rain. Additionally, temperatures within spinifex ranged approximately between 2° and 24°C (Körtner et al., 2008). It appears *D. blythi* burrows that are created underground beneath spinifex tussocks could be well buffered by extreme temperatures.

Home Range, foraging biology and activity patterns of L. kintorei

Liopholis kintorei is generally assumed to be a crepuscular species when active on the surface and spends most time sequestered inactive deep in their burrows (Moore et al., 2018a). Activity at burrow entrances is typically highest at dawn and dusk and lower during the middle of the day (Ridley, et al., 2020) when summer surface temperatures can exceed 55°C (Bruton et al., 2014) well above the CT_{Max} for *L. kintorei* (Moore et al., 2018a). During hot summer months the depth of *L. kintorei* burrows seem to facilitate their thermoregulatory needs. In a study at Newhaven Wildlife Sanctuary in central Australia, surface and burrow activity recorded between the spring and summer months of September to December showed that *L. kintorei* spent over half their time sequestered in their burrows at depths of 50 cm-1m, and 35% of their time at depths of 15-30 cm (Moore et al., 2018a). A small portion of daily activity was spent at the burrow entrance and only 4% of time was spent active outside the burrow, usually at dusk (Moore et al., 2018a). Body temperatures of *L. kintorei* when active ranged between 25.7 and what appeared to be the voluntary maximum body temperature of 39.6°C (Moore et al., 2018a).

Research on *L. kintorei* home range found that the average distance travelled between burrows was 83 m for males and 40 m for females. The maximum distance travelled by females and males is similar, with females travelling up to 180 m and males travelling up to 175 m. (Dennison, 2015). Although McAlpin (2000) observed that *L. kintorei* can move up to several hundred meters, genetic spatial analysis indicated that dispersal is male biased, with males moving between burrows significantly more often than females and juveniles (Dennison, 2015). Females generally remain monogamous while males are known to frequently sire offspring to various females in different burrow systems (McAlpin, 2011; McAlpin et al., 2011). The propensity for males to move further afield than females could possibly account for the species dispersal distances of generally 0-4 km but up to 9 km. (Dennison, 2015). At Uluṟu in central Australia, 3 adult male *L. kintorei* were recorded for every 5 females encountered (McAlpin, 2011). Assuming an unbiased sex ratio at hatching, the lower abundance of males could explain polygynous behaviour across a larger home range, although lower abundance could be due to higher levels of predation as a result more frequent roaming.

Food availability may also affect surface activity of *L. kintorei*, potentially lengthening crepuscular or nocturnal activity. *Drepanpterms perniger* termites form a major part of the diet of *L. kintorei* and Dennison (2015) found a significant relationship between active burrows and the presence of termite mounds. During periods of high humidity, termite swarms can be active between sunset and sunrise, encouraging *L. kintorei* to forage opportunistically for longer periods especially after rain (Andersen, 2005; McAlpin, 2011; Moore et al., 2018a).

Home Range, foraging biology and activity patterns of D. blythi

Dasycercus blythi are opportunistic predators that forage over large areas and can excavate a wide range of invertebrates and small vertebrates from their burrows, including small lizards (Chen et al., 1998; Thompson & Thompson, 2014). McAlpin (2001) suggested that *D. blythi* prey on *L. kintorei,* particularly on juveniles or when individuals are hibernating. As there is a reduced supply of invertebrates and other prey during winter months *D. blythi* would benefit from preying on high energy resources such as small reptiles (Pavey et al., 2009; Molyneux et al., 2018).

Compared to other small dasyurids *Dasycercus blythi* display high site fidelity and are relatively sedentary (Masters 2003). Research has shown that male and female home ranges at the Uluṟu- Kata Tjuṯa NP bore fields overlap, but can differ greatly between sexes (Körtner et al., 2007). Individuals interact frequently and can display a high degree of social tolerance with burrow sharing occurring between both the same and opposite sexes. (Körtner et al., 2007). Difference in home range could be influenced by seasonal changes, breeding, food availability and presence or lack of vegetation (Masters, 2003). In winter *D. blythi* can use up to 15 burrows and although they can move over 670 m between them, they typically move between 100-300 m on consecutive days (Körtner et al., 2007). Winter home range for male *D. blythi* is on average approximately 25 ha and females about 10 ha (Körtner et al., 2007), although another study found the average home range to be less (Masters, 2003). It is unknown if summer home range differs to winter months.

Aims

The thermal biology of a species greatly influences its behaviour and responses to changing environmental conditions. As such, ectotherms are less reliant on regular food availability, but their activity can be constrained by their thermal environment. Endotherms, on the other hand, can achieve a greater climatic independence, but at high energetic costs limited by food availability. Hence, understanding the thermal biology of species and how they function within their environment can inform us how particularly vulnerable organisms persist in ecosystems affected by environmental extremes (Stawski et al., 2015). Particularly for threatened species, such information can therefore assist land managers predict behavioural responses of species to threatening processes and mitigate immediate and long-term risks.

The aim of this study was to analyse the thermal biology of two arid zone burrowing species across seasons which share a number of traits; despite one being an ectotherm and the other a heterothermic endotherm. Both species are expected to interact to some degree so monitoring the movements of both species may determine levels of interspecific interactions. They also interact to some degree so monitoring both species may determine levels of interspecific interactions. Living a semi-fossorial existence, they spend large portions of their lives within burrows to regulate their body temperature and avoid predation. They are both impacted by feral predators. Although they share many similar traits and occur in the same habitat, differences lie in their physiology; one being heterotherm able to conserve energy by using torpor and sustain high levels of activity even in cold climates; the other a less active 'low-energy' ectotherm, able to control its own T_b behaviourally but unable to operate effectively in cold temperatures. It appears that both species use cold temperatures to either facilitate use of torpor or brumation throughout winter months however, understanding use of torpor in summer months is not well understood in free-living dasyurids and the extent of inactivity in a burrowing reptile to conserve energy in summer months should be further examined.

For *D. blythi* I aimed to quantify the energetic and fitness consequences of heterothermy in a free-living endotherm and for *L. kintorei* I aimed to further investigate its response to changing ambient temperatures. In monitoring both species I aim to understand more about their activity and movement patterns across seasons. While torpor expression during winter has been studied previously in *D. blythi*, no measurements are available outside winter and therefore no seasonal comparisons can be made. In *L. kintorei* some data are available on ecology and distribution (McAlpin, 2011; Ridley et al., 2020), social organisation and population genetics (Dennison et al., 2015; McAlpin et al., 2011), threatening processes such as predation and fire pressure (Cadenhead et al., 2016; Moore et al., 2015; Moore et al., 2018b) and operative temperatures in relation to T_b and activity budgets, along with projected effects of climate warming (Moore et al., 2018a). As for *D. blythi* a comparison of thermal biology of *L. kintorei* between seasons is lacking. By analysing the differences between the thermal biology of two sympatric species of different classes (an ectotherm and a heterothermic endotherm) across seasons, findings may provide land managers with relevant information to support management actions in the protection of these species.

The aims of my study are to i) determine seasonal patterns in thermal biology of *L. kintorei* and extent of activity and burrow use and ii) determine seasonal differences of torpor use and activity patterns by *D. blythi* during summer and winter.

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Chapter Two

Seasonal differences in the thermal biology and spatial behaviour of the great desert skink (*Liopholis kintorei*)

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Introduction

Australia's arid zone is characterised by long periods of drought interspersed with highly variable rainfall, low nutrients and reduced resources (Morton et al., 2011). Fauna occupying arid regions encounter extreme environmental conditions due to large variations in daily and seasonal ambient temperature (T_a) (Perry & Goodall, 1978), and have suffered the highest rates of vertebrate extinction in recent history (Molyneux et al., 2018). Despite this, the Australian arid zone is home to a wide array of flora and fauna with the most diverse species of lizards worldwide (Pianka, 1996) and a high diversity of snakes (Wilson & Swan, 2010). In particular, the diversity of lizard species in the arid interior is believed to be a result of an intricately linked relationship with fire succession cycles which create heterogeneous habitats (Pianka & Goodyear, 2012). As such, many species of arid zone reptiles rely on a semi fossorial existence to cope with such events and extreme annual temperatures (Kinlaw, 1999). Ectotherms, including reptiles have low metabolic rates (Hillenius & Ruben, 2004) which allows them to survive on low energy costs during long periods of reduced access to resources (Shine, 2005; Pough & Janis, 2019).

Reptile thermal biology differs greatly to endotherms as they generally thermoregulate behaviourally, for example by moving to warm areas to heat up or moving to shaded areas or burrows to cool down (Bogert, 1949), but this is however multifarious (Huey & Slatkin, 1976). For example, by increasing their heart rate and peripheral circulation they can increase heat absorption and by decreasing heart rate they can conserve body heat (Raske et al., 2012). A species' thermoregulatory behaviour defines how it functions within environments, so examining this can provide insights into how organisms are able to survive environmental extremes (Stawski et al., 2015).

Laboratory studies have shown that reptile body temperatures (T_bs) generally increase or decrease with fluctuating surrounding temperatures if there is enough time to reach equilibrium (Bogert, 1959; Spellerberg, 1972; Vickers & Schwarzkopf, 2016). However, field studies have shown clearly that reptiles can maintain T_b within narrow limits via behavioural thermoregulation despite wide variations in T_a and surface temperature (Bogert, 1959; Pough, 1980). Furthermore, some species have been found to regulate their T_b independently of the external environment (Raske et al., 2012). Thermoregulatory behaviour results in costs and benefits (Huey & Slatkin, 1976) which requires a balance between behavioural and physiological processes affected by the need to gather and digest food, to reproduce, and avoid predators (Huey, 1982).

Simple behaviour such as basking allows reptiles to achieve high T_bs (Shine, 2005) and the ability to heat up quickly reduces reaction time when approached by predators (Cowles & Bogert, 1944). Basking thus enables ectotherms to take advantage of heat gain from conduction and radiation to raise their T_b passively (Geiser, 2021). Similarly, when reptiles retreat underground their T_b, especially in small species can decrease rapidly.

Reptile species display preferred T_b ranges for optimal performance that support biological function (Raske et al., 2012). In general, the active body temperatures of reptiles fall within a relatively narrow range which fluctuates a few degrees above or below the mean (Bogert, 1949; Heatwole & Taylor, 1987). Brattstrom (1965) recorded lizard T_bs which ranged between 11.0 and 46.4°C with mean T_b at 29.1°C. Interspecific, conspecific and seasonal variation in mean T_b of active lizards however occurs and can be for example, as low as 20.3°C for the three-toed earless skink (*Hemiergis decresiensis*) from south eastern Australia (Huey & Bennett, 1987) or as high as 40.0°C in the desert iguana (*Dipsosaurus dorsalis*) from the Sonoran and Mojave Deserts (Brattstrom, 1965). Research on the Arizonan spiny lizard (*Sceloporus jarrovi*) recorded mean T_b at 34.0°C yet found that conspecific competition for optimal basking positions occurred where dominant males maintained higher mean T_bs of 35.7°C compared to smaller males which displayed mean T_bs of 32.1°C (Rusch & Angilletta, 2017). Seasonal differences have been recorded in Galapagos land iguanas (*Conolophus Pallidus*) where mean T_bs during hot and cool seasons vary between 36.6 and 32.2°C respectively (Christian et al., 1983) and also in the European wall lizard (*Podarcis guadarramae*) where mean T_b during summer is 28.7°C, in contrast to winter at 20.7°C (Ortega & Perez-Mellado, 2016).

Thermoregulatory behaviour in hot arid environments may include avoiding activity in the middle of hot summer days or increasing activity during cooler times of the year (Huey & Pianka 1977). When analysing body temperatures of reptiles, it is necessary to consider the period of time an animal remains within various thermal microhabitats, their body mass, rate of movement and operative body temperatures (Bakken & Gates, 1975; Seebacher & Shine, 2004).

Research has shown that once reptiles move underground for prolonged periods, soil temperatures provide a close approximation to T_b (Gregory, 1982) which is generally within 0.5°C of soil temperature (Moberly, 1963). Soil temperature is however far from uniform and changes with depth and time of day. However, Seebacher and Shine (2004) suggest that as body mass of ectotherms increases so does equilibration time within the operative environment. Because heat was found to transfer more quickly through a smaller body (15 minutes for a 0.01 kg lizard from T_b = 20°C to an operative temperature of 40°C), small reptiles equilibrate with their surrounding temperature much faster than larger individuals (90 minutes for a 5-kg lizard with the same temperature difference) which have slower rates of heating and cooling (Seebacher & Shine, 2004). It is therefore important to consider this when drawing conclusions about behaviour based on T_b alone. Additionally, some species of reptiles can maintain T_b above ambient temperatures (T_a) without the assistance of solar radiation, for example leatherback sea turtles (*Dermochelys coriacea)*, lizards of the genus *Liolaemus*, corn snakes (*Elaphe guttata*) during digestion, carpet pythons (*Morelia spilota*) and the females of several other python species which shiver to increase body temperature when incubating eggs (Raske et al., 2012).

In temperate environments energy availability and temperatures fluctuate predictably with season resulting in many species hibernating during winter (Geiser 2021; Ultsch, 1980). Such species experience seasonal cycles with temperatures well below their optimal activity threshold which affects their physiology and behaviour (Williams et al., 2015). For many ectotherms to survive cold and resource poor periods they need to remain inactive for extended periods of time in a state of dormancy known as brumation or hibernation (Ultsch, 1980; Gregory, 1982). This involves reduced metabolism, heart rate, and energy demands (Holden et al., 2021) and is often triggered by changes in photoperiod, a drop in temperature and reduced access to their usual food sources (Goodyear & Strine, 2022). Some species however interrupt winter dormancy by moving from within burrows to burrow entrances or emerging to move between burrows, for example rattlesnakes (*Crotalus horridus* and *Crotalus oreganus*;

Nordberg & Cobb, 2017), Rosenberg's goanna (*Varanus rosenbergi*; Rismiller & McKelvey, 2000) and several other lizard species (Gregory, 1982).

Because reptiles can potentially remain dormant for long periods of time, brumation signifies an important aspect of their lifecycles and maintenance of energy balance (Grant & Doherty, 2009; Holden et al., 2021). Brumating species rely on winter cues for entering and exiting dormancy (Williams et al., 2015) and the processes by which they achieve this is more than simply a state of dormancy brought about by cold conditions but involves complex suppression of metabolic processes (Gregory, 1982; Holden et al., 2021). A study on brumation patterns of desert reptiles showed they predominantly appear to brumate alone and in what appeared to be random locations (Cowles, 1941). Communal hibernation occurs in some species of snakes in the northern hemisphere however, research has shown that mainland Australia does not get cold enough to warrant communal hibernation (Shine, 1979). The summer version of dormancy is termed estivation and differs to brumation because higher temperatures increase metabolic rates which may result in increased water loss compared to winter dormancy (Christian et al., 1996).

In desert environments seasonal changes are compounded by extreme daily temperature fluctuations and lack of water availability. The T_bs can exceed well over 40°C and drop below 0°C in a single day (Shipley & Reading, 2006). For example, the Egyptian burrowing lizard (*Uromastyx aegypticus*), escapes surface temperatures of up to 55°C by retreating to burrows that can be 15-20°C cooler (Williams et al., 1999). Burrows of the great desert skink (*Liopholis kintorei*) are known to have temperatures ~40°C less than surface temperatures and provide close to 100% humidity (Moore et al., 2018). Moreover, the deep burrows of springhares (*Pedetes capensis*) and the aardwolf (*Proteles cristatus*) fluctuate just 5°C annually and maintain high levels of humidity which show that a buffered microclimate can reduce evaporative water loss (Whittington-Jones et al., 2011). In central Australia specifically, surface temperatures can reach 34.1°C in winter (Körtner et al., 2008) and be up to 78°C during summer (Moore et al., 2018). Burrows are therefore an essential refuge for a vast number of desert species effectively buffering them from extreme changes in T_a and helping to lower thermoregulatory energy expenditure and water loss (Moore et al., 2018).

One species surviving in the harsh arid zone of central Australia is the burrowing and viviparous great desert skink (*Liopholis kintorei*). They occur in patchy distributions across spinifex deserts in central Australia and are classified as 'Vulnerable' under the Environment

Protection and Biodiversity Conservation Act 1999 (EPBC). This is due to combined detrimental effects of wildfires, fragmented populations, feral predators), increased roadkill, reduced traditional land management practices and potentially excessive ground water extraction (McAlpin 2001; McGregor et al., 2014; Moore et al., 2017). Population sizes are low across their range and show distinct genetic variation, especially in populations around Uluru-Kata Tjuta National Park, and the risk of genetic diversity being lost over time can be compounded by a combination of threatening processes (Dennison, 2015; Dennison et al., 2015).

The burrows of the relatively sociable *L. kintorei* house family groups of up to four cohorts which use one to two communal latrines on the surface of the burrow system (McAlpin, 1997). The extensive burrow systems range over 10 m in diameter, can be 80-100 cm deep and are made up of interconnecting tunnels with several to a dozen entrances (Moore et al., 2015; McAlpin, 2015). The structure of the complex burrow systems supports highly related family groups and may encourage group stability, low juvenile dispersal and reduced intraspecific aggression (Dennison, 2015; McAlpin et al., 2011). Living in social aggregations occurs also in members of *Egernia sp.* which are closely related to *L. kintorei* and appears to support higher survival rates of offspring, predator avoidance (Chapple, 2003).

Liopholis kintorei are relatively large with snout-vent length up to 225 mm and can weigh up to 350 g (McAlpin, 2011). Individuals are sexually mature at about two years of age and when spring temperatures rise during September and October, *L. kintorei* arouse from brumation and begin mating over the following weeks. Male *L. kintorei* are highly polygynous whilst females appear to be monogamous and give birth to 1-7 young in late December to early January (McAlpin, 2011).

Within communities of *L. kintorei*, movement between, and occupation of new and previously abandoned burrows varies over time. Whilst new burrows can be excavated, abandoned burrows are often re-used as individuals within a burrow system leave to establish new breeding pairs, while continuing to shuttle to and from their original burrows (McAlpin, 2011). Activity patterns of *L. kintorei* differ between sexes and males move between a greater number of burrows than females (Dennison, 2015). The distances between burrows of related individuals generally range from 25-200 m but can be up to 500 m apart (McAlpin, 2011). Depending on seasonal conditions, active foraging becomes more extensive at dusk allowing *L. kintorei* to forage further from their burrows, at times up to several hundred metres (McAlpin

2011). At a local population level dispersal is generally up to 0-4 km but can be greater (McAlpin 2011) with a male bias (Dennison, 2015). The dispersal of females is less than males and they are more closely related and live closer together (Dennison, 2015; McAlpin 2011). This low level of dispersal results in clustered sub-populations of ~10-20 ha but can be up to ~300 ha (McAlpin 2011).

Male lizards often have larger home ranges than females, for example throughout most of the Autarchoglossa and Iguania clades (Perry & Garland, 2002) and male reticulate collared lizards (*Crotaphytus reticulatus*; Ryberg et al., 2019). Similarly, it has been found that the polygynous male *L. kintorei* are under pressure to establish new burrows, presumably to pair up with females with which to mate, causing them to move further afield and establish larger home ranges (McAlpin, 2011). Larger home ranges may improve chances of reproducing, but this increases energetic costs. While excavating new burrows and maintaining relationships by moving between burrows, increased foraging to fuel activity is required, potentially exposing them to greater risks of predation (McAlpin, 2011). Species such as pygmy bluetongues (*Tiliqua adelaidensis;* Fenner & Bull, 2011) and the lizard *Phrynocephalus vlangalii* from China (Qi et al., 2012) expend energy defending territories and guarding valuable resources such as burrows. Male *L. kintorei* may also incur additional energy costs while defending their offspring from unrelated males. Such attacks from outsiders are not exclusive to *L. kintorei,* and one study of a related *Egernia* species noted that highly aggressive interactions occurred between males when defending territories (While et al., 2009).

To cope with energy shortages and increased costs during long periods of low T_a, limited rainfall, and low food availability, *L. kintorei* spend much of the active season time deep in their burrows where temperatures are more stable and low, and humidity is high (Moore et al., 2018). One study found that during the first two months after exiting their winter dormancy period, *L. kintorei* spent 88% of their time sequestered within their burrows where they appeared to be inactive for 82% of that time. Furthermore, of the time spent within burrows, 52 % was at a depth ranging between 50 cm and 1 m and 35% of spent between 15 and 30 cm.

Reptiles often switch their daily mode of activity to experience similar thermal environments in summer and winter (Pianka, 1969). Bimodal activity comprises two well-separated activity peaks per day and unimodal activity as one activity peak per day (Foà & Bertolucci, 2001). A study on the large shingleback skink, *Tiliqua rugosa* demonstrated that activity was mostly unimodal during cooler days and bimodal on hotter days (Firth & Belan, 1997). Prior research on *L. kintorei* established that during warm periods, activity patterns are typically bimodal, with skinks being active for several hours from early to mid-morning and during the late-afternoon and into the evening. Henzell, (1972) recorded *L. kintorei* at dusk and during the evening only. Moore et al. (2018) determined that 8% of daily activity occurred at the burrow entrance and just 4% of activity was spent on the surface and patterns were predominantly crepuscular, or bimodal. They also found that there were equal proportions of diurnal and nocturnal surface activity.

Actively foraging species have been found to spend over half their active time moving, whereas sit-and-wait predators generally spend ~30% of their potential activity period moving (Hertz et al., 1988; Moore et al., 2018). McAlpin (1997) observed that most *L. kintorei* diurnal activity involves waiting in ambush for long periods of time at burrow entrances for prey, including a large variety insects and other arthropods, small reptiles or potentially small mammals to pass (McAlpin, 2011). In doing so *L. kintorei* thermoregulate by spending hours shuttling between basking at burrow entrance mounds to waiting just within the burrow entrance. These behaviours naturally vary between individuals and the composition of burrows in relation to vegetation. For example, *L. kintorei* may spend a greater amount of time outside burrows that are provided with cover near burrow entrances than when little or no cover is present (Ridley et al., 2020). The combined behaviour of shuttling in and out of the burrow to thermoregulate and opportunistic sit-and-wait foraging can reduce the amount of time required to forage beyond the safety of the burrow system and potentially reduce exposure to predation.

Preferred body temperatures of reptiles vary between species, depending on habitat and latitude (Huey & Pianka 1977; Dawson, 1975). Prior to Moore et al. (2018) recording T_b data of *L. kintorei* there were few T_b records for the species. Under laboratory conditions, mean T_b of *L. kintorei* is 33.6°C (31.8°C under dehydration; Henzell, 1972), with a single value of 25.2°C recorded by Pianka (1967). Moore et al. (2018) found that *L. kintorei* T_b ranged between 25.7 - 39.6°C for all activity between September and December 2013. The T_b range during surface activity was somewhat narrower between 27.1 and 37.6°C with mid 50% T_b ranging from 32.1 - 34.6°C. Seasonal difference can however occur and research on *T. rugosa* found that between spring and summer average T_b was 33.8°C and in autumn was 32.3°C (Firth & Belan, 1997).

A laboratory study that analysed T_b and activity of *L. kintorei* determined the critical thermal maximum T_b (CT_{Max}) to be 43.1°C by averaging the CT_{Max} of two *Liopholis* species, *L. inornata* (42.8°C; Spellerberg & Spellerberg, 1972) and *L. slateri* (43.5°C; unpublished). Moore et al. (2018) recorded voluntary maximum T_b of *L. kintorei* at 39.6°C during mid spring to early summer. Despite optimal T_b being as high as 33.6°C, prevention of evaporative water loss is particularly important for arid zone reptiles. Henzell (1972) suggested such species may prefer nocturnal activity when air temps are cooler and below typically preferred T_b. Additionally, McAlpin (1997) recorded *L. kintorei* activity outside of burrows when the air temperature was as low as 22°C. There has been no CT_{Min} recorded for *L. kintorei* however the related *L. inornata* was found to have a high summer CT_{Min} value of 9.8°C which would likely be ~1°C lower in winter (Spellerberg & Spellerberg, 1972).

The buffering effects from extreme arid temperatures of *L. kintorei* burrow systems can be extremely beneficial and during summer months can average between 34°C and 37°C at depths of ~80 cm and 40-50 cm, respectively (Moore et al., 2018). In contrast, Temperatures were found to be as high as 49°C at burrow entrances, requiring animals to retreat deeper within burrows. This research found that *L. kintorei* burrow temperatures never exceeded voluntary maximum T_b and that in July they were vastly lower, ranging from 14°C deep in burrows to 9°C at burrow entrances. This would likely restrict activity of *L. kintorei* during winter months.

Detailed research on *L. kintorei* has investigated the ecology, social organisation, population genetics and distribution, effects of fire and other threatening processes, operative temperatures, the buffering effects of burrows in relation to body temperature, activity budgets and the projected effects of climate warming. Two Recovery Plans for *L. kintorei* have been developed since 2001 which provide valuable information and recommendations on how to monitor and protect the species. The National Recovery Plan for the Great Desert Skink (*Liopholis kintorei*) 2023-2033 (DCCEEW, 2023) recommends monitoring surveys of *L. kintorei* should occur when skinks are active (October- March) and that abundance of subpopulations can be determined by the number of active burrows in an area. We have also learnt about the life history and behaviour of *L. kintorei* from Traditional Owners who grew up hunting them and continue to inform and participate in management actions. There is however a general lack of knowledge of reptile behaviour during winter (Holden et al., 2021). Reptiles can spend up to two thirds of their lives inactive (Etheridge et al., 1983) and according to Huey

(1957), research on reptilian ecology should focus equally on inactivity as much as activity. Further, it has been recommended that studies on the thermal ecology of reptiles should consider seasonal changes in availability of thermal habitats, acclimatization, hormonal rhythms and food supply (Schauble & Grigg, 1998). So, despite existing research on *L. kintorei*, there are gaps in knowledge of the thermoregulatory behaviour of this species during cooler months, particularly during brumation. Additionally, knowledge of how seasonal changes affect the home range of *L, kintorei* is limited, as is the frequency of movement between burrows and how seasonal change affects activity budgets.

Through use of implanted temperature sensitive radio transmitters, we hypothesised that the activity patterns of *L. kintorei* across seasons based on changes in T_b would indicate they are most active during spring and summer, less so in autumn, and brumating and inactive at their main burrows during winter. We also predicted that bimodal and crepuscular activity during warmer months would switch to unimodal and diurnal activity in cooler months.

Material and Methods

Location and field work period

Fieldwork was conducted during the summer season from 13 January 2018, through one austral winter season and into a second summer period until 11 January 2019. The study area was located at the bore fields area within Uluru-Kata Tjuta National Park (UKTNP) within the Great Sandy Desert, Northern Territory (NT), Australia (25°16'S, 130°56'E; Figure 1). The bore fields that provide the water supply for a nearby resort are located on a sand plain bordered by mulga (*Acacia aneura*) woodland and low dunes dominated by spinifex species (predominantly *Triodia basedowii*) a spiky grass forming dense hummocks ~50 cm high, interspersed with the sub-shrub *Androcalva loxophylla* and sparsely growing *Grevillea sp*. and desert oaks (*Allocasuarina decaisneana*). Seasons were defined by widely accepted quarterly periods for temperate Australia; Summer: December to February; Autumn: March-May; Winter: June-August; Spring: September- November (Rodo, Baert & Comin, 1997).

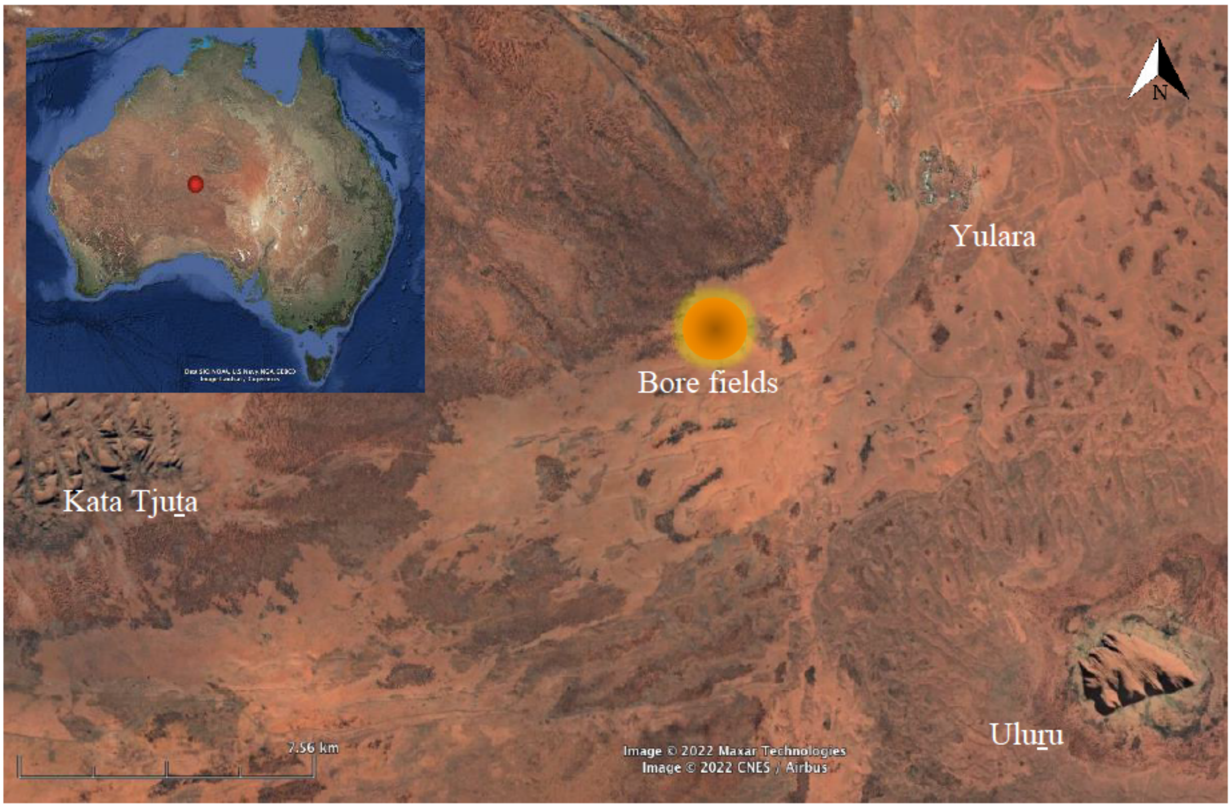


Figure 1. Field study site for great desert skinks (*L. kintorei*) within the bore fields area (orange circle) of Uluru-Kata Tjuta National Park, NT, Australia. Inset image shows the research site location within the arid zone of Australia.

Capture and surgery

Liopholis kintorei burrow systems were determined to be active if fresh tracks and recent excavations at burrows were visible and if latrines contained fresh scats (Moore et al., 2015). Up to four type A Elliott traps were set up at several active *L. kintorei* burrow systems (Dennison, 2015) for ~8 nights. In addition, four pitfall traps (~50 cm deep; Ø = 150 mm; narrow enough to prevent feral predators preying on caught specimens) were set along ~12 m lengths of fly-wire drift fence (~35 cm high and buried about 5 cm) positioned in an arc outside the area of *L. kintorei* burrow systems (Hobbs et al., 1994). Funnel traps were positioned along lengths of wire mesh at both ends of the pitfall trap line. Elliot traps were baited with a mixture of peas and corn (Dennison, 2015) and set within two hours of sunset and closed < two hours after sunrise. Once caught, all animals were weighed with an electronic scale to the nearest 0.1 g and kept one to two days in individual holding boxes (45 x 45 x 45 cm). Wood roaches and water were provided *ad libitum*.

During summer 2018, 18 *L. kintorei* were captured, only four of which were adults (247.1 g, 238.3 g, 203.9 g, 181.0 g) with the body mass of the remaining ranging between 11.3 - 136.3 g. The four adults were implanted with radio transmitters while the remaining animals were too young to implant transmitters, and these were released at the site of capture. Animals were anaesthetised with Isoflurane in oxygen and implanted with small, sterilised, wax coated, temperature-sensitive radio transmitters weighing 3.0 – 3.6 g (Sirtrack, Havelock, New Zealand). The transmitters weighed well below the recommended 5% of the animal's body mass (NSW Department of Primary Industries Animal Welfare Unit and Animal Research Review Panel, 2020) and were calibrated to the nearest 0.1°C over a temperature range of 9.6° – 41.6°C against a high-precision mercury thermometer (Rojas et al., 2010; Körtner et al., 2008).

The site of the incision was sterilised with alcohol and Betadine before a short (~1 cm) abdominal incision was slightly offset from the midline to avoid a major blood vessel, after which the transmitter was inserted intraperitoneally. Both muscle and skin layers were sutured separately with polyglycolic acid surgical sterile sutures followed by a local anaesthetic (10% Xylocaine pump spray/ 3M Vetbond glue) and an antibacterial spray bandage. The procedure lasted between 20-40 minutes per animal, plus a 60-minute recovery period. After recovery, animals were placed their own boxes and released the following day at their burrows on dusk at the site of capture.

Skinks were recaptured on the 28 February (skink 2), 8 April (skink 1), 21 June (skink 3) and 15 November (skink 4) to assess their condition of the surgical wounds. Skink 3 was inspected when found during the day while in the process of creating a new burrow in June. This individual's surgery had not healed well and because low temperatures can affect resistance to disease and bacterial infection (Adolph & Porter, 1993; Kluger, 1979) it was taken back to the researcher's residence where its condition was closely monitoring with additional treatment of antibiotics (Flagyl Suspension; 0.1 ml orally for 10 days). The transmitter was not removed, and the assumption was that the surgical wound would heal better in a sterile and warmer environment. When the wound had healed in October the skink was released at its main burrow after the other skinks had aroused from brumation. The surgical wounds for the other three skinks had all healed well and were still active after winter suggesting this procedure, apart from the one that did not heal quickly as the others, overall did not adversely affect them.

To determine sex of individual *L. kintorei* manual eversion of hemipenes was attempted but this was unsuccessful. Therefore, traits based on visual appraisal and sexual dimorphism were used based on the methodology of McAlpin (2011). Using this method, the ratio of head widths (HW) to snout-vent length (SVL) of males should average 16.7% and HW to SVL in females should average 15%. Photographs of *L. kintorei* captured for the study were provided to an experienced researcher of this species, Steve McAlpin for further visual appraisal and advice. As the study progressed behavioural traits further contributed to our assessment of the sex of each individual. The small pool of individuals was thus made up of probably 3 females and 1 male *L. kintorei* (Table 1).

Table 1. Measurements used to determine sex based on head width (HW) and snout-vent length (SVL) ratios. Head length (HL) and behavioural information was also used to determine sex with more confidence.

Individual	Body Mass (g)	SVL (mm)	HW (mm)	Head length (mm)	Ratio HW to SVL	Sex based on SVL-HW ratio	Sex after additional assessment
Skink 1	247.1	215	30	34	13.90%	Female	Female
Skink 2	238.3	193	30	35	15.50%	Female	Female
Skink 3	203.9	175	26.5	32	15.14%	Possibly female	Male
Skink 4	181.0	187	27	30	14.40%	Female	Female

Radio-tracking and temperature logging

Tracking was carried out on foot or in a vehicle using 3-element Yagi antennas (Sirtrack, Titley and ATS models), at times affixed to a 2.4 m pole standing on the tray of a utility vehicle and attached to Icom IC-R10 receivers (Icom inc.). Each radio-transmitter had a unique frequency so different individuals could be identified and the intervals between pulses changed with temperature, which is why it can be used to determine temperature from pulse rate. Tracking was used to identify individual animals, daytime refugia, $T_{b,}$ and movement patterns.

Provided an animal could be located daily, T_b was recorded by positioning mobile data loggers ~1.5m from each individual animal's burrow. The loggers measured and stored the transmitter's pulse interval every 10 min (Körtner & Geiser, 1998) and these data were downloaded to a laptop computer every few days. Pulse intervals were then converted to body temperature based on transmitter-specific calibrations (Körtner & Geiser, 2011). The ability to conduct research during the year was limited at times so loggers were left in the field to record T_b where skinks remained at burrows and downloaded when possible. Data gaps however occurred where *L. kintorei* moved to different burrows when the researcher was unable to visit the site.

Once animals were located each morning their location was marked and recorded with a hand-held GPS (Garmin GPSmap 62S). The location of daytime refugia of each *L. kintorei* was recorded to determine their movement between burrows. Minimum convex polygons (MCP) were created using the burrows as edge points and minimal home range area was calculated for each specimen in Google Earth Pro. Because waypoints were not recorded when *L. kintorei* were active we consider the area of the polygons to only be a conservative estimate of the core home range. Even with limited field visits, sufficient *L. kintorei* movement was recorded throughout winter because they were largely dormant. Despite the inability to record daily observations between October 2018 and January 2019, a substantial amount of T_b data were obtained in addition to movement patterns between burrows based on transmitter signal recordings on different loggers.

Burrow temperatures were recorded in three active *L. kintorei* burrows throughout the study period by positioning iButton data loggers along lengths of cable feeder and inserting them into burrow openings. Because depth of burrows does not necessarily correlate to length, data loggers were affixed with cloth tape at various lengths ranging between 0 cm (burrow entrance), 50 cm, 100 cm, 150 cm and 200 cm. Soil temperature (T_s) was recorded by taping data loggers at seven depths on timber stakes (5, 10, 20, 35, 50, 80, 100 cm) and burying them in the ground at two areas withing the study site. Depth of brumation chambers was determined by matching *L. kintorei* T_b with T_s and confirming that by digging into the chambers after the skinks had aroused and moved back to their main burrows.

Ambient temperature was recorded using temperature and relative humidity loggers (iButtons) held within polystyrene cups and positioned ~1.6 m high in shrubs and beneath clumps of spinifex (*T. basedowii)*. This data was used to correlate with body temperature data at increments of 30 mins. Rainfall data were collected from the Bureau of Meteorology (BoM) weather station at Yulara (Station number 015635) ~7 km from the field site. Where there were gaps in the logger data set, T_a, data from BoM were used for statistical analysis.

Activity

To investigate thermoregulatory behaviour, we compared T_b of *L. kintorei* with T_a and where required, soil (T_s), burrow temperature and particularly burrow entrance temperature ($T_{b\text{-}e}$) data. Data were visualised on a day-by-day basis using a custom-written program in Visual Basic 6 (Microsoft Corporation, WA; Figure 2). T_b was correlated with T_a to determine how changes in seasonal temperatures affected activity and dormancy. Maximum, minimum and average T_b data for each 24-hour period was calculated using the same Visual Basic 6 program. Only days with more than 200 minutes of T_b recordings (<20 readings) were included in further analyses. Comparing soil temperatures with body temperature corroborated hibernacula depth with measurements of hibernacula taken after skinks had returned to their main burrows. Additional behavioural information was collected by installing Reconyx motion sensor cameras at 22 active *L. kintorei* burrows.

Temporal patterns of T_b in conjunction with T_a were used to determine activity. Generally, activity periods were characterised by rapidly changing T_b patterns especially noticeable after long periods of inactivity, represented by lines of consistent T_b values. End of activity was determined by the last T_b value towards the end of a period of activity before resting T_b values became consistent for at least 60 minutes (Figure 2-1). Individuals were regarded as inactive if T_b fluctuations of 1°C or less occurred over several hours (Figure 2-2). Daily activity was split into distinct periods (up to three) if separated by at least 240 minutes of rest (Figure 2-3).

Confidence in assessing activity start and end times was increased by comparing change in T_a, $T_{b\text{-}e}$ or T_s at a depth of 5 cm with *L. kintorei* T_b (Figure T-4). This was further validated by matching calculations with individual *L. kintorei* exiting or entering burrows photographed on motion sensor cameras (Figure 3). Duration of activity was recorded using this same method and days where activity could not be determined with a high level of confidence were disregarded for analysis.

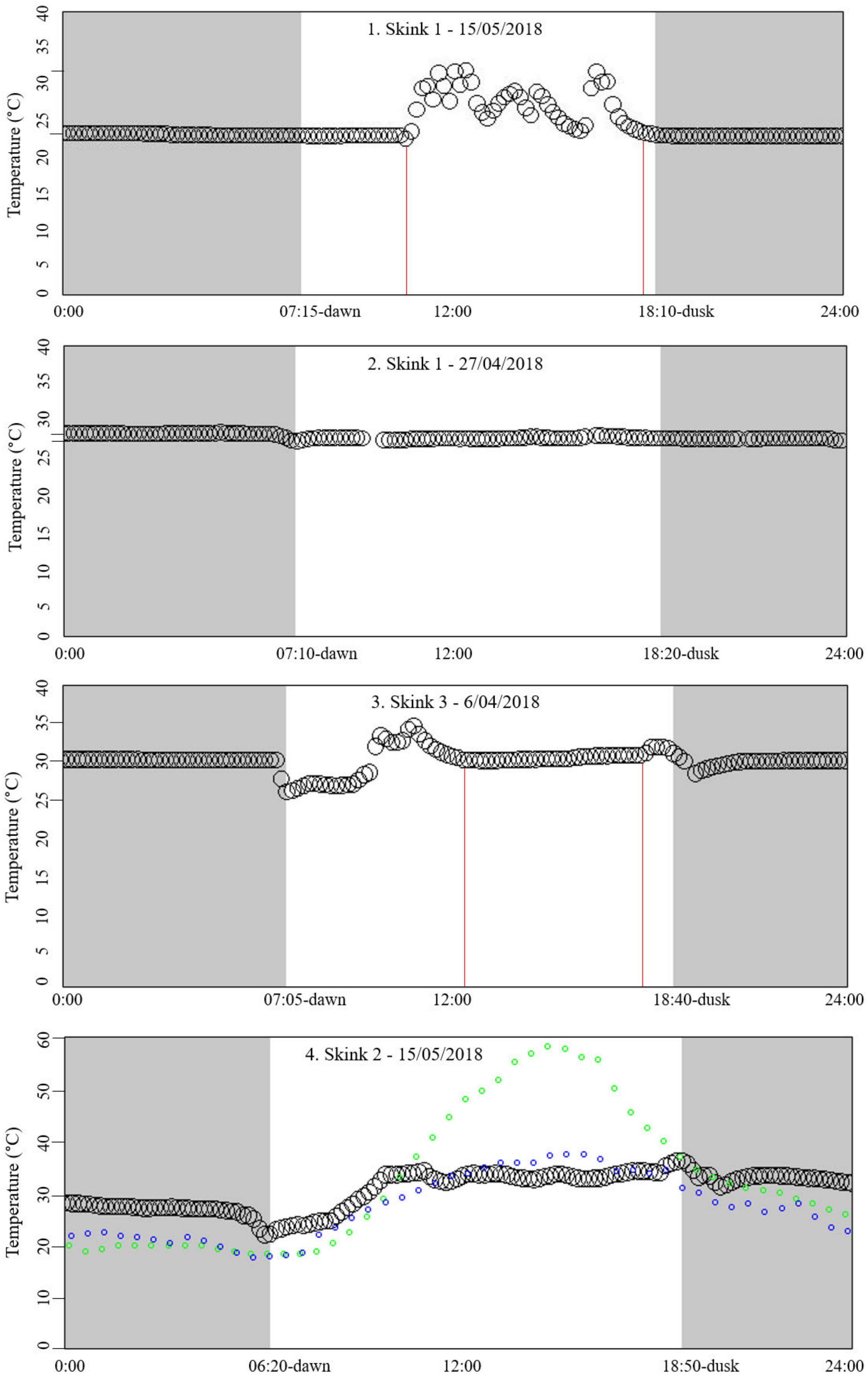

1. Skink 1 - 15/05/2018
Temperature (°C)
0
5
10
15
20
25
30
35
40
0:00
07:15-dawn
12:00
18:10-dusk
24:00
2. Skink 1 - 27/04/2018
Temperature (°C)
0
5
10
15
20
25
30
35
40
0:00
07:10-dawn
12:00
18:20-dusk
24:00
3. Skink 3 - 6/04/2018
Temperature (°C)
0
5
10
15
20
25
30
35
40
0:00
07:05-dawn
12:00
18:40-dusk
24:00
4. Skink 2 - 15/05/2018
Temperature (°C)
0
10
20
30
40
50
60
0:00
06:20-dawn
12:00
18:50-dusk
24:00

Figure 2. Plots of individual *L. kintorei* body temperature (black circles) for 24-hour periods from midnight to midnight. The white bar delineates dawn to dusk.

1, Unimodal activity patterns with red lines indicate activity start and end times.

2, Day without activity where change in T_b < 1°C. This constitutes one day of dormancy.

3, Bimodal activity patterns; Two bouts of activity separated by an inactive period of > 240 minutes. Morning and evening resting T_b = 30.0°C.

4, Burrow entrance temperature (green circles; range 18.5 to 58°C) and T_a (blue circles; range 17.9 to 37.4°C) in relation to T_b (range 22.1 to 36.1°C). Graph was generated in a custom program written in Visual Basic 6.

Activity recorded on camera corresponding with change in T_b

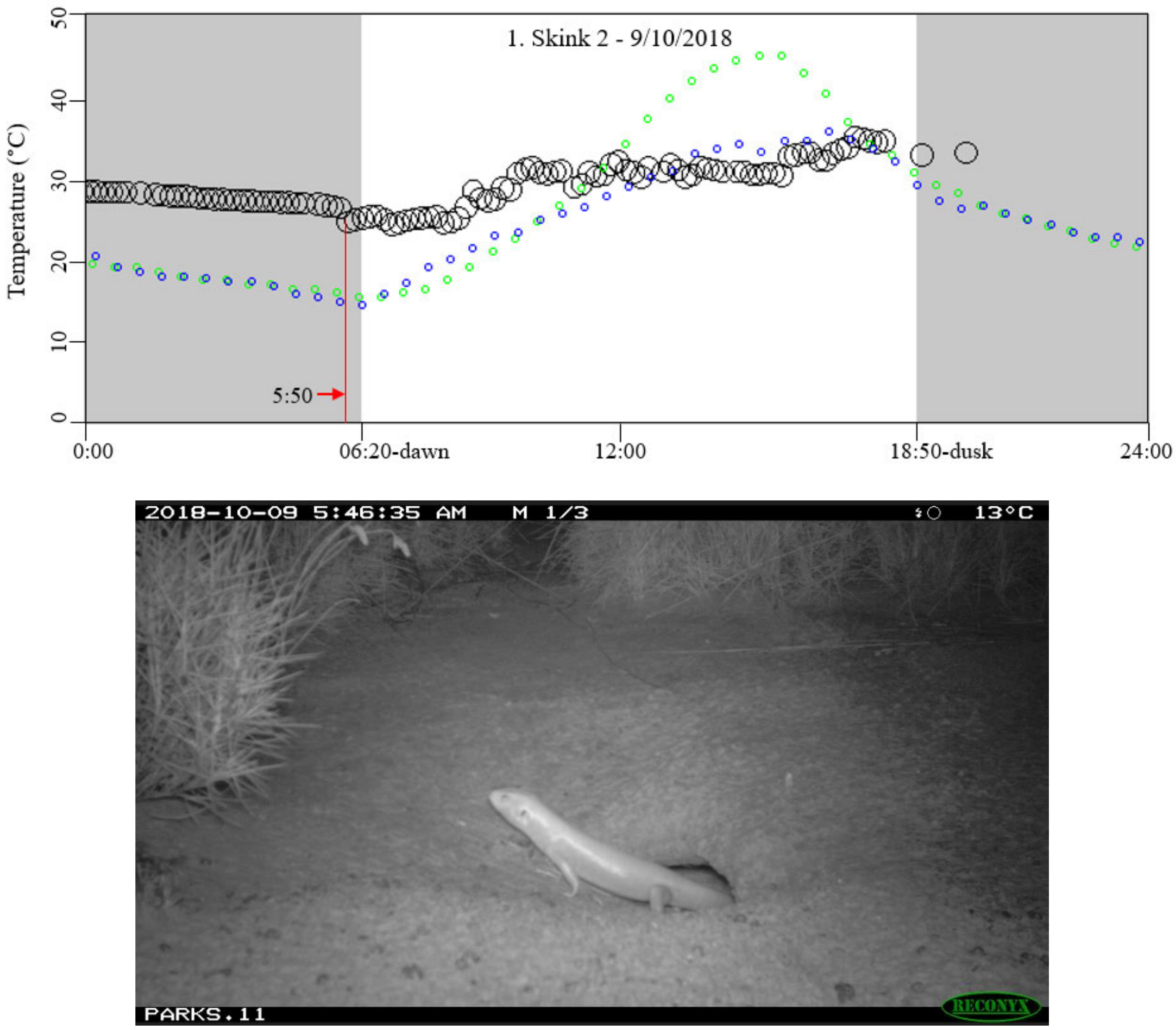


Figure 3a. Example of *L. kintorei* (skink 2) activity captured on motion sensor camera used to validate onset of activity based on matching T_b data for the same individual. Burrow entrance temperature (green circles) and T_a (blue circles) are shown in relation to T_b (black circles) at 10-minute intervals. The image was taken at 5:50 a.m. as indicated by the red arrow and corresponds with recorded change in T_b.

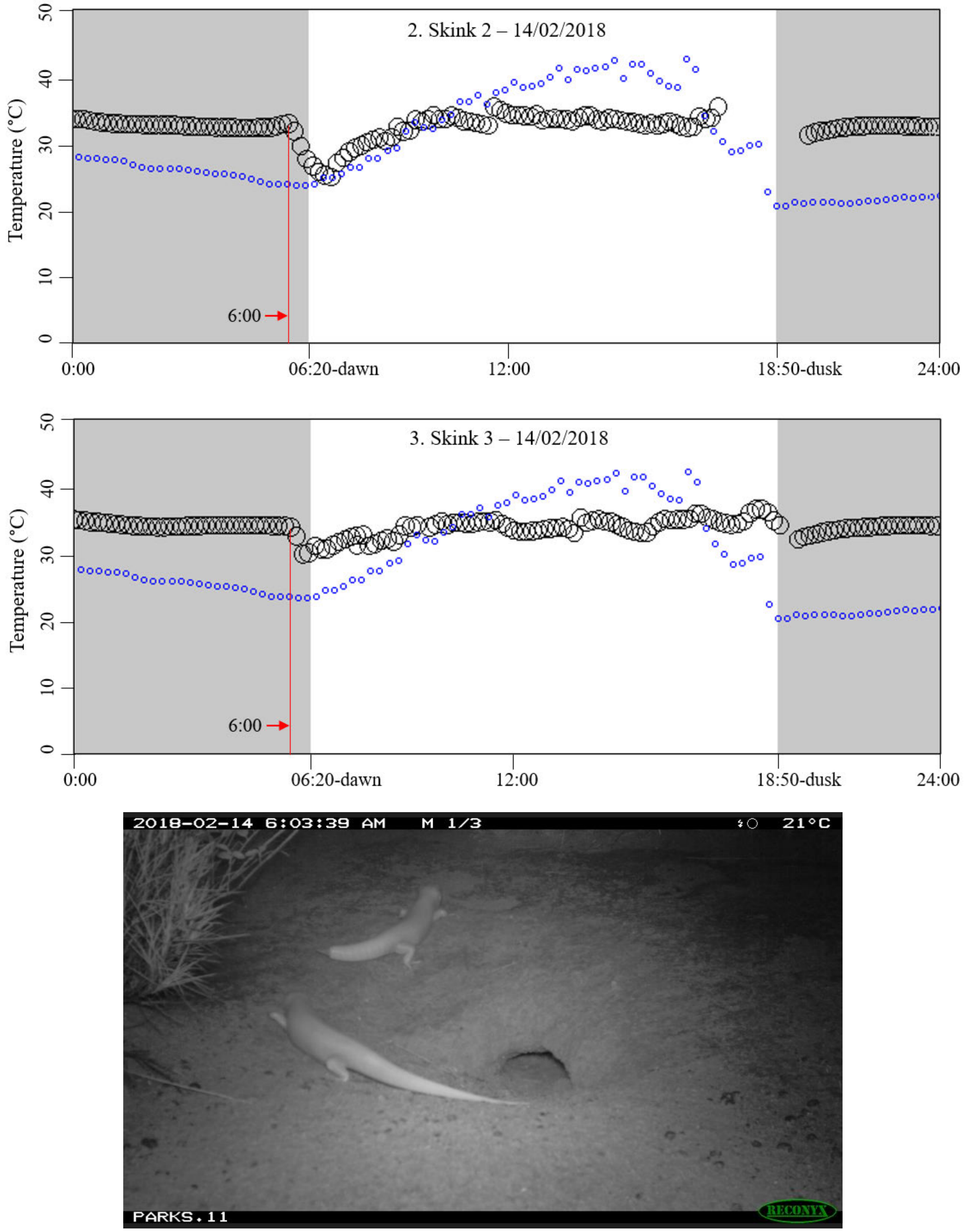


Figure 3b. Examples of *L. kintorei* (skink 2 and skink 3) activity captured on motion sensor camera, used to validate onset of activity based on change in T_b data. Burrow entrance temperature (green circles) and T_a (blue circles) are shown in relation to T_b (black circles) at 10-minute intervals. Both skinks are easily identifiable in the image as they leave their burrow.

Brumation and dormancy

For the purposes of this study brumation was defined as the period of dormancy experienced by *L. kintorei* over winter. Dormancy was defined as periods of inactivity greater than 24 hours. Inactivity related to time that *L. kintorei* were not moving during periods less than 24 hours. Location and duration of brumation was determined using the same tracking methods above. The complete set of T_b data were visualised using as double plots to illustrate seasonal changes in T_b and to determine onset and end of brumation (Figure 5).

Statistical analyses

All statistical analyses were carried out in the R (R Core Team, 2019) and Excel. Days with T_b less than 200 minutes of continuous records were excluded from statistical analysis. To test activity of *L. kintorei* using T_b data we analysed;

- The frequency of unimodal (single activity bout) and bimodal (2-3 activity bouts per day) activity across seasons (summer, autumn, winter, spring)
- When activity occurred in relation to sunrise and sunset across seasons
- Duration of activity per day
- Differences between daily maximum body temperature (T_{bMax}) and maximum ambient temperature (T_{aMax}) across seasons
- Differences between when T_{aMax} occurred and when T_{bMax} occurred across seasons.

Percentages of unimodal and bimodal activity across seasons were calculated and analysed using the R-package 'emmeans' (v1.4.6; Lenth, 2021). Unimodal and bimodal activity patterns were categorised as per Foà & Bertolucci (2001) where bimodal activity refers to two daily peaks of activity and unimodal pattern is characterized by one peak of activity each day. Because *L. kintorei* can be nocturnal as well as diurnal modality for this study does not only pertain to day-time periods. Because inactivity was determined as a period of consistent T_b for at least 240 minutes, unimodal activity could potentially span into the evening and across a whole day in the absence of period of rest. Occasions where three bouts of activity occurred were classed as bimodal. To test the differences between activity and inactivity between seasons a general linear mixed effects model (nlme) (Pinheiro, 2012) was used with the fixed effects: season and average T_a. The dependent variable is T_b and the random factor is ID (individual skink). A post hoc Tukey HSD pair wise similarity test was run to analyse those differences and 'emmeans' were calculated. We used two-way comparisons and Tukey multiple comparisons of means to analyse differences between activity start and end times either side of sunrise and sunset across seasons and duration of activity.

Seasonal differences between minimum, maximum and average T_b were tested using a mixed effects model and an ANOVA, followed by a post-hoc Tukey's HSD test for pairwise seasonal differences adjusting for multiple comparisons. A Welch Two Sample t-test was used to compare movement between burrows before and after brumation (mid-January to mid-June; September-December). In all analyses we assigned the significance level at $\alpha = 0.05$. Data are presented as the mean ± standard deviation (SD); n represents the number of individuals, and N the number of measurements.

Results

Fieldwork and tracking

Liopholis kintorei were monitored for 347 days throughout summer autumn, winter and spring periods for a total of 1135 tracking days (Table 2). Implanted radio transmitters functioned for the entire tacking period (up to 350 days) due to the low T_bs of *L. kintorei* and therefore low click frequency which prolongs the battery life of the transmitters. Although loggers recorded T_b in the absence of field visits at various stages during the year, the quantity of T_b and movement data were reduced due to interruptions in fieldwork.

Overall, T_a ranged between -2.7 to 46.8°C (BoM) and -4.7 to 49.3°C (iButtons) throughout the study period (13 January 2018 to 11 January 2019). Due to the gaps in the iButton records the averages of daily means form the Yulara weather station were used to report mean annual and seasonal T_a. Mean daily T_a throughout the year was 22.8 ± 7.6°C. Average humidity was 33.9 ± 13.3% across the study period and the total rainfall was 147.6 mm. Average daily T_a during the summer fieldwork period was 31.0 ± 3.3°C (range; 12.5°C to 46.8°C; $N = 89$; 2018 & 2019). Average autumn T_a was 23.2 ± 5.5°C (range; 5.0 to 40.4°C; $N = 91$; 2018). Average winter T_a was 13.2 ± 3.3°C (range; -2.7 to 31.7°C; $N = 92$; 2018) and average spring T_a was 24.0 ± 4.3°C (range; 5.2 to 41.4°C; $N = 91$; 201; Bureau of Meteorology, 2019).

Table 2. Number of *L. kintorei* tracking days and periods individuals were tracked at Uluru-Kata Tjuta National Park bore fields, NT, Australia.

Individual	Days tracked	Dates
Skink 1	347	19/01 - 11/01/2019
Skink 2	299	23/01 - 12/12/2018
Skink 3	171	26/01 - 18/06/2018; 19/10 - 2/12/2018
Skink 4	318	26/01 - 11/01/2019
Total skink days	1135	19/01/18 - 11/01/2019

Soil, burrow and spinifex temperature

Soil temperatures (T_s), burrow entrance temperatures (T_{b-e}) and spinifex temperatures (T_{spin}) were not used for statistical analyses but are included because they were used to highlight differences between ambient and surface temperatures and compare with depths of hibernacula (Appendices, Table A1). The greatest range of maximum and minimum T_s occurred at a depth of 5 cm (46.0 ± 4.9 to 26.7 ± 1.8°C; Table 3) and at this depth occurred before average maximum T_a in summer (54.3 ± 69.7 minutes) and before maximum T_a (12.3 ± 71.7 minutes) in winter (Appendices, Table A2). Maximum T_s always occurred after maximum T_a for all other soil depths during summer and winter months (Appendices, Table A2). T_s at depths of 5 cm were on average higher than maximum T_a during both summer (3.9 ± 3.0°C) and winter (1.1 ± 5.3°C). At a depth of 5cm the soil heated up faster than T_a and at greater depths the opposite occurred.

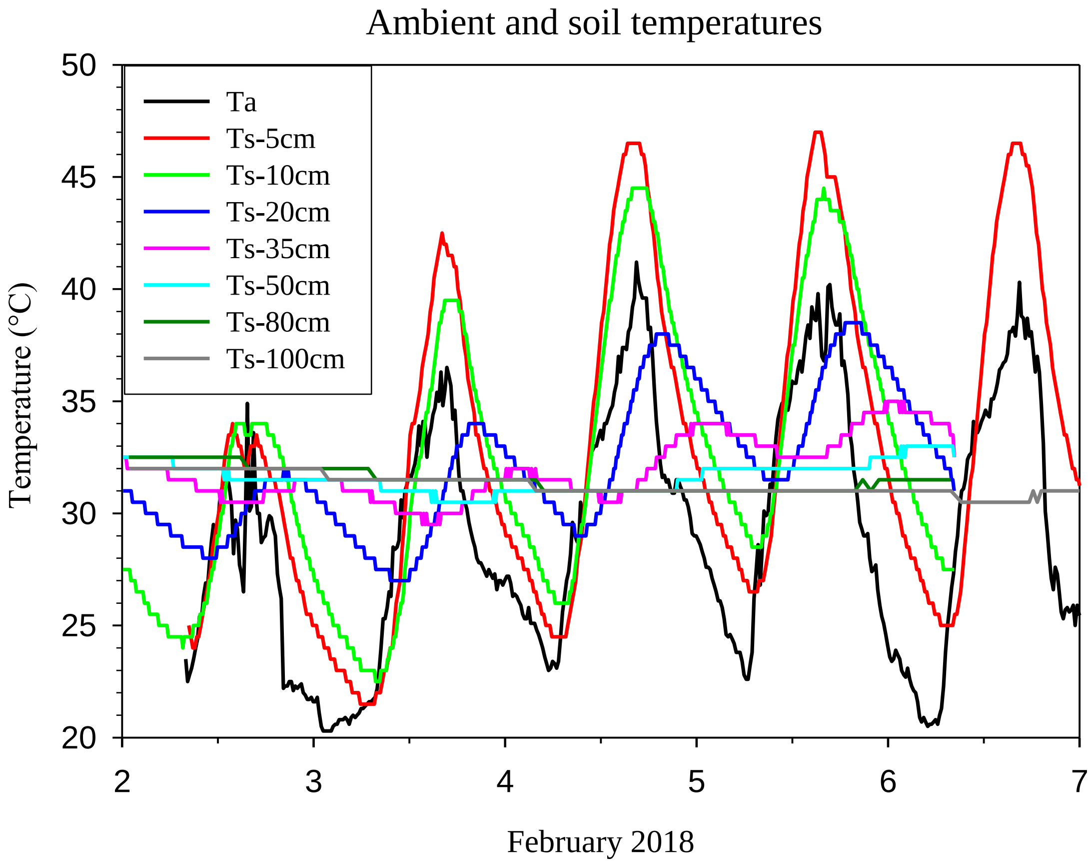


Figure 4. Plot showing T_a (black line) against soil temperature (T_s) at various depths below surface level over 5 days at the Uluru-Kata Tjuta NP bore fields during February 2018. Soil temperatures below 50 cm are relatively stable with greater fluctuations occurring closer to the surface.

At depths of 10 cm in summer, maximum T_s was typically delayed by ~2.3 hours (± 86.9 minutes) following maximum T_as, and at depths of 35 cm the delay increased to ~5.8 hours (± 151.4 minutes). Minimum T_s during winter at a depth of 10 cm was 13.4 ± 2.8°C higher than minimum T_a and delayed by ~3.2 hours (194.4 ± 136.7 minutes) showing that soil depths below 10 cm buffer effectively against maximum and minimum T_as. Change in time between T_a and T_s could not be determined at depths of 50 to 100 cm due to the low resolution of the loggers. Differences between maximum and minimum T_s and T_a at depths of 80 and 100 cm in both summer and winter were negligible (Figure 1; Table A2).

Table 3. Average, maximum and minimum soil temperatures (T_{s}) at depths of 5, 10, 20, 35, 50, 80 and 100 cm during summer and winter months.

Summer soil temperatures (°C)						
	AvT_s	SD	$MaxT_s$	SD	$MinT_s$	SD
5 cm	34.9	2.5	46.4	4.9	26.7	1.8
10 cm	35.5	1.9	38.6	1.7	32.5	2.5
20 cm	34.6	1.5	35.6	1.2	33.5	1.8
35 cm	33.6	1.2	33.9	1.1	33.1	1.3
50 cm	32.0	1.1	32.2	1.1	31.9	1.1
80 cm	31.3	0.8	31.4	0.8	31.3	0.8
100 cm	31.3	0.8	31.4	0.8	31.3	0.8

Winter soil temperatures (°C)						
	AvT_s	SD	$MaxT_s$	SD	$MinT_s$	SD
5 cm	20.5	6.5	31.7	6.8	12.4	6.6
10 cm	18.9	3.3	20.4	3.1	17.4	3.4
20 cm	19.7	2.5	20.0	2.5	19.5	2.5
35 cm	20.2	2.0	20.4	2.0	20.0	2.0
50 cm	21.6	1.2	21.7	1.2	21.5	1.3
80 cm	21.5	1.2	21.6	1.2	21.5	1.2
100 cm	21.5	1.2	21.6	1.2	21.5	1.2

High maximum T_{b-e} and T_{spin} were useful indicators of when *L. kintorei* were likely inactive during summer and potentially active during cooler months. Maximum T_{b-e} during summer (February) reached over 65°C (Table 4) and maximum T_{spin} reached as high as 54.5°C during December (Table 5).

Table 4. Average, maximum and minimum monthly *L. kintorei* burrow entrance temperatures (T_{b-e}) during the 2018 field season at Uluru-Kata Tjuta NP bore fields.

	Burrow entrance temperatures (°C)					
	Mean	SD	Range	Min.	Max.	Count
January	-	-	-	-	-	-
February	32.9	8.5	50.5	16.0	66.5	2048
March	-	-	-	-	-	-
April	27.7	1.2	5.5	24.5	30.0	731
May	20.8	2.1	10.0	17.0	27.0	1317
June	-	-	-	-	-	-
July	15.6	7.4	36.5	2.5	39.0	1469
August	16.8	5.8	38.0	0.0	38.0	1465
September	23.7	9.3	48.0	7.0	55.0	1433
October	29.0	11.5	49.0	14.0	63.0	1296
November	36.1	10.9	42.5	19.0	61.5	272
December	32.1	9.2	41.5	19.5	61.0	737

Table 5. Average, maximum and minimum monthly temperatures within spinifex at the study site throughout 2018.

	Spinifex temperature (iButton)				
	Mean	SD	Range	Min.	Max.
January	32.4	6.9	36.0	17.5	53.5
February	30.8	5.6	23.5	21.5	45.0
March	29.8	6.1	27.5	17.5	45.0
April	28.3	6.4	25.5	15.5	41.0
May	-	-	-	-	-
June	-	-	-	-	-
July	13.8	7.7	31.0	0.5	31.5
August	15.4	6.8	30.0	1.0	31.0
September	21.3	7.1	29.5	9.5	39.0
October	25.1	6.8	35.0	12.5	47.5
November	27.7	6.8	30.0	15.0	45.0
December	32.2	7.7	36.5	18.0	54.5

Summary of L. kintorei body temperature

Overall, 145,956 T_b values were recorded for the four skinks. Average T_b as well as minima and maxima were highest during summer followed by autumn and spring and lowest during winter (Table 6). Absolute minimum T_b was 7.8°C and absolute maximum T_b was 40.4°C (N = 145956; n = 4). Average, minimum and maximum *L. kintorei* T_b was significantly different between seasons ($P < 0.001$; see Appendix *Table A3*). Average T_b during summer was 32.5 ± 1.6°C (average T_a 31.0 ± 3.3°C), average T_b during autumn 28.4 ± 2.9°C (average T_a 23.2 ± 5.5°C), average T_b during winter 18.4 ± 3.2°C (average T_a 13.2 ± 3.3°C) and average T_b during spring was 27.7 ± 3.1°C (average T_a 24.0 ± 4.3°C; see *Figure A1*). A Tukey post-hoc tests confirmed that *L. kintorei* T_b was significantly different between all seasons ($P < 0.001$; spring and autumn $P = 0.003$).

Table 6. Summary of mean seasonal *L. kintorei* T_b (°C) with mean T_a (°C) and standard deviation (± SD) during field work at Uluru-Kata Tjuta NP bore fields (January 2018- January 2019).

	Summer (°C)		Autumn (°C)	
	T_b	T_a	T_b	T_a
Max	35.8 ± 1.7	39.3 ± 3.7	31.2 ± 3.0	31.4 ± 5.8
Min	28.8 ± 2.7	22.6 ± 2.9	25.9 ± 2.7	15.0 ± 5.5
Mean	32.5 ± 1.6	31.0 ± 3.3	28.4 ± 2.9	23.2 ± 5.5
	Winter (°C)		Spring (°C)	
	T_b	T_a	T_b	T_a
Max	23.7 ± 4.0	23.0 ± 5.8	32.9 ± 3.3	32.8 ± 4.8
Min	14.6 ± 4.1	3.6 ± 4.2	23.6 ± 3.7	15.8 ± 4.9
Mean	18.4 ± 3.2	13.2 ± 3.3	27.7 ± 3.1	24.0 ± 4.3

Initial observations of T_b and T_a data showed that there was a significant positive correlation between average T_b and average T_a throughout the year (Pearson $R = 0.80$, d.f. = 1, $t = 67.65$, $P < 0.001$, $N = 1114$, $n = 4$; y = 0.71(X) + 10.5; Figure 4). T_{bMax} was frequently higher than T_{aMax} only during May and early June (Figure 5). Changes in when T_{bMax} occurred relative to T_{aMax} throughout the year were analysed statistically below.

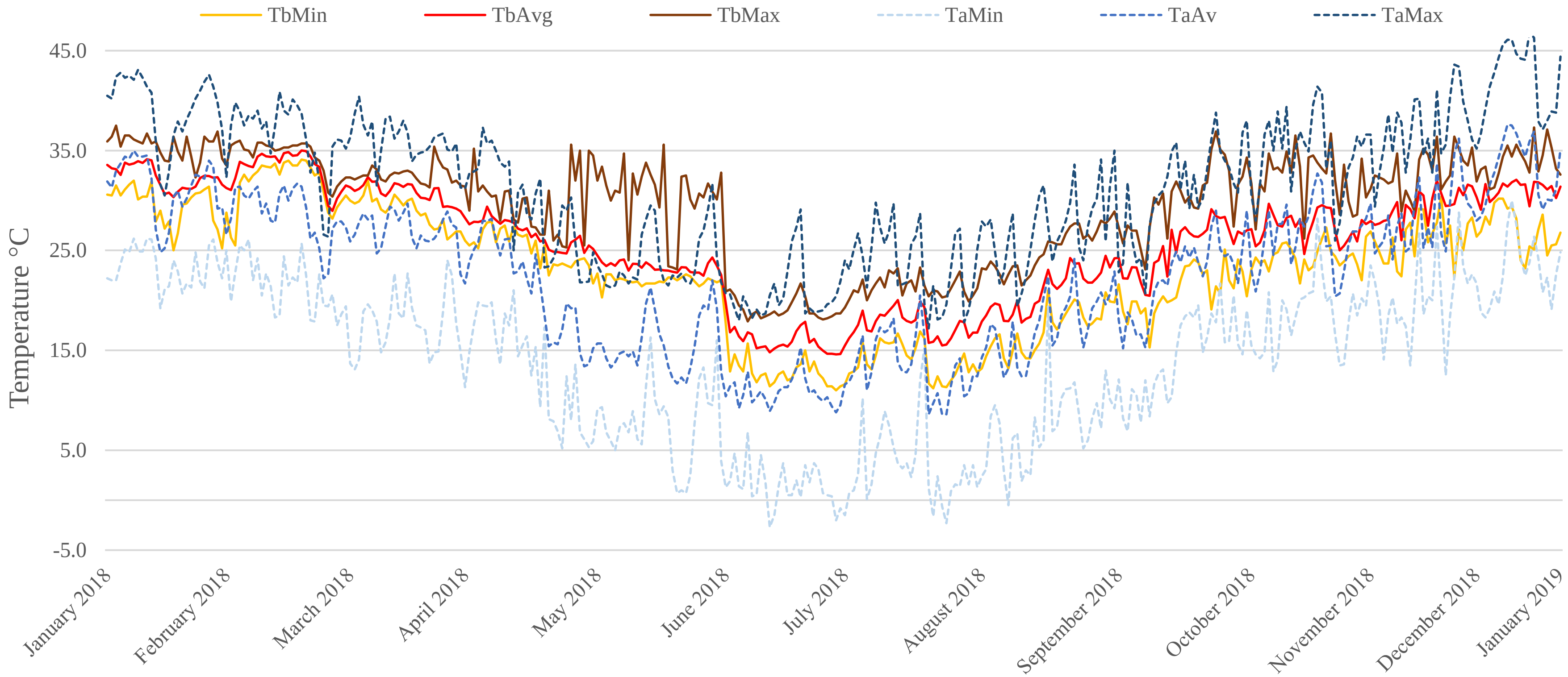


Figure 5. Plot showing T_a against the T_b of one individual *L. kintorei* (Skink 1) throughout the study period at Uluru-Kata Tjuta NP bore fields (January 2018-January 2019).

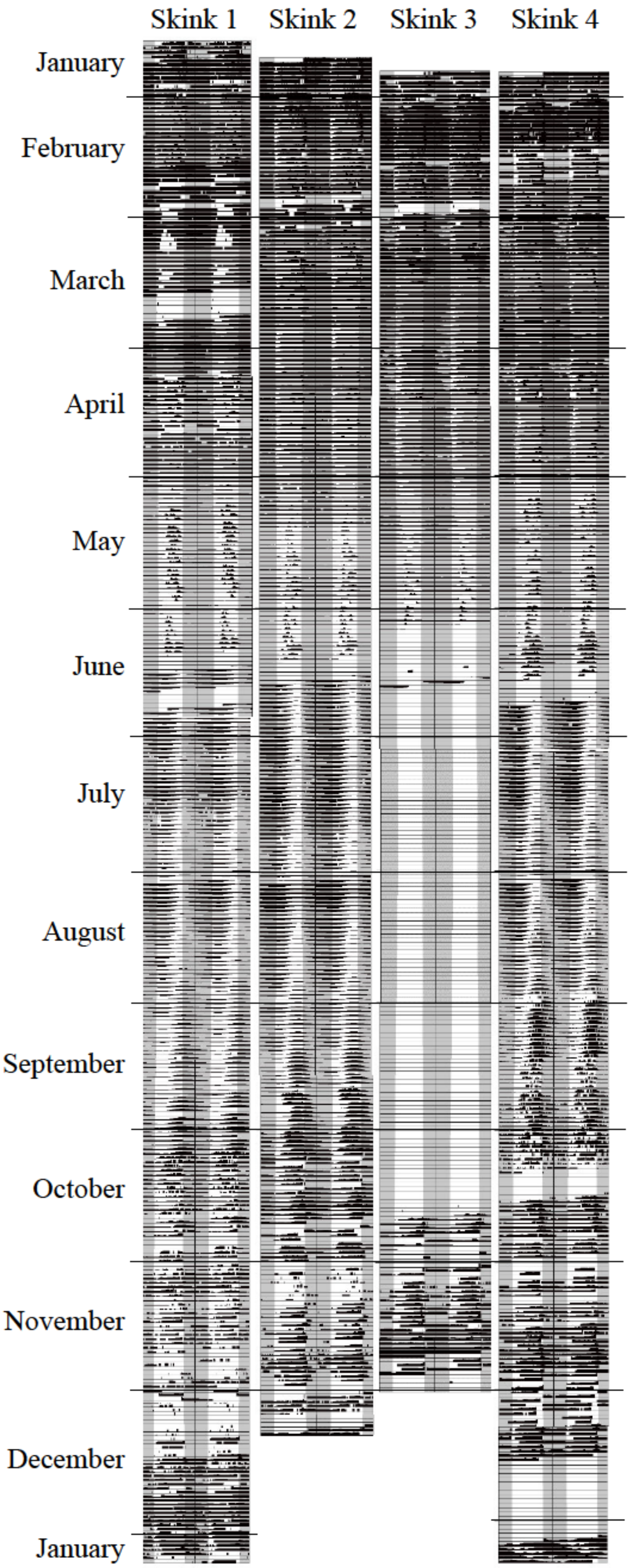


Figure 6. Plots used to view T_b data for four *L. kintorei* monitored from 19 January 2018 to 11 January 2019. Each line shows a 48-hour period with the first column replicating the previous 24-hour period and displays temperature range above and below 21°C and up to 40°C.

Differences between maximum T_b and maximum T_a

Δ Temperature (T_{bMax} and T_{aMax})

When *L. kintorei* were active, mean T_{bMax} in summer was 5.6 ± 3.8°C cooler than mean T_{aMax}. In autumn and spring T_{bMax} was 2.7 ± 4.8°C and 2.8 ± 5.7°C cooler than T_{aMax} respectively, and in winter mean T_{bMax} was 3.5 ± 4.8°C warmer than T_{aMax}. There was a significant difference between T_{bMax} - T_{aMax} differential across seasons ($F = 41.2$, d.f. = 3, $P < 0.001$). The T_a-T_a differential was similar between autumn and spring whereas it differed between all other seasons (Table 7).

Table 7. Summary of Tukey multiple comparisons of means between seasons when analysing Δ temperature (°C) between T_{aMax} and T_{bMax}.

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Season	3	2964	988	41.17	< **2e-16** ***
Residuals	429	10294	24		

	diff	lower 95%	upper 95%	p adj
Spring-Autumn	-0.1	-2.0	1.8	0.999
Summer-Autumn	-2.9	-4.9	-0.9	**0.001**
Winter-Autumn	6.3	3.8	8.8	< **0.001**
Summer-Spring	-2.8	-4.2	-1.4	< **0.001**
Winter-Spring	6.4	4.3	8.4	< **0.001**
Winter-Summer	9.1	7.0	11.3	< **0.001**

Δ Time ($T_{b\ Max}$ and $T_{a\ Max}$)

Means generated from an ANOVA showed that T_{bMax} of *L. kintorei* occurred 76.0 ±197.8 minutes later than T_{aMax} in summer, 38.0 ± 158.7 minutes later in autumn, 79.0 ± 188.1 minutes later in winter, and 83.0 ± 138.2 minutes earlier than when mean T_{aMax} occurred in spring. A Tukey multiple comparisons of means confirmed a seasonal difference between when T_{bMax} and T_{aMax} occurred. There was no significant difference between summer and autumn, summer and spring and autumn and spring. All other two-way comparisons between when T_{bMax} and T_{aMax} occurred across seasons were significant (Table 8).

Table 8. Summary of Tukey multiple comparisons of means between seasons when analysing Δ time (mins) when T_{aMax} and T_{bMax} occurred.

	Degrees of freedom	F value	Pr(>F)
Season	3	10.6	**1e-06** ***

	diff	lower 95%	upper 95%	p adj
Spring-Autumn	41.7	-30.4	113.9	0.443
Summer-Autumn	37.8	-36.6	112.1	0.557
Winter-Autumn	-121.0	-215.1	-26.8	**0.005**
Summer-Spring	- 4.0	-56.3	48.4	0.997
Winter-Spring	-162.7	-240.6	-84.8	< **0.001**
Winter-Summer	-158.7	-238.7	-78.8	< **0.001**

Unimodal and bimodal activity across seasons

Unimodal activity was more frequent than bimodal activity across all seasons (Figure 6). Bimodal activity was highest in summer (49.4 % activity; emmean = -0.02, SE = 0.20) and spring (37.5 % activity; emmean = -0.51, SE 0.20) and was reduced in autumn (18.8 % activity; emmean = -1.4627, SE = 0.224) and occurred least in winter (0.1 % activity; emmean = -2.7353, SE = 0.613). A pairwise comparison between emmeans found that bimodal activity was significantly greater in summer compared to winter and autumn ($P < 0.001$). However, there was no statistical difference between summer and spring ($P = 0.136$). Bimodal activity was significantly greater in spring than in autumn ($P < 0.00$) and winter ($P = 0.002$) and there was no statistical difference between winter and autumn ($P = 0.175$) and therefore autumn and winter were highly unimodal.

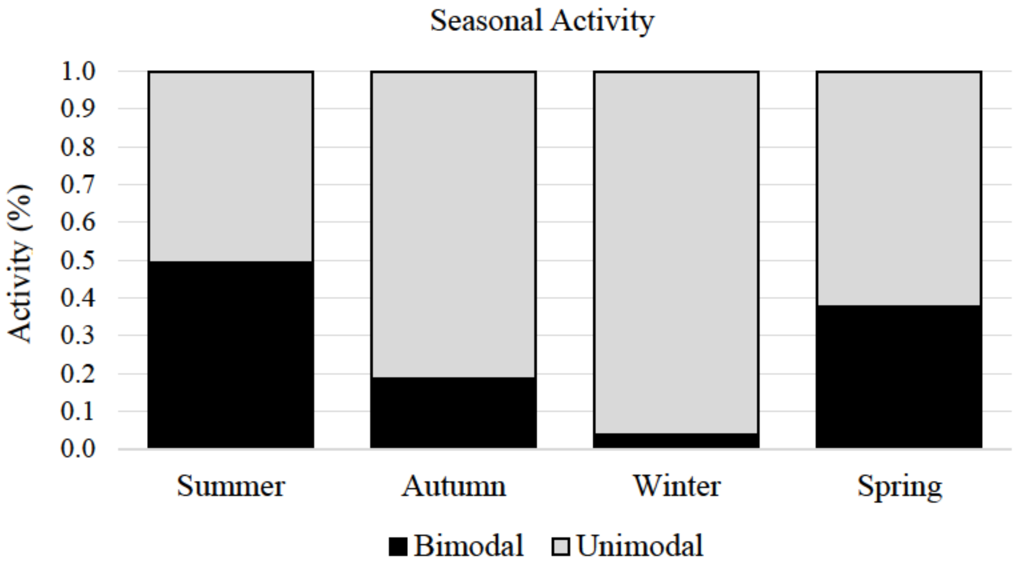


Figure 7. Plot of unimodal (grey) and bimodal (black) activity for *L. kintorei* across seasons at Uluru- Kata Tjuta NP bore fields for the austral year 2018-2019.

Activity relative to sunrise

In summer skinks began activity on average 0.5 ± 235.1 minutes after sunrise, in autumn 40.6 ± 253.3 minutes after sunrise, in winter (5 to 17 days in June only) 195.3 ± 119.8 minutes after sunrise and in spring 148.9 ± 271.2 minutes after sunrise. This delay in respect to sunrise differed significantly between seasons (Table 9). However, there was no significant difference in time from when activity began around sunrise between summer and autumn as well as winter and spring. For all other two-way comparisons between seasons, the differences between activity start times around sunrise were significant.

Table 9. Onset of activity either side of sunrise of *L. kintorei* at Uluru- Kata Tjuta NP bore fields across all seasons for the austral year 2018-2019.

	Df	Sum Sq	Mean Sq	F	Pr(>F)
Season	3	2804063	934688	15.34	**1.15E-09**
Residuals	669	4.1E+07	60920		

Tukey multiple comparisons of means: Activity sunrise				
	diff	Lower 95%	Upper 95%	p adj
Spring-Autumn	108.3	46.5	170.1	< **0.001**
Summer-Autumn	-40.1	-101.8	21.5	0.337
Winter-Autumn	154.7	53.9	255.4	< **0.001**
Summer-Spring	-148.4	-218.3	-78.5	< **0.001**
Winter-Spring	46.4	-59.6	152.4	0.673
Winter-Summer	194.8	88.9	300.7	< **0.001**

Activity relative to sunset

In summer, activity of *L. kintorei* ceased on average 35.9 ± 203.1 minutes after sunset, in spring 81.2 ± 122.8 minutes after sunset, in autumn 171.9 ± 265.5 minutes before sunset and in winter (5 to 17 days in June only) 43.6 ± 197.9 minutes before sunset. Significant seasonal variation in differences occurred between end of activity either side of sunset (Table 10). There was no significant difference when activity ended either side of sunset between summer and spring and no significant difference between summer and winter). For all other two-way comparisons between seasons, the differences between activity end times around sunset were significant.

*Table 10***.** Statistical summaries for end of activity either side of sunset of *L. kintorei* at Uluru-Kata Tjuta NP bore fields across all seasons for the austral year 2018-2019.

Test – aov (Activity-sunset~Season)					
	Df	Sum Sq	Mean Sq	F	Pr(>F)
Season	3	7793233	2597744	52.71	**<2e-16**
Residuals	622	30652207	49280		

Tukey multiple comparisons of means: Activity sunset				
	diff	Lower 95%	Upper 95%	p adj
Spring-Autumn	253.1	193.5	312.7	**0.000**
Summer-Autumn	207.8	151.2	264.4	**0.000**
Winter-Autumn	128.3	33.9	222.6	**0.003**
Summer-Spring	-45.3	-112.6	22.09	0.308
Winter-Spring	-124.8	-225.9	-23.7	**0.008**
Winter-Summer	-79.5	-178.9	19.9	0.167

Activity duration

On days when *L. kintorei* were active, mean duration of activity was highest in summer and spring (507 ± 349 and 555 ± 299 minutes), and less in autumn and winter (313 ± 250 and 404 ± 210 minutes. 5 to 17 days only in June; Table 11). Significant variation was found in the difference of duration of activity between seasons (Table 12). There was no significant difference in mean duration of activity between summer and winter or between winter and autumn, or between summer and spring. For all other two-way comparisons of activity duration between seasons was significant.

Table 11. Average duration of activity (minutes) per season for four *L. kintorei.*

	Summer	Autumn	Winter	Spring
Mean	507	313	404	555
SD	349	250	210	299
Range	1456	1420	1035	1510
Minimum	20	20	110	21
Maximum	1476	1440	1145	1531
Count	201	361	41	151

Table 12. Statistical summaries for activity duration of *L. kintorei* at Uluru- Kata Tjuta NP bore fields across all seasons for the austral year 2018-2019.

Test: aov (Activity duration~Season)					
	Df	Sum Sq	Mean Sq	F	Pr(>F)
Season	3	8008194	2669398	31.97	**<2e-16**
Residuals	753	62873516	83497		

Tukey multiple comparisons of means: Activity duration				
	diff	lower 95%	upper 95%	p adj
Spring-Autumn	238.5	166.6	310.4	**0.000**
Summer-Autumn	185.4	120.1	250.8	**0.000**
Winter-Autumn	83.2	-38.1	204.5	0.291
Summer-Spring	-53.1	-132.9	26.8	0.319
Winter-Spring	-155.3	-285.0	-25.6	0.011
Winter-Summer	-102.3	-228.4	23.9	0.158

Winter brumation

The transition from regular diurnal activity of *L. kintorei* between May and June ceased when winter brumation began in mid-June (Table 13). At the start of winter (beginning of June), when individuals were not active during the day, they were consistently inactive or resting for the majority of each 24-hour period. Nevertheless, during this period skinks still maintained an average and maximum T_b (average: 22.9 ± 0.5°C; maximum: 30.1 ± 1.2°C) above T_a (average:

14.3 ± 3.8°C; maximum: 23.3 ± 3.4°C). Overall, June was the coldest month at the study site with T_as as low as -2.7°C. Soil temperatures also fell but stayed above 15°C at a depth of > 10 cm. Consequently, skinks entered brumation about mid-June close to winter solstice.

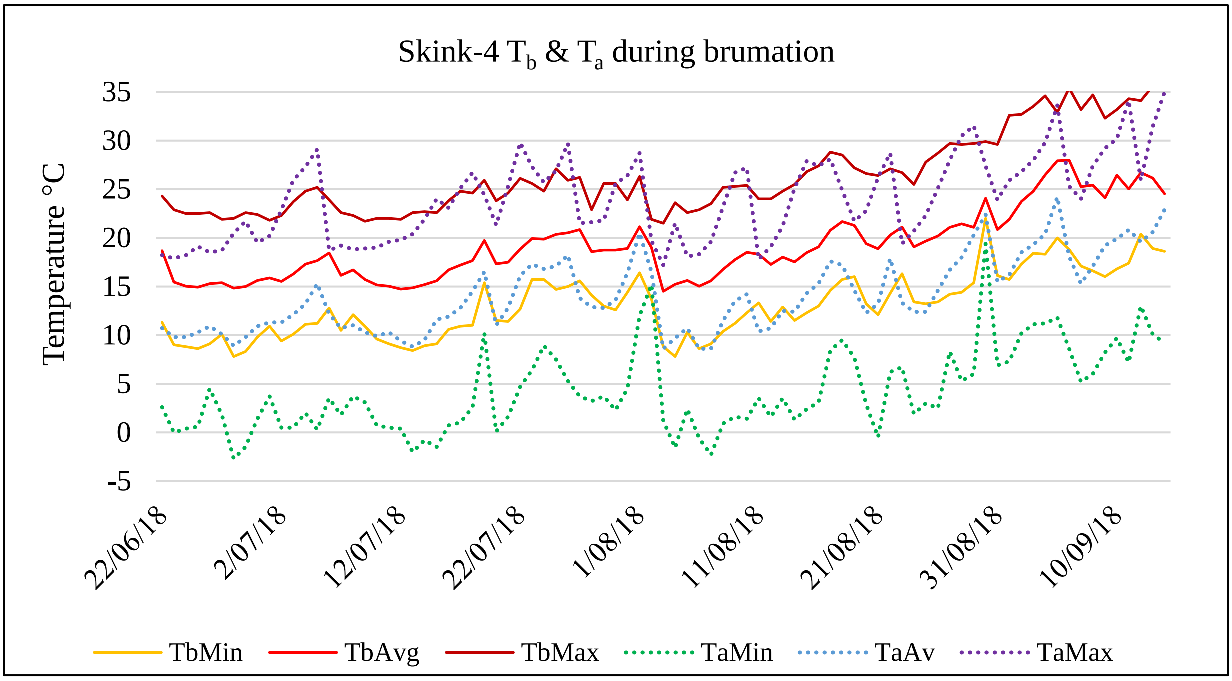
Before entering brumation, all *L. kintorei* left their main burrows and travelled between 72 m and 226 m away to where they dug shallow brumation hibernacula. No discernible patterns in the location of hibernacula were detected, all spread in different directions, and none close to one another. The average number of days spent in brumation for three *L. kintorei* was 98.0 ± 14.1 days ($N = 294$, $n = 3$) with individuals arousing from brumation between 14 September and 5 October. Body temperatures of *L. kintorei* during brumation ranged between 7.8 and 37.2°C while average ambient temperatures fluctuated between -2.7 and 35.8°C ($N = 291$; $n = 3$).

There were significant positive correlations between T_b of *L. kintorei* and minimum, maximum and average T_a during winter brumation. The strongest significantly positive correlation was between average T_{bMin} and average T_a ($N = 290$, $n = 3$, $t = 24.93$, $P < 0.001$, d.f. = 289, Figure 7).

Table 13. Dates *L. kintorei* departed their main burrows to commence brumation and when they aroused from brumation at Uluru-Kata Tjuta NP bore fields between 2018-2019. The distance each skink moved between their main burrows and hibernacula is also listed.

* Skink 3 was excluded from winter brumation statistics.

Individual	Date left for winter hibernacula	Distance- main burrow to hibernacula (m)	Date started winter brumation	Date aroused from winter brumation	No. days in brumation
Skink 1	~12/06/2018	83	~15/06/2018	5/10/2018	113
Skink 2	13/06/2018	T_bMin	~17/06/2018	21/09/2018	96
Skink 3	6/06/2018	130	*	*	*
Skink 4	17/06/2018	106	22/06/2018	14/09/2018	85



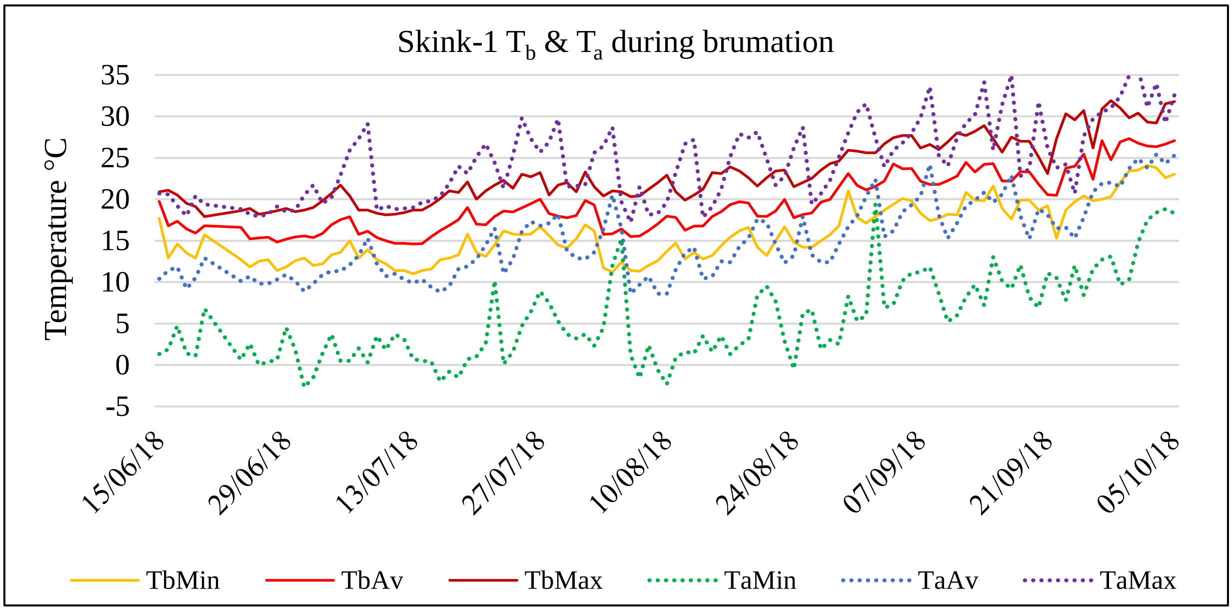


*Figure 7***.** Fluctuations between minimum, maximum and average T_b of two *L. kintorei* during winter brumation (Skink 1-15 June to 5 October; Skink 4 - 22 June to 14 September 2018) against minimum, maximum and average T_a at Uluru-Kata Tjuta National Park bore fields, NT.

Winter hibernacula

The average depth of hibernacula from the surface of the ground to top of the chamber was 10.7 ± 2.5 cm, and from the surface to the base of the chamber was 17.3 ± 2.9 cm ($N = 3$; $n = 3$, Table 14). The length of the tunnels from entry at the surface to hibernacula chambers was 106.7 ± 30.6 cm. Two hibernacula were located in open sandy areas away from spinifex and without vegetation cover. One individual was buried beneath a mix of *Aristida* grass and *Androcalva loxophylla* and the other, which was removed from the study, was in the process of digging a winter chamber in centre of an aged clump of old spinifex. All chambers were situated less than 1 m from the nearest clumps of spinifex.

Table 14. Depth and tunnel length of winter brumation hibernacula used by *L. kintorei* at Uluru-Kata Tjuta NP bore fields during 2018.

Individual	Depth from surface to top of chamber (cm)	Depth from surface to base of chamber (cm)	Length of brumation tunnel (cm)
Skink 1	11	19	140
Skink 2	8	~14	80
Skink 4	13	~19	~100

The midpoint between the top of hibernacula and the base was ~14 cm. When *L. kintorei* T_b was plotted against T_a and T_s at 5, 10, 20 cm its closest match was T_s at 10 cm, close to hibernacula depth measured in the field (Figure 8).

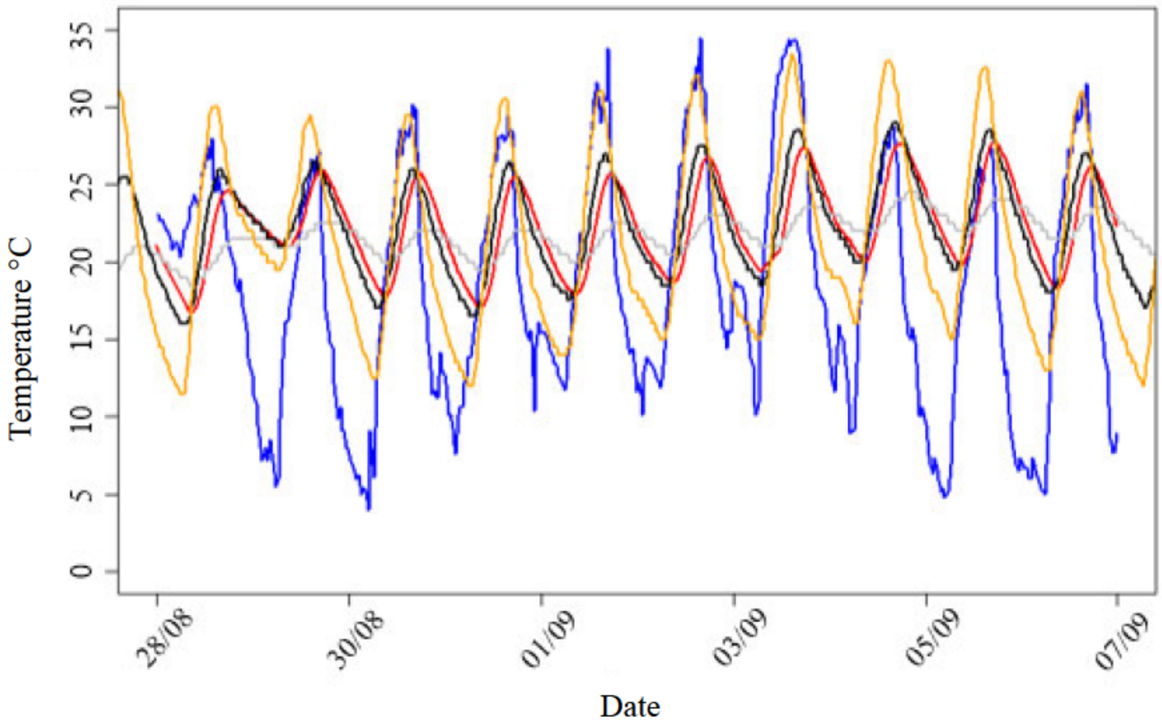


Figure 9. Relationships between T_b of one *L. kintorei* (Skink 4; red line red line) for 6 days during the start of brumation (24 to 30 June 2018) with T_a (blue line) and soil depth at 10 cm (black line). The orange line = T_s at a depth of 5 cm. The grey line = T_s at a depth of 20 cm.

Dormancy (general)

At times dormancy was exhibited for periods > 24 hours during the year other than during brumation, and *L. kintorei* became dormant on average 9.9 ± 11.3% of days tracked ($N = 884$, $n = 4$; Table 15). These periods of dormancy spanning days only occurred between February and the onset of brumation (Figure 9). There were no day-long bouts of dormancy recorded between spring and January. Dormancy throughout the year, including winter brumation, was on average 37.7 ± 11.3% of days tracked ($N = 1008$, $n = 3$; Table 15) with one individual remaining dormant for over 50% of the time.

Table 15. Dormancy during summer/warmer months (D) and brumation during winter (B) in *L. kintorei* at Uluru-Kata Tjuta NP bore fields.

	1 day D	2 days D	3 Days D	≥ 4 days D	Total days D excl. B	% days excl. B	Total days B	Total days D-B combined	% days D-B combined
Skink 1	5	2	1	1	62/235	26.4	113	348	50.3
Skink 2	6	2	2	4	20/246	8.1	96	342	33.9
Skink 3	4	0	0	0	4/170	2.4	-	-	-
Skink 4	4	1	0	0	6/233	2.6	85	318	28.6

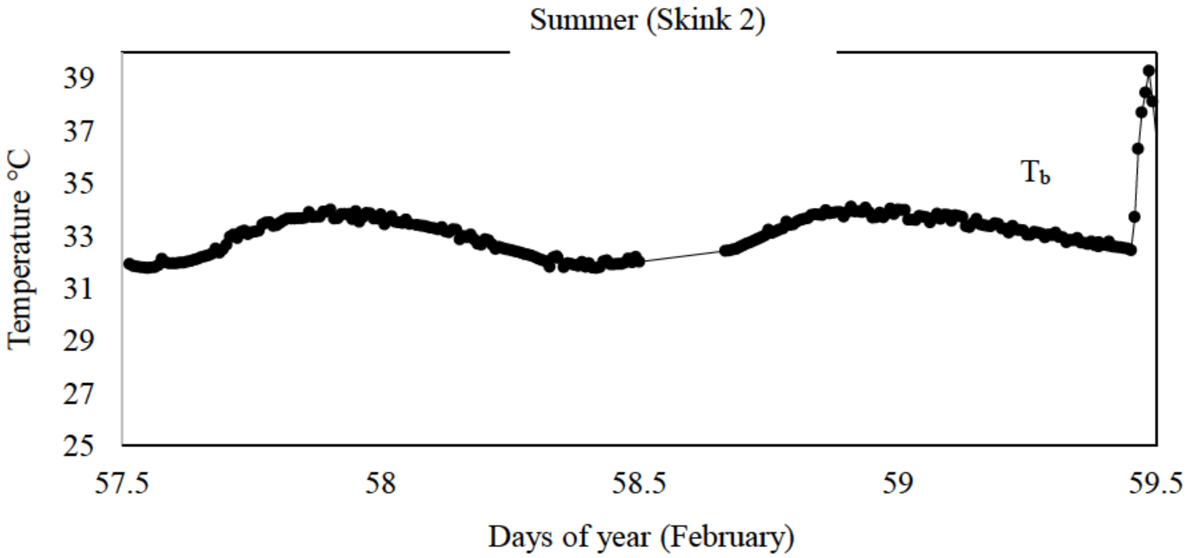


Figure 10. Example of the body temperature of *L. kintorei* (Skink 2) in a dormant state for two days (mid-day 26 February to mid-day 28 February 2018) at Uluru-Kata Tjuta NP bore fields. Arousal from dormancy is indicated by the steep rise in T_b just before mid-day 28 February.

Summer dormancy (estivation)

Two individual *L. kintorei* (Skink 1 and Skink 2) displayed long periods of dormancy in the summer period. Skink-1 estivated within its main burrow system for 50 consecutive days (17 February to 8 April). It was dug up to check if it had died, however, it was alive in a chamber offset from one of the main tunnels at a depth of 21cm from the surface (28 cm to the base). The chamber was ~35 cm long. On inspection its surgical wound had healed.

Skink-2 moved 83 m away from its main burrow 24 February and buried itself into a chamber within what appeared to be a mulgara burrow system, remaining dormant for 4 days at a depth of ~23 cm from the surface (27 cm to the base). The chamber was ~34 cm long and the length from the entry hole on the surface to the chamber was 120 cm. The skink's surgical wound beneath the outer scales had healed and it was released within the same burrow.

Both were dug up due to 'uncharacteristic' inactivity, and because Skink-2 had left its main burrow it had been assumed it had fallen prey to a mulgara, python, goanna or other burrowing species. Summer estivation is assumed to have continued for both individuals if not disturbed. Skink-2 returned to its main burrow and both individuals remained active with bouts of inactivity up to three days within the same burrow system until entering winter brumation in mid-June. The two other individuals did not enter prolonged states of estivation during this period however all individuals displayed some days of dormancy between January and early winter (Table 15). Body temperatures experienced by *L. kintorei* during summer estivation averaged 32.3 ± 1.8°C (*N* = 46) and 33.2 ± 0.5°C (*N* = 4) and ranged from 31.1 ± 1.9°C – 35.3 ± 2.7°C. These average T_bs closely matched average T_{soil} which was 32.8°C at a depth of 20 cm (February to March) and ranged between 26.5 and 37.5°C.

Home range

Home ranges were 0.13 ha (Skink 1- female), 0.91 ha (Skink 2 - female), 4.14 ha (Skink 3 - male) and 2.29 ha (Skink 4- female; Figure 10). The distance between known burrows used by all individuals ranged from 21 m to 226 m (*N* = 25; *n* = 4). The largest female (247.1 g, SVL = 215 cm) had the smallest home range. Home range overlap between individuals only occurred between the two *L. kintorei* that shared a main burrow (Skink 2 and Skink 3).

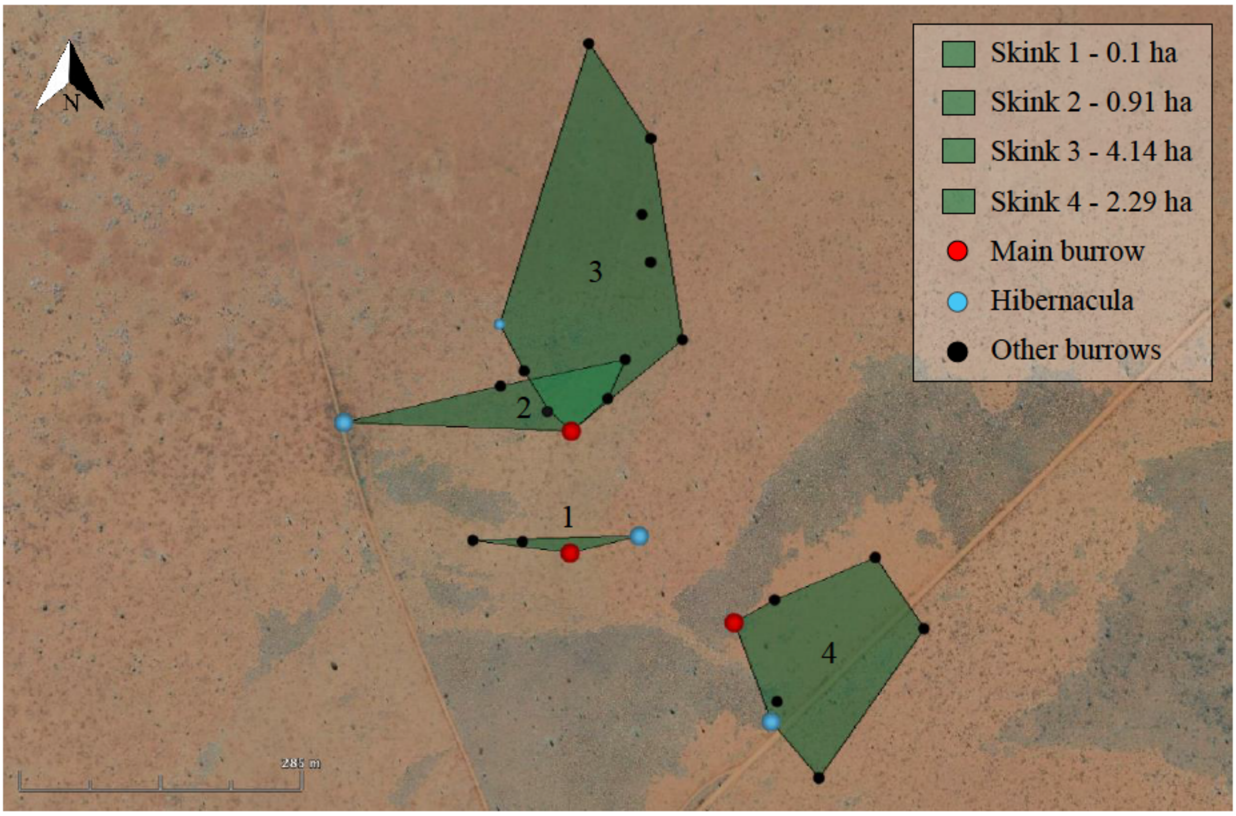


Figure 11. Minimum home range of great desert skinks (*L. kintorei*) and burrows used by each individual at the UKTNP bore fields tracked from 19 January - 11 January 2019. Polygons were created around skinks movement between burrows using minimum convex polygons (MCP) in Google Earth.

Movement between burrows

Individual skinks occupied between four and nine burrows during the overall observation period. Skink 3 was excluded from the study during the brumation period and was therefore removed for this analysis. An ANOVA was used to compare number of burrows used per season and found there was no significant difference ($F = 3.35$, d.f. = 3, $P = 0.056$). *Liopholis kintorei* spent on average 65.8 ± 2.0% of days throughout the study period in their main burrows, 30.1 ± 4.2% of days in their brumation chambers and 4.1 ± 2.2% of days in other burrows ($N = 16$ (burrows), $n = 3$; Figure 11).

Collectively, four *L. kintorei* used 25 burrows during the study period, including hibernacula used when dormant. Average number of burrows used during summer was 2.3 ± 1.3 and during winter 2.8 ± 1.0 burrows. Each individual used only one burrow in autumn and on average 3.8 ± 1.5 burrows in spring (Figure 12). The minimum distance between burrows was ~21 m and the maximum distance was ~226 m (average distance = 100.7 ± 58.7 m). The maximum linear distance between one individual's main burrow and the furthest point away was ~386 m. A polygon drawn around the known active burrows in the bore fields and home ranges of four tracked individuals was at least ~22 ha but could be up to ~30 ha if considering movement of ~100 m beyond burrows. The estimated area of all active burrows at the bore fields during 2018 was estimated between 35 and 45 ha.

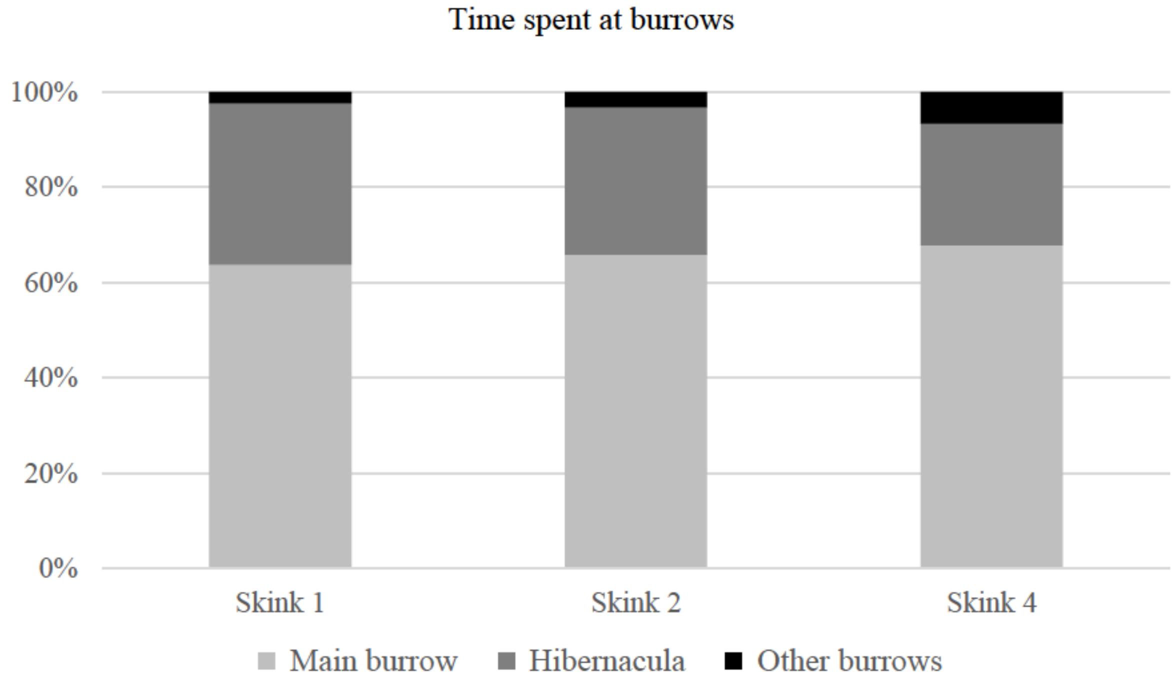


Figure 12. Percentage of days *L. kintorei* spent at their main burrow, winter hibernacula and other burrows combined at the Uluru-Kata Tjuta NP bore fields between January 2018 - January 2019).

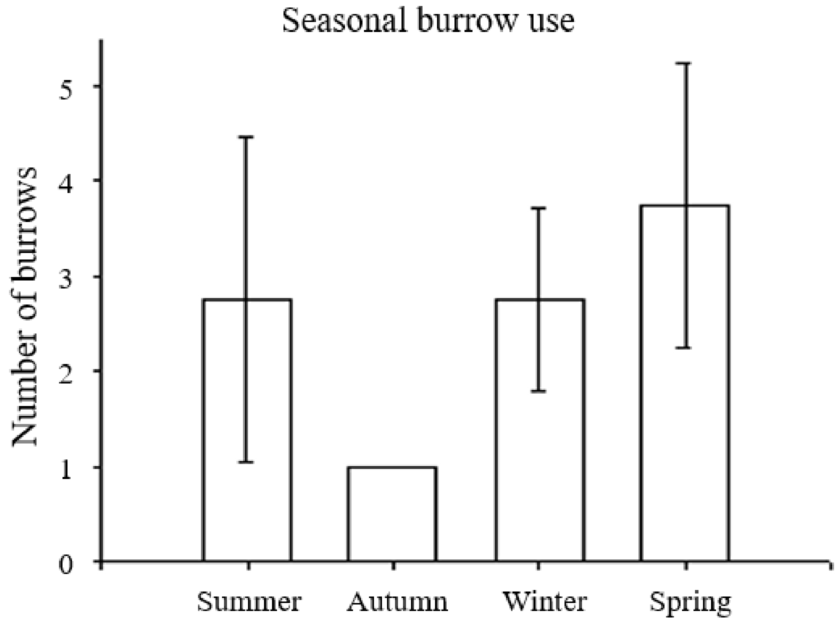


Figure 12. Plot showing average number of burrows used per season by four great desert skinks (*L. kintorei*) at Uluru-Kata Tjuta NP between January 2018-January 2019.

Liopholis kintorei moved between burrows during spring (after brumation) on average 16.5 ± 2.4 occasions ($N = 66$, $n = 4$) and movement between burrows from January to brumation was 2.3 ± 2.1 occasions ($N = 9$, $n = 4$; Table 12). The frequency of movement between burrows during spring and early summer was 7-fold higher than from January to brumation and this difference was statistically significant ($t = 9.29$, d.f. = 5.70, $P < 0.001$).

Table 16. Summary of number of burrows used and times moved between burrows by *L. kintorei* before and after brumation. Pre- brumation = mid-January to brumation. Post brumation = late September to early January).

Individual	Burrows used before brumation	Times moved between burrows before brumation	Burrows used after winter brumation	Times moved between burrows after brumation
Skink 1	2	2	2	14
Skink 2	2	2	3	18
Skink 3	1	0	6	19
Skink 4	4	5	4	15

Discussion

Our year-long study of great desert skinks (*Liopholis kintorei*) in the Great Sandy Desert of Australia provides new information on several aspects of its seasonal thermal biology and activity patterns. The study revealed that (i) *L. kintorei* were dormant for three months in winter from June to September in shallow hibernacula away from their main burrows when their T_b largely tracked soil temperature, however after their emergence from winter brumation in spring, (ii) they were actively thermoregulating every day until mid-summer (February), and (iii) displaying more frequent movement between different burrows until December, but then (iv) moved in and out of shorter to extended periods of dormancy between February and June when (v) there was a trend from bimodal to unimodal patterns of activity as the ambient temperature cooled.

Activity- general

Outside the winter brumation period skinks were active for an average of 5 (autumn) to 9 hours per day (spring), although there was considerable variation within seasons. Spring is a busy time in the annual life cycle of *L. kintorei*. It is the season where burrows are cleaned out after winter and mating occurs (Paltridge, personal observation, 2020). Although skinks were generally found to have high site fidelity, males are known to breed with females from multiple burrows (McAlpin et al., 2011), and this resulted in more movement between burrows than in other seasons. It has previously been assumed that males travel between burrows to seek out females, but as all skinks visited other burrows in the breeding season, it is possible that females may also seek out males in other burrows.

Our result that skinks were active for an average of 9 hours per day in the spring, equates to 37% of their daily activity budget. This is substantially greater than that found using a similar method in the only other study to have attempted using body temperature to describe activity patterns of skinks (Moore et al., 2018), where 10 skinks were found to be active for only 28% of the day over a 2-month period in spring, and only 4% of the daily activity budget was spent on the surface. The below-average rainfall conditions (148 mm compared to the annual average of 316 mm) that prevailed during that study were acknowledged as potential reasons for the low activity with higher risk of desiccation and reduced availability of termite prey during dry conditions (Moore et al., 2018).

Although motion sensor camera data confirmed frequent activity outside burrows, we could not always determine whether activity based on T_b alone was either above or below ground. Activity budgets for the purpose of this study therefore represent movement underground as well as movement at burrow entrances and on the surface within the immediate vicinity of burrows (up to ~30 m).

Being underground does not preclude animals from being active. Behaviour exhibited within the burrow system includes shuttling between different depths to thermoregulate, defending burrows from other species and undertaking maintenance of burrows. For example, *L. kintorei* are known to excavate up to four tonnes of sand throughout the life of a large burrow system (up to 7 years) which would naturally involve much underground activity (McAlpin, 2011).

Liopholis kintorei has previously been described as a predominantly crepuscular species, with peak activity in the early morning, and again around dusk, sometimes extending into the evening (Chapple 2003, McAlpin 2011) although this primarily relates to activity on the surface. Activity inferred from body temperature data also suggested a crepuscular activity pattern, with more surface activity at dusk (Moore et al., 2018). In a laboratory study where a heat gradient was provided with temperatures ranging between 24 and 50°C *L. kintorei* was also observed to emerge around dawn, retreat to its burrow for most of the day and resurface in the late afternoon (Henzell 1952).

In this study we found the *L. kintorei* displayed diurnal, nocturnal and crepuscular activity, and this included underground activity. Skinks were also found to be more active during daylight hours than expected. To confirm this, we were able to match motion sensor camera images of individual skinks outside their burrows at any hour between sunrise and sunset with T_b data patterns. We therefore reject the notion that they are a strictly crepuscular species, but rather have flexible activity patterns incorporating both day-time and night-time movements and ranging from bimodal to unimodal patterns in behaviour.

As expected, skinks became active earlier in the day in the summer months, typically within minutes of the sun rising. Activity generally extended into the hour after sunset in spring and summer but ceased several hours prior to sunset in the autumn. In the hottest months there was usually a period of inactivity in the middle of the day, giving rise to a bimodal activity pattern whereas in the cooler months when skinks were primarily active in the middle of the day, their activity was predominantly unimodal.

Nocturnal activity was primarily confined to spring and summer when searing daytime temperatures restricted activity in the middle of the day. The related species *Liopholis slateri* was also found to increase its nocturnal activity as ambient temperatures increased (Treilibs, 2017). Increased activity in the evenings is probably an adaptation to reduce evaporative water loss in very dry conditions (Scantlebury, 2011) and such activity may be facilitated by the capacity of the desert sandy substrate to retain its warmth after sunset and radiate heat into the atmosphere. This study found that maximum afternoon temperatures were absorbed by the soil and at depths of 35 cm the delay in temperature gradient was up to several hours into the evening. Such transitions between activity patterns may also be facilitated if *L. kintorei* are already pre-adapted to low-light conditions because of their semi-fossorial nature.

Reptiles that employ a crepuscular or nocturnal foraging strategy may endure suboptimal performance due to less than preferred body temperatures to take advantage of increased prey availability and/or reduced vulnerability to predators (Gordon et al., 2010). The preferred food source of *L. kintorei*, termites of the species *Drepanotermes perniger* are primarily nocturnal, and occasionally appear in large numbers on the surface after rain (McAlpin, 2011; Anderson, 2005).

Most predators are adapted to foraging in either darkness or daylight, as specially adapted eyesight is required for nocturnality. However, some species like the cat (*Felis catus*) can adapt to both low level and bright illumination. The elliptic pupil of the congener *Liopholis striata* is believed to be an adaptation to nocturnality and the observation that the *L. kintorei* pupil is circular under normal daylight conditions, but contracts to a vertically elliptical form under torchlight, has been suggested as a trait that may allow them to forage at night (Chapple 2003).

Observations during this study suggest that activity levels of *L. kintorei* are higher than previously recorded and the main reasons for this could be that activity was recorded across four seasons. We confirmed our hypothesis that unimodal-diurnal activity would be most prominent in cooler months as reflected by the high frequency of unimodal-diurnal activity during autumn and particularly winter. Although unimodal activity was high, *L. kintorei* displayed almost equal proportions of bimodal and crepuscular activity during summer.

Activity in spring was highest with predominantly unimodal activity but also with a high frequency of bimodal activity. We determined that variations in ambient temperature and photoperiod impact the time that activity occurs either side of dawn and dusk. Hot summer temperatures increased crepuscular and nocturnal activity and colder autumn and winter temperatures increased diurnal activity.

Summer-autumn dormancy

Despite extended periods of favourable temperatures between February and June, skinks intermittently retreated to periods of dormancy during late summer and autumn. The slightly deeper hibernacula used for summer estivation compared to winter brumation, appears to have prevented *L. kintorei* from overheating while simultaneously supporting necessary thermal regulation. Bouts of inactivity typically lasted from 1-4 days, however one animal remained inactive for 50 days from February. This individual and one other, both may have remained dormant for longer if they were not disturbed when presumed dead.

Estivation is a state of inactivity in response to high temperatures or lack of water (Cowles and Bogert 1944). It is an important drought survival adaptation for many frog species and some reptiles and can be a short or long-term phenomenon. For example, Sonoran mud turtles (*Kinosternon sonoriense*) survive periods of drought by estivating for up to 34 days (Ligon & Stone, 2003). Other species such as the long-neck turtle (*Chelodina rugosa*) estivate under drying mud on floodplains during tropical dry seasons and achieve this by reducing their standard metabolic rate by ~28% to conserve energy and water (Kennett & Christian, 1994). Couch spadefoot toads (*Scaphiopus couchii*) from north America can remain in a state of estivation for up to 10 months per year and also use metabolic depression and reduce oxygen consumption by 70-80% of their resting rate (Storey et al., 1999).

It is plausible that the reproductive and energetic requirements of the estivating *L. kintorei* had been met by mid-summer. By entering a dormant state of estivation, they were likely able to conserve energy, water and reduce the risk of exposure to predators. Studies on populations of the eastern fence lizard (*Sceloporus undulatus*) found that mortality rates were reduced 10-fold by avoiding being active, and that mortality rates of populations of adult females were lower where seasonal activity was shorter (Adolph & Porter, 1993).

Activity- autumn and winter

Our study revealed that *L. kintorei* remained mainly active throughout autumn and deeper into winter than had previously been documented (McAlpin, 1997), maintaining six hours of activity on most days even in the first two weeks of June. Activity never occurred before dawn in winter but occasionally extended past dusk, possibly due to the delay of latent afternoon heat in the soil. Similarly, *Agama hispida* lizards in the Kalahari are active at midday during winter (Huey & Pianka, 1977) and a number of central Australian arid zone reptile species such as the central netted dragon, *Ctenophorus nuchalis*, some geckos (Schlesinger et al., 2010), and snakes *Furina ornata* and *Suta suta* (McDonald, 2012) can also be active during winter, despite the generally low biomass of invertebrates during that period (Paltridge & Southgate, 2001).

The completeness of the data logger records in autumn-winter indicates that *L. kintorei* were not venturing far from their burrows (beyond the range of the receivers) and this was supported by camera trap images which showed that much of this autumn-winter diurnal activity was predominantly based around basking at burrow entrances or on burrow entrance mounds, with some movement on the surface around the burrow system.

Radiant surface heat from the sandy substrate apparently made it possible for *L. kintorei* to thermoregulate during the hottest period of a mild winter day. Basking enabled skinks to elevate their body temperature to 7°C above the maximum winter ambient temperature, enabled by surface temperatures which can reach over 30°C (Körtner et al., 2008). Basking is also seen in other species during days leading up to hibernation, such as the Rattle snake (*Crotalus viridis*; Macartney et al., 1989).

The ability to sustain this basking behaviour during winter may have become unattainable when daily minimum temperatures dropped below 4°C and average temperatures fell below 12°C. Average T_a in June was the lowest of all months in the year (12.6 °C) and also presented the lowest minimum temperature (-2.7°C). This was accompanied by a substantial drop in average soil temperature from May which gradually dropped further until July where temperatures of 16.5°C and 17.6°C respectively were recorded at depths of 10 and 20cm. With ambient temperatures and soil temperatures declining to this degree, *L. kintorei* is unlikely to have been able to thermoregulate sufficiently to remain active and during the month of June all four skinks left their main burrows to enter winter brumation.

Winter brumation

As the transition to brumation also coincided with the shortest days of the year, it is possible that brumation was triggered by a combination of low temperatures and minimum day length. Although short-horned lizards (*Phrynosoma hernandesi*) commenced winter brumation just prior to subzero night-time temperatures in Colorado (Mathies & Martin, 2008) and a sudden drop in both mean and maximum T_as triggered brumation in the desert iguana (*Dipsosaurus dorsalis*) in the Sonoran and Mojave deserts (Moberly, 1963), a large European lizard, *Lacerta viridis,* was found to commence brumation in response to changing photoperiod. These *L. viridis* were exposed to a natural change in photoperiod in captivity while living in a thermal gradient that permitted selection of high or low T_bs throughout the year, but selected high T_bs when the photoperiod was long in summer and constant low T_bs when the photoperiod was short in winter (Rismiller & Heldmaier, 1982). Other studies suggest brumation is triggered by a combination of factors including temperature extremes, availability of prey, rainfall and photoperiod (Goodyear & Strine, 2022).

The discovery that all four *L. kintorei* monitored in this study left their main burrows and constructed completely separate brumation chambers at distances of 72-226m from their normal homes was novel information that had not been previously documented. We can only speculate why they would travel to another site to brumate, rather than set up a shallow chamber within their main burrow as has previously been suggested/observed by McAlpin (2011). One possibility is to reduce the chance of predation during winter dormancy. A study on movements and shelter-site selection by free-ranging brownsnakes (*Pseudonaja textilis*, Elapidae) suggested that the selection of winter hibernation sites away from their usual active home range may be to avoid predation (Whitaker & Shine, 2006). While hibernation and brumation are normally considered a safe way of avoiding predation (Turbill et al., 2011; Turbill et al., 2019), some predators take advantage of the dormancy of hibernating animals, for example badgers dig up hibernating squirrels (Michener, 2004) and great tits hunt hibernating pipistrelle bats (Estók et al., 2010). During periods of activity, photos captured on motion-sensor cameras throughout this study, and those captured by Paltridge (personal observation, 2022), show that adult *L. kintorei* actively chase smaller predators such as sand goannas, brush-tailed mulgaras and some snakes away from their burrows. However, *L. kintorei* burrows with their obvious latrines are highly conspicuous to predators such as the dingo which are capable of excavating burrows. Shallow brumation chambers at only ~10-15 cm below the surface, could consequently make them quite susceptible to predation. The creation of inconspicuous brumation chambers away from their main burrow with plugged entrances and no obvious spoil heaps or latrines may therefore be a way of remaining hidden from potential predators while the skinks are dormant.

During the brumation period when outside air temperatures fluctuated between -2.7°C and 35.0°C, the body temperatures of skinks in their hibernacula ranged between 7.8 and 35.6°C with average daily body minimum and maximum temperatures between 14 and 24°C. Hibernacula at depths of only 10 cm below the surface effectively buffered *L. kintorei* against temperature extremes while allowing sufficient warmth to penetrate the soil as ambient temperature increased in the spring. Shallow hibernacula are typical of species overwintering in mild to warm climates whereas in extremely cold climates reptiles must retreat to hibernacula deep underground to avoid freezing (Huey, 2021).

Activity- spring

After three-months of winter brumation skinks emerged from their hibernacula between mid-September and early October and returned to their original communal burrows. Body temperatures on emergence were 31.8, 31.0 and 35.6°C and the egress of two of the three skinks followed overnight rain. This supports the assertion by local Aboriginal people that *L. kintorei* are aroused from brumation by spring storms (M. Teamay, personal communication, 2018). While photoperiod may trigger the onset of brumation (Rismiller & Heldmaier, 1982), reptiles overwintering underground would receive no exposure to such cues, and therefore rely on environmental temperatures (and possibly rain) to trigger emergence from dormancy (Etheridge et al., 1983; Moss & McLeod 2022).

Burrow use and home range

Liopholis kintorei predominantly used one main burrow throughout the year with interspersed movement between four to nine burrows. Movement between burrows increased seven-fold during spring in response to reproductive behaviour. The home range of males was much greater than females, probably due to the need to establish breeding partners and to construct and maintain burrows. The minimum and maximum distance between burrows (21 to 226 m) was similar to previous findings of 25 to 200 m recorded by McAlpin (2011). However, the maximum linear distance recorded between one individual’s main burrow and the furthest burrow away (~386 m) was less than some burrows previously recorded up to 500 m apart.

The area of the four individuals tracked in this study was slightly larger than the average area (10-20 ha) of clustered sub-populations recorded by McAlpin (2011). The estimated area of active burrows at the bore field (35 to 45 ha) at the beginning of 2018 was however much smaller than the potential 300 ha for some sub-populations previously recorded. Further, this is apparently much smaller than the area of *L. kintorei* burrows recorded ~20 years earlier by McAlpin (1997), indicating a decline in population size at this location.

Management implications

The National Recovery Plan for *L. kintorei* (DCCEEW, 2023) recommends monitoring surveys should occur when skinks are active (October- March) and relative abundance of sub-populations can be determined by the number of active burrows in an area. This study showed that adult skinks appeared to be most active during spring, and from February some had entered an extended period of dormancy. Although the sample size was low this could mean that monitoring populations may be skewed a) in excess if monitoring takes place during spring (September- November) due to increased movement between burrows and b) underestimated if carried out between February and March due to a proportion of adults being potentially dormant. It appears then that the most suitable months to undertake surveys could be from late December, after young are born, to early February when both adults and juveniles are most likely present and active.

Recording the home range of individual *L. kintorei* helps with the interpretation of tracking and burrow survey data. Positioning of track plots for monitoring purposes should therefore be at least ~1 km apart to maintain independence. The National Recovery Plan (DCCEEW, 2023) recommends some flexibility in the size of track plots for monitoring populations depending on how extensive a population is and how much effort can be put into it. Where larger sub-populations are known to occur, or appear to be declining, plot sizes and search effort should be greater to better identify subtle changes over time if required. The plan suggests using motion sensor cameras to record behaviour and assess predation pressure at burrows. In addition to this, cameras could also be set up at the extent of estimated home range zones to capture predator access to sites to inform prompt predator management actions. Additionally, where developments are planned e.g., for mining or infrastructure, consideration must be given not just to the location of active burrows but also of abandoned burrows which could be being used temporarily by individual skinks. The potential home range beyond burrows should also be considered including during winter when *L. kintorei* move away from their burrows to brumate.

Undertaking appropriate small-scale patch burning within *L. kintorei* habitat seems to be an important factor in maintaining diversity of vegetation and prey species within a localised ecosystem supporting populations of *L. kintorei*. Because *L. kintorei* and other species are known to be easily preyed upon when moving about on bare earth after large fires, small patch burning within skink habitat is essential to maintain vegetation cover, combined with carrying out larger fire breaks beyond skink populations. Cool fires likely promotes fresh growth of plants necessary to supplement the diet of *L. kintorei*, including fresh grasses required by termites, which are essential for the survival of skinks.

Conclusion

This research contributes greatly to the current pool of knowledge about a cryptic arid zone threatened species. During the one-year study period we recorded substantial body temperature and movement pattern data of *L. kintorei* at the Uluru-Kata Tjuta National Park bore fields in central Australia. Novel information was obtained about home range for individuals and activity patterns prior to, during and after winter brumation.

Observations during this study suggest that activity levels of *L. kintorei* are temporarily higher than previously recorded that as activity was recorded across four seasons. We confirmed our hypothesis that unimodal-diurnal activity would be most prominent in the cooler months as high ambient temperatures imposed crepuscular and nocturnal activity and colder autumn and winter temperatures diurnal activity.

This research is the first to determine that *L. kintorei* entered prolonged dormancy in shallow burrows up to 230 m away from their main burrows during winter and also summer, possibly as a way of avoiding predation during dormancy. Hibernacula were deep enough to buffer against extremely cold temperatures but shallow enough to trigger emergence when temperatures increased in spring. The slightly deeper hibernacula used for summer estivation prevented *L. kintorei* from overheating yet appeared to support necessary thermal regulation. Individuals remained in a state of estivation for up to 50 days during warm summer months and afterwards remained inactive for days at a time intermittently from mid-summer to the onset of winter brumation.

Body temperature data provided novel information about periods of activity and inactivity of *L. kintorei* and their responses to seasonal change. *Liopholis kintorei* were shown to regulate body temperatures at specific depths seen in brumating, estivating and inactive individuals. During late autumn and early winter, skinks rested at depths in burrows that appeared to maintain minimum voluntary T_bs until cooling winter T_as appeared to initiate the onset of brumation. During brumation and summer estivation skinks seemed to be positioned at depths which would allow awareness of changes in ambient and surface temperatures while remaining below critical maxima and minima temperatures.

Novel findings from this research project will assist land managers make decisions about monitoring *L. kintorei* and *D. blythi* across different seasons to better understand changes in behaviours that may trigger populations to decline. Continued research and monitoring of activity, inactivity and dormancy patterns in both species should look for subtle differences in their response to changing seasonal temperatures and over consecutive years. Combining western science with traditional Aboriginal knowledge, tracking skills and ability to read changes occurring in the environment may help predict potential effects of climate change and prompt improved fire and feral predator management programs to maintain healthy habitats and country necessary for the survival of all species.

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Appendices

Table A1. Average, maximum and minimum ambient temperatures (T_a) and soil temperatures (T_s) at depths of 5, 10, 20, 35, 50, 80 and 100 cm at the Uluru-kata Tjuta bore fields NP.

Soil temperatures

	Summer						Winter					
	Av Ta	Max Ta	Min Ta	Av Ts	Max Ts	Min Ts	Av Ta	Max Ta	Min Ta	Av Ts	Max Ts	Min Ts
	Summer T_{soil} 5 cm (°C)						Winter T_{soil} 5 cm (°C)					
Mean	31.0	42.6	22.2	34.9	46.4	26.7	18.0	30.1	7.7	20.5	31.7	12.4
SD	1.8	2.8	2.3	2.5	4.9	1.8	6.4	6.5	7.6	6.5	6.8	6.6
Min	26.3	36.4	18.3	27.5	31.0	22.0	7.3	17.1	-4.7	10.8	21.5	1.5
Max	35.1	46.7	26.0	38.8	52.5	29.0	32.2	45.3	25.7	34.2	47.0	26.5
Count	19	19	19	19	19	19	143	143	143	143	143	143
	Summer T_{soil} 10 cm (°C)						Winter T_{soil} 10 cm (°C)					
Mean	32.2	42.8	22.0	35.5	38.6	32.5	15.0	27.5	4.0	18.9	20.4	17.4
SD	2.8	3.6	3.3	1.9	1.7	2.5	4.4	4.4	5.2	3.3	3.1	3.4
Min	27.3	36.1	13.8	30.5	35.0	26.5	7.3	17.1	-4.7	14.5	16.0	12.5
Max	38.2	49.3	29.0	38.8	41.0	36.5	25.3	38.3	17.8	26.5	27.5	25.5
Count	47.0	47.0	47.0	47.0	47.0	47.0	101	101	101	101	101	101
	Summer T_{soil} 20 cm (°C)						Winter T_{soil} 20 cm (°C)					
Mean	32.2	42.8	22.2	34.6	35.6	33.5	15.0	27.3	4.3	19.7	20.0	19.5
SD	2.9	3.6	3.3	1.5	1.2	1.8	4.4	4.5	5.5	2.5	2.5	2.5
Min	27.3	36.1	13.8	30.7	32.5	29.0	7.3	17.1	-4.7	16.3	16.5	16.0
Max	38.2	49.3	29.0	37.0	37.5	36.5	25.3	38.3	20.3	25.5	26.0	25.5
Count	46	46	46	46	46	46	105	105	105	105	105	105
	Summer T_{soil} 35 cm (°C)						Winter T_{soil} 35 cm (°C)					
Mean	32.1	42.7	22.2	33.6	33.9	33.1	15.0	27.3	4.1	20.2	20.4	20.0
SD	3.0	3.7	3.3	1.2	1.1	1.3	4.4	4.4	5.3	2.0	2.0	2.0
Min	26.3	36.1	13.8	31.1	31.5	30.5	7.3	17.1	-4.7	17.5	17.5	17.5
Max	38.2	49.3	29.0	35.7	36.0	35.5	25.3	38.3	17.8	24.9	25.0	24.5
Count	47	47	47	47	47	47	106	106	106	106	106	106
	Summer T_{soil} 50 cm (°C)						Winter T_{soil} 50 cm (°C)					
Mean	32.5	42.8	21.8	32.0	32.2	31.9	15.4	27.4	4.7	21.6	21.7	21.5
SD	3.1	3.9	3.5	1.1	1.1	1.1	4.6	4.7	5.4	1.2	1.2	1.3
Min	27.3	36.1	13.8	30.0	30.5	29.0	8.3	19.9	-4.7	19.5	19.5	19.0
Max	38.2	49.3	29.0	33.5	33.5	33.5	25.3	38.3	17.8	23.5	23.5	23.5
Count	43	43	43	43	43	43	84	84	84	84	84	84
	Summer T_{soil} 80 cm						Winter T_{soil} 80 cm					
Mean	32.3	43.0	22.1	31.3	31.4	31.3	15.0	27.3	4.0	21.5	21.6	21.5
SD	2.9	3.6	3.2	0.8	0.8	0.8	4.4	4.5	5.2	1.2	1.2	1.2
Min	26.3	36.1	13.8	29.5	29.5	29.5	7.3	17.1	-4.7	20.0	20.0	19.5
Max	38.2	49.3	29.0	32.5	32.5	32.5	25.3	38.3	17.8	24.0	24.0	24.0

Count	54	54	54	54	54	54	106	106	106	106	106	106
	Summer T_{soil} 100 cm (°C)						Winter T_{soil} 100 cm (°C)					
Mean	32.3	43.0	22.1	31.3	31.4	31.3	15.0	27.3	4.1	21.5	21.6	21.5
SD	2.9	3.6	3.2	0.8	0.8	0.8	4.5	4.5	5.3	1.2	1.2	1.2
Min	26.3	36.1	13.8	29.5	29.5	29.5	7.3	17.1	-4.7	20.0	20.0	19.5
Max	38.2	49.3	29.0	32.5	32.5	32.5	25.3	38.3	17.8	24.0	24.0	24.0
Count	54	54	54	54	54	54	107	107	107	107	107	107

Table A2. Change in time between T_sMax - T_aMax (minutes) and change in time between T_sMin -T_aMin (minutes) across summer and winter. Soil temperatures at depths ≥ 50 cm remained constant (within 0.5°C throughout the day) and were therefore not calculated. Negative change in time values indicate that maximum T_s occurred before maximum T_a and negative values for change in T_s-T_a indicate that T_s was lower than T_a.

Time differences between T_a and T_s

Summer **Winter**

	Change in time T_sMax - T_aMax (mins)	Change in time T_sMin - T_aMin (mins)	Change in temp. T_sMax - T_aMax (°C)	Change in temp. T_sMin - T_aMin (°C)	Change in time T_sMax - T_aMax (mins)	Change in time T_sMin - T_aMin (mins)	Change in temp. T_sMax - T_aMax (°C)	Change in temp. T_sMin - T_aMin (°C)
	Summer- T_{soil} 5 cm				**Winter T_{soil} 5 cm**			
Mean	-54.3	69.4	3.9	4.5	-12.3	59.2	1.1	5.3
SD	69.7	72.7	3.0	1.7	71.7	78.2	2.9	2.0
Min	-246.0	-6.0	-5.4	1.5	-151.0	-22.0	-5.7	-0.8
Max	84.0	279.0	6.8	7.7	308.0	449.0	7.6	9.4
Count	19.0	19.0	19.0	19.0	103	103	103	103
	Summer- T_{soil} 10 cm				**Winter- T_{soil} 10 cm**			
Mean	142.5	216.8	-4.2	10.5	188.3	194.4	-7.0	13.4
SD	86.9	105.4	2.8	2.8	95.2	136.7	3.2	2.8
Min	4.0	72.0	-9.3	5.5	26.0	2.0	-13.0	6.2
Max	394.0	484.0	0.9	16.7	512.0	602.0	1.1	19.2
Count	47	47	47	47	104	104	104	104
	Summer- T_{soil} 20 cm				**Winter- T_{soil} 20 cm**			
Mean	334.7	378.3	-7.2	11.4	333.5	351.1	-8.0	15.1
SD	123.8	221.1	3.2	2.9	144.8	283.7	3.5	3.9
Min	14.0	207.0	-13.2	6.2	1.0	-97.0	-13.7	0.2
Max	604.0	1654.0	-1.1	18.2	631.0	1854.0	-1.0	21.9
Count	45	46	45	46	73	68	74	105
	Summer- T_{soil} 35 cm				**Winter- T_{soil} 35 cm**			
Mean	348.8	492.5	-8.8	11.0	507.0	568.1	-6.9	15.8
SD	151.4	93.6	3.7	3.1	45.3	145.9	4.0	4.1
Min	99.0	304.0	-15.2	5.0	475.0	415.0	-14.3	6.2
Max	604.0	634.0	-2.1	18.7	539.0	955.0	2.7	22.7
Count	23	15	46	47	2	11	105	105
	Summer- T_{soil} 50 cm				**Winter- T_{soil} 50 cm**			
Mean	NA	NA	-10.6	10.1	0.0	0.0	-5.7	16.8
SD	NA	NA	3.7	3.2	0.0	0.0	4.5	5.0

Range	NA	NA	12.6	14.7	0.0	0.0	18.0	20.7
Min	NA	NA	-17.2	3.0	0.0	0.0	-15.3	5.7
Max	NA	NA	-4.6	17.7	0.0	0.0	2.7	26.4
Count	NA	NA	43	43	0	0	84	84
	Summer- T_{soil} 80 cm				**Winter- T_{soil} 80 cm**			
Mean	NA	NA	-11.5	9.1	0.0	0.0	-5.7	17.5
SD	NA	NA	3.7	3.1	0.0	0.0	4.5	5.0
Range	NA	NA	13.9	14.7	0.0	0.0	17.8	21.7
Min	NA	NA	-18.3	2.0	0.0	0.0	-15.3	5.2
Max	NA	NA	-4.4	16.7	0.0	0.0	2.5	26.9
Count	NA	NA	54	54	0	0	105	106
	Summer- T_{soil} 100 cm				**Winter- T_{soil} 100 cm**			
Mean	NA	NA	-11.5	9.1	0.0	0.0	-5.8	17.4
SD	NA	NA	3.7	3.1	0.0	0.0	4.5	5.1
Range	NA	NA	13.9	14.7	0.0	0.0	17.8	21.8
Min	NA	NA	-18.3	2.0	0.0	0.0	-15.3	5.1
Max	NA	NA	-4.4	16.7	0.0	0.0	2.5	26.9
Count	NA	NA	54	54	0	0	106	107

Table A3: R script used to test seasonal T_b differences for *L. kintorei* using a mixed effects model.

```
> View(Skink_Tb_Min_Max_Avg_vs_Season)

> ModelTbMax<-lme(TbMax~Season,

random=~1|Individual,data=Skink_Tb_Min_Max_Avg_vs_Season)

> summary(ModelTbMax)

Linear mixed-effects model fit by REML

  Data: Skink_Tb_Min_Max_Avg_vs_Season

       AIC          BIC            logLik

  5609.981   5640.054    -2798.99

Random effects:

 Formula: ~1 | Individual

               (Intercept)    Residual

StdDev:    1.168894   2.966964

Fixed effects:  TbMax ~ Season

                          Value               Std.Error     DF        t-value      p-value
```

```
(Intercept)     31.179927    0.6048411    1107   51.55061     0
SeasonSpring   1.765925     0.2398569    1107   7.36241      0
SeasonSummer  4.577018     0.2606192    1107   17.56209     0
SeasonWinter -7.408601     0.2451081    1107   -30.22585    0
 Correlation:
                    (Intr)      SsnSpr     SsnSmm
SeasonSpring        -0.167
SeasonSummer       -0.154      0.402
SeasonWinter        -0.164      0.446       0.402
Standardized Within-Group Residuals:
        Min                Q1                  Med               Q3                 Max
-2.9371912424   -0.6560460350    -0.0002763907    0.6064035681     3.4243713320
Number of Observations: 1114
Number of Groups: 4
> anova(ModelTbMax)
            NumDF       denDF          F-value         p-value
(Intercept)    1        1107           2713.3041      <.0001
Season         3        1107           730.8731       <.0001
> ModelTbMin<-lme(TbMin~Season,
random=~1|Individual,data=Skink_Tb_Min_Max_Avg_vs_Season)
> summary(ModelTbMin)
Linear mixed-effects model fit by REML
  Data: Skink_Tb_Min_Max_Avg_vs_Season
      AIC            BIC          logLik
  5857.079     5887.152     -2922.54
Random effects:
 Formula: ~1 | Individual
             (Intercept)    Residual
StdDev:     0.69275       3.321709
Fixed effects:  TbMin ~ Season
                    Value            Std.Error        DF       t-value          p-value
```

```
(Intercept)      25.886339     0.3877841     1107   66.75451      0
SeasonSpring  -2.243346      0.2683121     1107   -8.36096      0
SeasonSummer          2.961867       0.2916373      1107    10.15599       0
SeasonWinter          -11.257572     0.2737767      1107    -41.11954      0
 Correlation:
                    (Intr)              SsnSpr     SsnSmm
SeasonSpring     -0.293
SeasonSummer  -0.269              0.402
SeasonWinter    -0.287              0.444       0.401

Standardized Within-Group Residuals:
       Min              Q1              Med               Q3               Max
-2.51293457    -0.71877371   -0.08556488    0.59146063    2.83445878
Number of Observations: 1114
Number of Groups: 4
> anova(ModelTbMin)
                 numDF      denDF             F-value          p-value
(Intercept)       1          1107              4189.717         <.0001
Season             3          1107              849.703          <.0001



ModelTbAvg<-lme(TbAvg~Season,
random=~1|Individual,data=Skink_Tb_Min_Max_Avg_vs_Season)
> summary(ModelTbAvg)
Linear mixed-effects model fit by REML
  Data: Skink_Tb_Min_Max_Avg_vs_Season
      AIC          BIC          logLik
  5431.792   5461.865    -2709.896
Random effects:
 Formula: ~1 | Individual
              (Intercept)       Residual
```

```
StdDev:   0.7884784      2.740372
Fixed effects:  TbAvg ~ Season
                    Value        Std.Error     DF     t-value           p-value
(Intercept)         28.428219    0.4196614     1107   67.74084     0e+00
SeasonSpring        -0.778038    0.2214723     1107   -3.51303     5e-04
SeasonSummer        4.101186     0.2406731     1107   17.04048     0e+00
SeasonWinter        -9.999675    0.2261993     1107   -44.20735    0e+00
 Correlation:
              (Intr)    SsnSpr    SsnSmm
SeasonSpring    -0.223
SeasonSummer  -0.205    0.402
SeasonWinter    -0.218    0.445     0.402

Standardized Within-Group Residuals:
       Min           Q1           Med          Q3          Max
-2.58300656  -0.69061257  0.03428004   0.71860994   2.63168793
Number of Observations: 1114
Number of Groups: 4
> anova(ModelTbAvg)
             numDF    denDF    F-value     p-value
(Intercept)     1        1107     4411.872    <.0001
Season          3        1107     1154
```

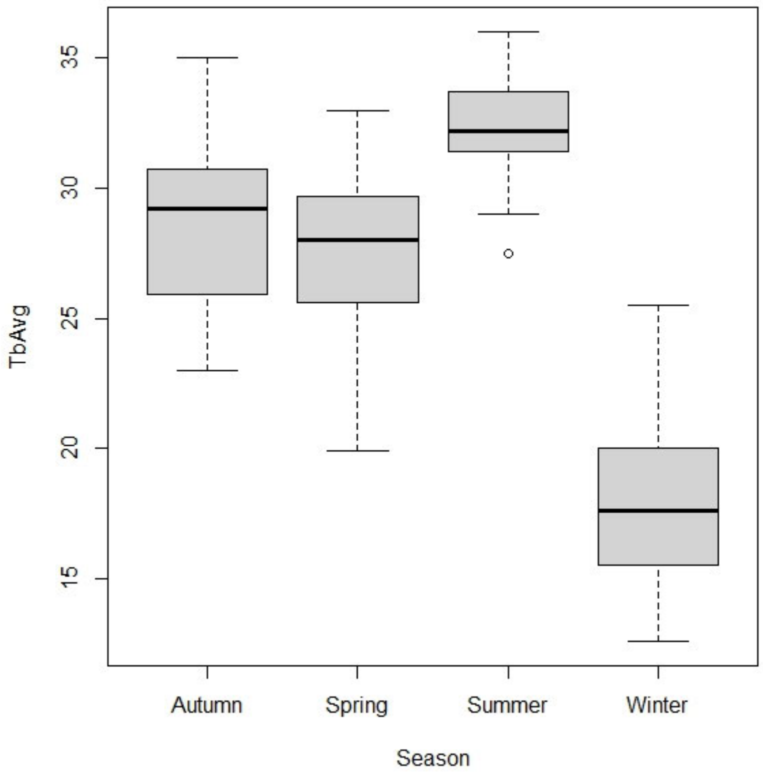

Figure A1: Plot showing distribution of *L. Kintorei* T_b values. The dark line indicates the median (°C) for each season and error bars indicate maximum and minimum values per season.

Higher Degree Research Thesis by Publication

University of New England

STATEMENT OF AUTHORS' CONTRIBUTION

(To appear at the end of each thesis chapter submitted as an article/paper)

We, the Research Master candidate and the candidate's Principal Supervisor, certify that all co-authors have consented to their work being included in the thesis and they have accepted the candidate's contribution as indicated in the *Statement of Originality*.

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Chapter Three

Seasonal differences in the thermal biology of mulgaras (*Dasycercus blythi*).

To be published by: Martin Campbell, Gerhard Körtner, Rachel Paltridge, Zenon Czenze,
Fritz Geiser

Introduction

Ectotherms, with their low metabolism and water loss may appear to be ‘pre-adapted’ for life in the desert. Endotherms on the other hand (i.e., mainly mammals and birds) fundamentally differ from ectotherms (i.e., reptiles, amphibians, fish and most insects) in their ability to maintain a high, stable body temperature (T_b) via metabolic heat production (MHP; Withers et al., 2016; Geiser et al., 2017). The basal metabolic rates (BMR; the minimum metabolic rate of normothermic animals measuring under thermoneutrality) of birds and mammals are generally 20 to 30-fold higher than similarly sized reptiles (Hillenius & Ruben, 2004), but can be 100-fold or more in small species (< 50 g) in the cold (Geiser, 2021). However, MHP is energetically costly and the maintenance of a high and stable T_b requires a constant supply of food energy (Geiser, 2004). The ambient temperature (T_a) an individual experiences impacts their energy balance, with low T_as the T_b-T_a differential is increased leading to greater heat loss to the environment and therefore higher energy demands (Lovegrove, 2012).

The impact of ambient temperature on energy balance is especially pronounced in small endotherms that quickly lose heat to the environment due to the high surface area to volume ratios of their bodies (Geiser, 2010; 2021). As a result, many species of small endotherm employ several behavioural and physiological adaptations to decrease energy expenditure in periods of low T_a or resource availability (Geiser, 2004; Ruf & Geiser, 2015). Behavioural adjustments include huddling, which reduces the surface area of individuals and therefore heat loss (Gilbert et al., 2010). A highly efficient physiological adaptation is torpor, a physiological state characterized by substantial decreases in metabolic rate and T_b (Geiser, 2004). Torpor is common in small endotherms and allows them to minimize energy and water loss during periods of low T_a or energy scarcity (Wang, 1989; Grigg et al., 2004; Ruf & Geiser, 2015), but also to deal with many other challenging situations (Nowack et al., 2017).

In temperate environments energy availability and temperature fluctuate predictably with season and many species can prepare accordingly, fatten in autumn and hibernate during winter (Heller, 1983; Geiser, 2020). However, in desert environments, seasonal changes are compounded by extreme daily T_a fluxes and lack of water availability. For example, in the arid zone of central Australia, organisms experience arid conditions with highly unpredictable rainfall, and T_a ranging between -4.1 to 47.1 °C (Uluru, BoM 2021). As a result, many arid zone species cope with these conditions via a semi-fossorial existence (Kinlaw, 1999) and the use of daily torpor in burrows (Körtner et al., 2007). Burrows effectively buffer and individual from changes in T_a and help lower thermoregulatory energy expenditure (Moore et al., 2018). In arid environments, burrows can be 15-20 °C cooler than surface temperatures, and maintain relatively stable temperatures (Williams et al., 1999; Whittington-Jones et al., 2011) yet be warmer at night (Cortés et al., 2000).

Small burrowing endotherms such as dasyurid marsupials use daily torpor via lowering MR and T_b to conserve energy but also water, thus increasing their survival when resources are limited (Geiser & Masters, 1994; Cooper et al., 2005; Körtner et al., 2008a). Individuals can further increase their energy savings by behavioural mechanisms including basking and huddling (Geiser, 2021). Basking enables individuals to passively rewarm from torpor to normothermic T_b and can reduce rewarming costs by 85% (Geiser & Drury, 2003; Warnecke et al., 2008). Huddling can also reduce energy expenditure by up to 50% by effectively reducing an individual's surface area exposed to the environment (Langer, 2005). These behaviours are prominent in several desert mammals including dasyurids (Langer, 2005; Gilbert et al., 2006; Schradin et al., 2006) and may be an important adaptation as many small dasyurids are under considerable pressures to reduce their time above ground to avoid predation (Geiser & Pavey, 2007).

With the loss of the western quoll (*Dasyurus geoffroii*) across arid Australia, and severely reduced numbers of kowari (*Dasyuroides byrnei*), the largest remaining dasyurids in central Australia, are the crest-tailed (*Dasycercus cristicauda*), and the brush-tailed mulgara (*Dasycercus blythi*), which weigh less than 150 g. Brush-tailed mulgaras (hereafter "mulgaras") inhabit locations across sandy deserts in Australia (Körtner et al., 2008b) where they are a dominant predator amongst small native mammals, reptiles and invertebrates (Dickman et al., 2001). Their nocturnal carnivorous lifestyle means mulgaras are energetically challenged during periods of low T_a as their energy expenditure is high because heat loss to the environment is increased. Since their energy availability is reduced as prey are less abundant/available when it is cold, they cannot afford to maintain a constant high T_b via physiological thermoregulation. To cope with energy shortages/increased costs during long periods of low T_a, limited rainfall, and low food availability, mulgaras use daily torpor within their burrows (Körtner et al., 2008a). During daily torpor their torpor metabolic rates (TMR) can be as low as 30% of BMR (Geiser, 2004). Using daily torpor provides mulgaras a means to offset energetic costs and lower daily energy expenditure during food shortages to maintain body mass, particularly during the winter reproductive period when they require extra energy for mating and the production of young (June – August; Geiser & Masters, 1994; Körtner et al., 2008a). Torpor use is therefore not solely a response to low T_as, but also allows reallocating energy towards reproduction, as seen in bats where delayed parturition may be beneficial until conditions are suitable for survival of offspring (Willis et al., 2006).

Both male and female mulgaras use torpor during the winter reproductive period. However, there is considerable intersexual variation due to differing natural selection pressure (Körtner et al, 2008a). Prior to gestation, females display lower T_bs and longer torpor bouts than males resulting in higher energy savings and a build-up of fat stores in preparation for parturition and lactation (Geiser & Masters, 1994; Körtner et al.,2008a). This strategy could lead to females increasing body mass while also reducing their foraging time and exposure to predators (Geiser & Körtner, 2010; Turbill et al., 2003). Conversely, as males are under pressure to find females with which to mate, they have large home ranges, and use shorter torpor bouts (Körtner et al., 2008a). The enlarged home range of males during this period leads to greater fitness opportunities, but also increased foraging demand to fuel activity exposing them to greater predation risks. However, no data exist on whether these intersexual differences in home range and energy expenditure persist during the non-reproductive season when the natural selection pressures acting on both sexes are likely similar.

Free-living mulgaras are known to differ between males and females with regard to activity patterns and thermoregulation during winter however, the understanding of activity behaviour and especially physiological adaptations during summer is lacking. In other species of arid zone marsupials such as dunnarts (*Sminthopsis* spp.) and kowaris (*D. byrnei*) studies of captive individuals demonstrated use of daily torpor during both winter and summer months especially when food was withheld (induced torpor), whereas spontaneous torpor in summer was regularly observed in the small dunnarts, but only rarely in the much larger kowaris (Geiser and Baudinette, 1987). Summer torpor has also been observed in other species such as numbats (*Myrmecobius fasciatus*; Cooper & Withers, 2004), echidnas (*Tachyglossus aculeatus*; Brice et al., 2002) and many insectivorous bats in the arid zone (Bondarenco et al., 2014). It is therefore possible mulgaras use torpor during summer to some extent.

Torpor use in mulgaras has been found to be affected by T_a and survival during winter may involve an intricate balance between torpor metabolic rate and use of relatively shallow burrows during periods of low T_a (Körtner et al., 2008a). Extended periods of gestation in female mulgaras have also been linked to low T_a and their likely use of torpor (Geiser & Masters, 1994). However, where daily T_a was a significant factor influencing torpor use in the western pygmy-possum (*Cercartetus concinnus*; Turner et al., 2012a), daily mean T_a was not found to be related to torpor bouts in the related eastern pygmy-possum (*Cercartetus nanus*; Turner et. al., 2012b). Nevertheless, for mulgaras we hypothesised that both season and average daily T_a will have a significant effect on use of daily torpor. Körtner et al. (2008a) predicted that torpor use in summer should be restricted by high soil temperatures and that mulgaras would therefore be unable to cool their T_bs sufficiently within their burrows to use torpor. I therefore tested the hypothesis that torpor use in mulgaras during summer is limited and shallow.

Differences of movement between the sexes and seasons can provide relevant information in understanding population composition and dynamics (Bos & Carthew, 2007). Investigation of home range and activity patterns of females and male mulgaras in conjunction with thermoregulation patterns during summer and winter was therefore required to better the understanding of their biology in nature. I tested the hypothesis that the activity and thermoregulation patterns of mulgaras would reflect energy availability and predation risk differently for male and female mulgaras.

Material and Methods

Location and field work period

Fieldwork was conducted during two austral summer seasons (13 January – 31 March 2018; 1 December - 12 January 2019), and one austral winter season (29 June – 30 September 2018). Field research was carried out at the bore fields area within Uluṟu-Kata Tjuṯa National Park (UKTNP), Northern Territory (NT), Australia (25°16'S, 130°56'E; Figure 1). The bore fields are located on a sand plain covered predominately by sparse to mature dense spinifex (*Triodia basedowii*), a spiky grass that forms dense tussocks, and bordered by low dunes and mulga shrubs *(Acacia aneura).* Temperature and rainfall data were collected from a weather station at Yulara ~7 km from the field site.

Figure 1. Field study site within the bore fields area of Uluṟu-Kata Tjuṯa National Park, NT, Australia. The red circle indicates the location in Australia and the pale shaded polygon with red outline indicates the area mulgaras were tracked during the study.

Capture and surgery

Mulgaras were captured by setting up 4 lines of type A Elliott traps with 25 traps per line within an area of ~20 ha. Two parallel and three perpendicular lines were positioned either side the road passing through the site. Traps were baited with a mixture of peanut butter and oats (Körtner et al., 2007) and set within two hours of sunset and closed within two hours after sunrise. A small ball of polyester fibre was placed in each trap to provide insulation. Once caught, all animals were sexed and weighed with an electronic scale to the nearest 0.1 g and kept one to two days in individual holding boxes (35 x 20 x 25 cm). A mixture of peanut butter, oats, fresh minced meat, and water were provided *ad libitum*.

During summer 2018, we captured two adult females (62.6 g, 65.5 g) and three adult males (68.8 g, 80.0 g, 90.3 g). Similarly, during winter 2018, two adult females (65.0 g, 73.3 g), and three adult males were captured (77.5 g, 78.8 g, 83.5 g). During a summer recapture in November 2018 one male had reduced mass from 77.5 g to 71.1 g and another from 78.8 g to 75.3 g. One female had reduced mass from 65.0 g to 58.4 g, but this was within the range of body mass of females we captured without transmitters. Together this suggests the procedure does not adversely affect individuals.

Animals were anaesthetised with Isoflurane in oxygen and implanted with small, sterilised, wax coated, temperature-sensitive radio transmitters weighing 3.0 – 3.6 g (Sirtrack, Havelock, New Zealand). The site of the incision was shaved and sterilised with alcohol and Betadine before a short (~1 cm) midline abdominal incision was made, after which the transmitter was inserted intraperitoneally. Both muscle and skin layers were sutured separately with polyglycolic acid surgical sterile sutures followed by a local topical anaesthetic (10% Xylocaine pump spray) and an antibacterial spray bandage. Animals were then provided with a few drops of children's (1 month – 2-year-old) liquid Panadol. The procedure lasted between 10-30 minutes per animal, plus a 30-minute recovery period. After recovery, animals were placed their own holding boxes and released the following day at dusk at the site of capture. Two males trapped during summer 2018 were re-captured in winter 2018. These individuals did not lose mass, showing an increased mass of 8.7 g and 3.5 g, again suggesting no adverse effects. As such these individuals had their transmitter extracted and a new one inserted.

Radio-tracking and temperature logging

The transmitters weighed well below the recommended 5% of the animal's body mass (NSW Department of Primary Industries Animal Welfare Unit and Animal Research Review Panel, 2020) and were calibrated to the nearest 0.1°C over a temperature range of 9.6 – 41.6°C against a high-precision mercury thermometer (Rojas, Körtner & Geiser, 2010; Körtner et al., 2008a). Tracking was carried out on foot or in a vehicle using 3-element Yagi antennas (Sirtrack, Titley and ATS models), at times affixed to a 2.4 m pole standing on the back of a utility vehicle and attached to Icom IC-R10 receivers (Icom inc.). Each radio-transmitter has a unique frequency and the interval between pulses changed with temperature. Tracking was used to identify individual animals, daytime refugia, T_b, and movement patterns.

Once animals were located each morning their location was marked and recorded with a hand-held GPS (Garmin GPSmap 62S). The location of each mulgara's daytime burrow refugia was recorded to determine the outer limits of an area within which they moved. We created a polygon using the burrows as edge points and several opportunistic night-time tracking locations and calculated the area of the polygon using minimum convex polygons (MCP) calculated in Google Earth Pro. For the purposes of this study, we consider the area of this polygon to be a conservative estimate of home range. This is partly due to the short range of the receivers and radio transmitters, and also because we generally did not track individuals during their active period at night. On five occasions, however, mulgaras were tracked during the active phase and on all occasions their locations were within our estimate of home range. On several occasions during the day, individuals could not be tracked despite extensive searches beyond their area of typical burrow use.

If two individuals were recorded in the same burrow during the day, we assumed the individuals were huddling or potentially together for the purpose of mating. The term 'shared burrows' refers to burrows used by more than one mulgara at different times. To record incidental behaviours such as basking or interactions between individuals, motion sensor cameras were erected at the entrance of 8 burrows at various stages during summer and winter.

Provided an animal could be located in the morning, T_b was recorded by positioning mobile data loggers ~1.5m from each individual animal's burrow. The loggers measured and stored the transmitter's pulse interval every 10 min (Körtner & Geiser, 1998) and this data was downloaded to a field computer every few days. Pulse intervals were then converted to body temperature based on transmitter-specific calibrations (Körtner & Geiser, 2011).

Burrow temperatures were recorded in three active mulgara burrows during summer and 8 mulgara burrows in winter by positioning iButton data loggers along lengths of cable feeder. Because length of burrows does not indicate depth, data loggers were positioned roughly halfway along the cable feeder and at the end of the feeder of various lengths ranging between 91- 134 cm long with cloth tape to provide variation. Average burrow temperatures were calculated from all burrow temperature records combined. Soil temperature was recorded by taping data loggers at seven depths on timber stakes (5, 10, 20, 35, 50, 80, 100 cm) and burying them in the ground at two areas within the study site.

Torpor and activity

Although the use of a torpor threshold is somewhat contentious (Brigham et al., 2011), a torpor threshold of 30°C is commonly used (Körtner et al., 2007; Körtner & Geiser, 2011). However, we selected a torpor threshold based on a frequency distribution of the T_b data as described by McKechnie et al. 2007 (Figure 2). The vast majority of T_b recordings were from around the burrow systems and hence represent rest phase normothermia or torpor. To determine the threshold between these two stages, the frequency distribution of all T_b records was calculated per individual. It was assumed that the bin with the most common T_b recordings represented normothermic resting values (T_b = ~36.5°C) with a normal distribution around it. Hence the right had side of this proposed bell curve that included only normothermic values was mirrored to the left and the lower end of the mirrored curve was assumed to be the threshold between normothermia and torpor. This method suggested a threshold value of 32.4°C, similar to a torpor threshold of 32.5°C used by Stawski & Rojas (2016) for a another dasyurid species, which we reduced to a more conservative 32.0°C. Our definition also agrees with a reduction of 5°C or more below resting T_b for defining torpor (Geiser 2021). Further, we only classified an individual as torpid if T_b fell below this threshold for 30 min or longer. Body temperature translated from pulse intervals can sometimes be unreliable (e.g., missed pulse resulting in very low T_b). Therefore, all values were manually checked, and all unrealistic data were deleted.

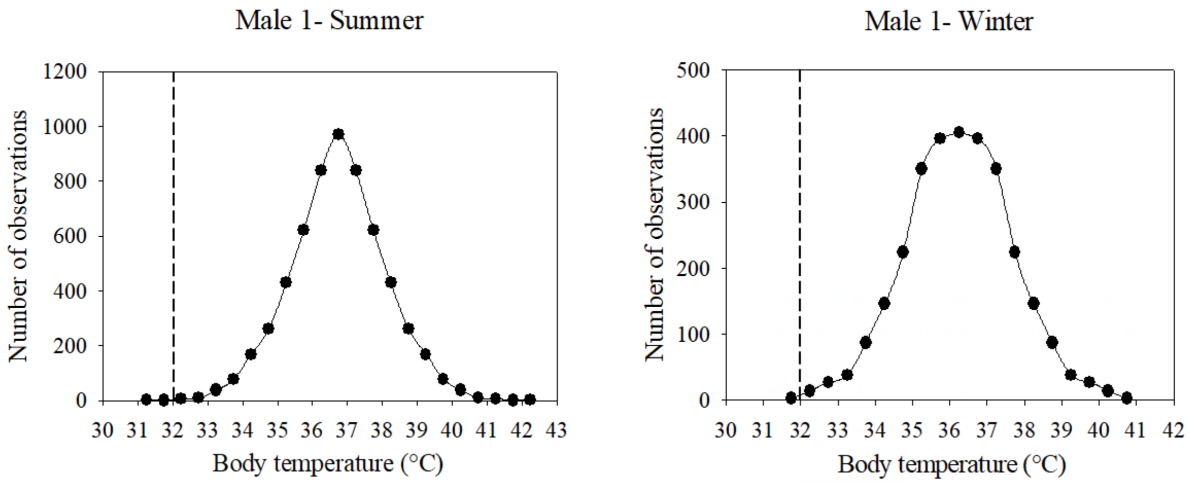

Figure 2. Frequency distribution of a male mulgara (*D. blythi*) during winter and summer based on the most common T_b frequencies which were found to be ~36.5°C for all mulgaras for this study. These values represented normothermic resting values and were then mirrored as per McKechnie et al. (2007) to determine torpor threshold cut off.

Using a custom-written program in Visual Basic 6 (Microsoft Corporation, WA) we extracted maximum, minimum and average T_b for each 24-hour period. Only 24-hour periods with more than 200 minutes of T_b recordings were included in further analyses. The program also extracted torpor bout length (based on the 32°C and 30 min threshold), average and maximum rewarming rates (degrees/minute), and length of arousal time from torpor. Rewarming rate was calculated by averaging the time taken between rewarming from the minimum T_b to the maximum T_b. Where the rewarming was irregular the end of arousal was chosen when T_b plateaued.

Since mulgaras usually move quickly out of range of logger reception (~30 m) once leaving a burrow, we calculated the activity bout length based on the absence of animals from their burrow. Activity bout length began with the final T_b record on departure and ended when animal returned and displayed a typical T_b resting pattern inside the burrow. Although the start of activity was recorded for most days, end of activity could only be assessed if an animal returned to a burrow already monitored by a logger.

Statistical analyses

All statistical analyses were carried out in R (R Core Team, 2019). To test for the influence of abiotic and biotic factors on torpor bout length and activity bout length we created linear mixed effects models using ‘nlme’ (Pinheiro, 2012) with the fixed effects: season (summer or winter), sex (male or female) and average ambient temperature. Maximum, minimum and average temperatures were correlated (Pearsons correlation, $R = 0.64 – 0.90$) and we chose average temperature because it had the lowest AIC score. In the models, individual ID was included as a random effect to account for pseudoreplication due to multiple data points per animal. Global models included all fixed effect interaction terms and model reduction as we were testing a hypothesis and thus modelling for inference, we selected which predictor variables to retain in the final models based on null hypothesis testing (Tredennick et al., 2021). The estimated marginal means of activity bout length for each sex and season and torpor bout length for each sex were calculated using the "emmean" package (v1.4.6; Lenth, 2021). We also created a generalised linear mixed effect model to analyse torpor frequency (percentage of days an individual used torpor) with the same fixed and random effect structure, and model reduction procedure as above. In all analyses we assigned the significance level at $\alpha = 0.05$. Unless otherwise stated, data are presented as the mean ± SD; *n* represents the number of individuals, and *N* the number of measurements.

Results

Weather data were collected over 121 days during summer and 94 during winter. T_as ranged from -2.7°C in winter to 46.8°C in summer and the total annual rainfall for 2018 was 147.6 mm (mean rainfall = 316.6 mm; Australian Bureau of Meteorology http://www.bom.gov.au). were 18 days of rain during the summer season and four during the winter period. The maximum daily rainfall was 22 mm in summer and 2.8 mm in winter. Total rainfall during the summer fieldwork period was 91.6 mm and 7.4 mm in winter. The daily average T_a during the summer fieldwork period was 30.1 ± 3.4°C with a maximum T_a of 46.8°C, and minimum T_a of 12.5°C. Average winter T_a was 15.4 ± 4.3°C with a maximum T_a of 35.8°C and minimum T_a -2.7°C.

Mulgara data were collected from 8 animals used in summer and 5 animals used in winter for a total of 701 mulgara-days (summer 359, winter 342) and ranged from 9-85 days per individual per season. This included additional summer data which were obtained from the winter study animals whose transmitters were still active in the early part of the second summer period (two females for 34 and 36 days and two males for 8 and 6 days).

Soil and burrow temperature

Mulgara burrow temperatures were averaged across various depths and therefore do not indicate burrow depth. Mulgara burrows are known to be ~25 to 30 cm in depth (Körtner et al., 2007). During summer, mulgara burrow temperatures averaged 31.4 ± 2.7°C but ranged from 18.9 to 44.1°C (*N* = 10950; *n* = 3). During winter, burrow temperatures fluctuated between 0.8 and 33.1°C (Mean 17.2 ± 3.9°C; *N* = 21026; *n* = 8).

In summer T_s at a depth of 20 cm ranged from 29.0 to 37.5°C (mean 34.6 ± 1.5°C) and at 35 cm were more stable and ranged from 30.5 to 36°C (mean 33.9 ± 1.1°C). T_s at a depth of 50 cm during summer was on average 32.1 ± 1.1°C and only slightly cooler than at 35 cm (Table 7).

During winter, T_s at depths of 20 cm ranged between 16.0 and 25.5°C (Mean 19.7 ± 2.5°C), and at 35 cm ranged between 17.5 and 24.5°C (mean 20.2 ± 2.0°C). T_s at a depth of 50 cm during winter was on average 21.6 ± 1.2°C (Table 7).

Table 1. Average, maximum and minimum ambient temperatures (T_a) and soil temperatures (T_s) at depths of 5, 10, 20, 35, 50 cm during summer and winter months at the Uluṟu-Kata Tjuṯa bore fields.

Soil temperatures

	Summer						**Winter**					
	Av T_a	Max T_a	Min T_a	Av T_s	Max T_s	Min T_s	Av T_a	Max T_a	Min T_a	Av T_s	Max T_s	Min T_s
	Summer T_{soil} 5 cm (°C)						Winter T_{soil} 5 cm (°C)					
Mean	31.0	42.6	22.2	34.9	46.4	26.7	18.0	30.1	7.7	20.5	31.7	12.4
SD	1.8	2.8	2.3	2.5	4.9	1.8	6.4	6.5	7.6	6.5	6.8	6.6
Min	26.3	36.4	18.3	27.5	31.0	22.0	7.3	17.1	-4.7	10.8	21.5	1.5
Max	35.1	46.7	26.0	38.8	52.5	29.0	32.2	45.3	25.7	34.2	47.0	26.5
Count	19	19	19	19	19	19	143	143	143	143	143	143
	Summer T_{soil} 10 cm (°C)						Winter T_{soil} 10 cm (°C)					
Mean	32.2	42.8	22.0	35.5	38.6	32.5	15.0	27.5	4.0	18.9	20.4	17.4
SD	2.8	3.6	3.3	1.9	1.7	2.5	4.4	4.4	5.2	3.3	3.1	3.4
Min	27.3	36.1	13.8	30.5	35.0	26.5	7.3	17.1	-4.7	14.5	16.0	12.5
Max	38.2	49.3	29.0	38.8	41.0	36.5	25.3	38.3	17.8	26.5	27.5	25.5
Count	47.0	47.0	47.0	47.0	47.0	47.0	101	101	101	101	101	101
	Summer T_{soil} 20 cm (°C)						Winter T_{soil} 20 cm (°C)					

Mean	32.2	42.8	22.2	34.6	35.6	33.5	15.0	27.3	4.3	19.7	20.0	19.5
SD	2.9	3.6	3.3	1.5	1.2	1.8	4.4	4.5	5.5	2.5	2.5	2.5
Min	27.3	36.1	13.8	30.7	32.5	29.0	7.3	17.1	-4.7	16.3	16.5	16.0
Max	38.2	49.3	29.0	37.0	37.5	36.5	25.3	38.3	20.3	25.5	26.0	25.5
Count	46	46	46	46	46	46	105	105	105	105	105	105

	Summer T_{soil} 35 cm (°C)						Winter T_{soil} 35 cm (°C)					
Mean	32.1	42.7	22.2	33.6	33.9	33.1	15.0	27.3	4.1	20.2	20.4	20.0
SD	3.0	3.7	3.3	1.2	1.1	1.3	4.4	4.4	5.3	2.0	2.0	2.0
Min	26.3	36.1	13.8	31.1	31.5	30.5	7.3	17.1	-4.7	17.5	17.5	17.5
Max	38.2	49.3	29.0	35.7	36.0	35.5	25.3	38.3	17.8	24.9	25.0	24.5
Count	47	47	47	47	47	47	106	106	106	106	106	106

	Summer T_{soil} 50 cm (°C)						Winter T_{soil} 50 cm (°C)					
Mean	32.5	42.8	21.8	32.0	32.2	31.9	15.4	27.4	4.7	21.6	21.7	21.5
SD	3.1	3.9	3.5	1.1	1.1	1.1	4.6	4.7	5.4	1.2	1.2	1.3
Min	27.3	36.1	13.8	30.0	30.5	29.0	8.3	19.9	-4.7	19.5	19.5	19.0
Max	38.2	49.3	29.0	33.5	33.5	33.5	25.3	38.3	17.8	23.5	23.5	23.5
Count	43	43	43	43	43	43	84	84	84	84	84	84

Torpor patterns Winter

During winter both male and female mulgaras regularly displayed daily torpor. Mean T_a in July was 12.9 ± 2.6°C and increased gradually towards the end of September to 19.8 ± 2.9°C. Males (average torpor frequency per individual = 88.0 ± 10.6%, 150 days tracked, 3 individuals monitored) used torpor more frequently in winter than females (average torpor frequency per individual = 85.4 ± 5.8%; 151 days tracked, 2 individuals monitored). Winter T_bs in torpid mulgaras were also lower for females than males (19.6 ± 5.1; 23.3 ± 4.2). Torpor was observed in female mulgaras essentially daily from July to mid-September and during this period minimum T_bs generally corresponded with fluctuations in T_a (Figure 3). The two females ceased using torpor 11 September and 21 September respectively and T_b remained consist between normothermic and active values after that time. During winter the daily torpor patterns of male mulgaras were not as deep as displayed by females and minimum T_bs generally fell to just below ~20°C when T_as approached 0°C (Figure 4). The lowest T_b experienced by a male was 15.4°C on 21 August.

The most pronounced expression of torpor was observed in female 2 in August, winter (Figure 5). This female reduced its T_b from 37.3°C mid-afternoon and entered torpor around dusk after which its T_b fell to a minimum of 13.0°C during the night. It then aroused around midday after a torpor bout of 20.5 hours. On the following day the female was not in range of the receiver for much of the night, but when she was tracked on the following morning her T_b was as low as 11.7°C, the lowest T_b measured for any individual and again she aroused after midday.

Mean maximum T_b recorded during winter was 37.8 ± 1.3°C. During activity mulgaras typically left their burrows around dusk to forage and if they returned to the same burrow, onset of torpor could be recorded. If they moved to another burrow out of range of the receiver, then tracking T_b resumed once they were located the next morning. Activity began once T_bs reached ~36.5°C and maximum T_bs corresponded with departure from burrows and when mulgaras were out of range of receivers.

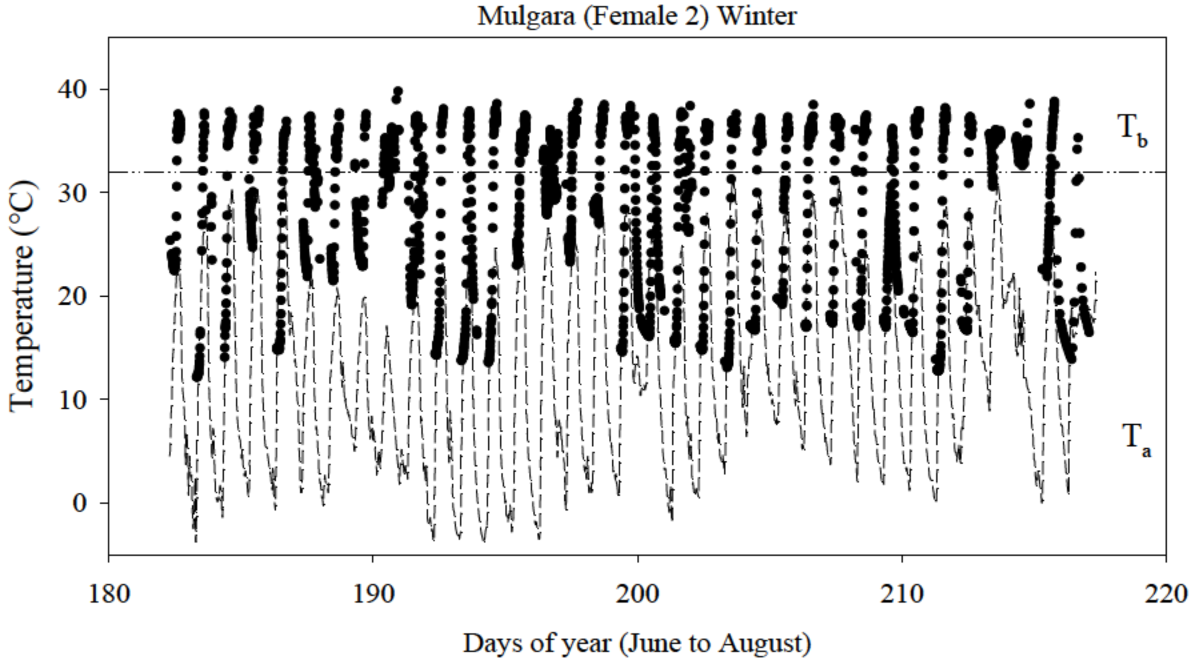

Figure 3. Fluctuations of body temperatures (T_b) and ambient temperatures (T_a) over five weeks in winter between 29 June (day 180) and 8 August (day 220). The dash-dotted line represents the torpor threshold.

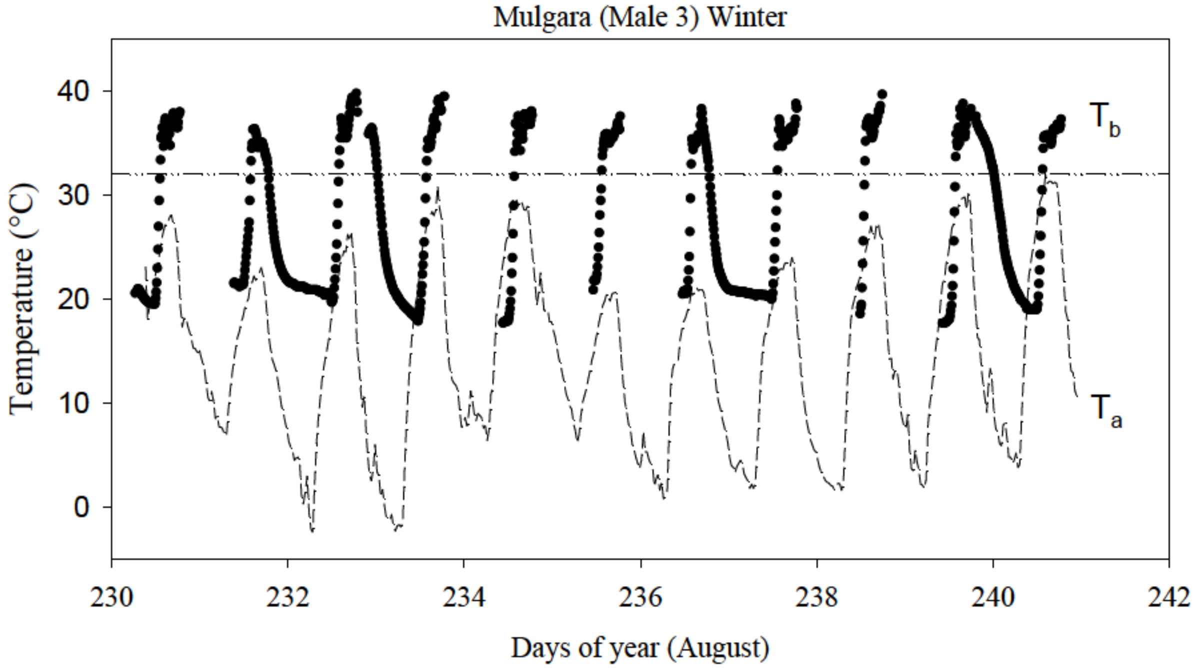

Figure 4. Daily torpor patterns of a male mulgara during winter between 18th August (day 230) and 29th August 2018 (day 241). During this period torpor bouts are not as deep as displayed by females, with minimum T_bs falling to just below ~20°C when T_as approached `0°C. The dash-dotted line represents the torpor threshold.

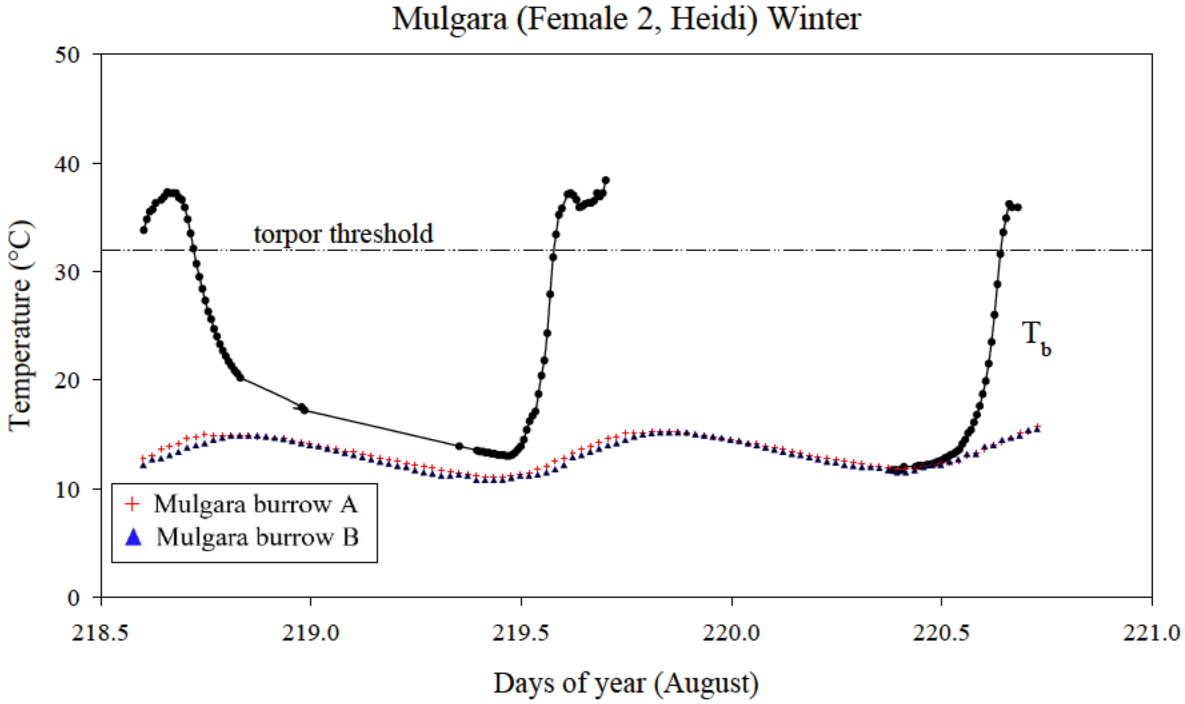

Figure 5. Body temperature (T_b) fluctuations of female 2 in August. Torpor commenced at about dusk on 6 August (~18:00, day 218), continued throughout the night reached a minimum of 13.0°C before arousing from torpor about mid-day 7 August (day 219). After rewarming to ~36°C it briefly cooled then T_b increased to 38.4°C at departure close to dusk (~219.6). A similar torpor pattern was displayed the following day prior to T_b falling to a minimum of 11.7°C when the animal was located.

Torpor patterns Summer

Torpor in summer was rare and observed on only 8 occasions. Most of these events occurred in females (5 events, torpor frequency per individual = 3.0 ± 2.8%, 157 days tracked, 4 individuals observed), slightly more often than in males (3 events, torpor frequency per individual = 1.6 ± 1.9%, 163 days tracked, 4 individuals observed). Torpor bouts occurred once in January, twice in February and five times in March. Summer T_b in torpid mulgaras did not fall below 30°C (mean = 31.1 ± 0.7°C), despite minimum T_as on days torpor occurred falling to 22.3°C in January, 21.4 and 20.7°C in February and ranging between 14.8 and 22.5° during March. Overall, minimum T_a throughout the summer months averaged 21.6°C ± 3.3°C. Mean T_a in January 2018 was 31.9 ± 3.3°C and by the end of March mean T_a decreased to 27.5 ± 2.2°C (Appendices, Table A1). Some individuals were not observed entering torpor during summer and T_b did not fall below the torpor threshold despite minimum T_a falling below 20°C (Figure 6).

One female mulgara displayed three shallow bouts of torpor in summer (Figure 7) and on each occasion this occurred when maximum T_as were relatively low. After being active until 4:30 a.m., she reduced her T_b from 39.5°C to 30°C at about mid-day when T_b increased as a result of rising T_as. This was the lowest T_b experienced during torpor in summer (Figure 8). Maximum T_bs recorded on arrival to and at departure from burrows during summer indicate active T_bs which were higher than during winter and averaged 39.1 ± 0.9°C.

Rain did not appear to influence use of torpor as only five torpor bouts in winter coincided with rain events and only one torpor bout in summer coincided with rainfall.

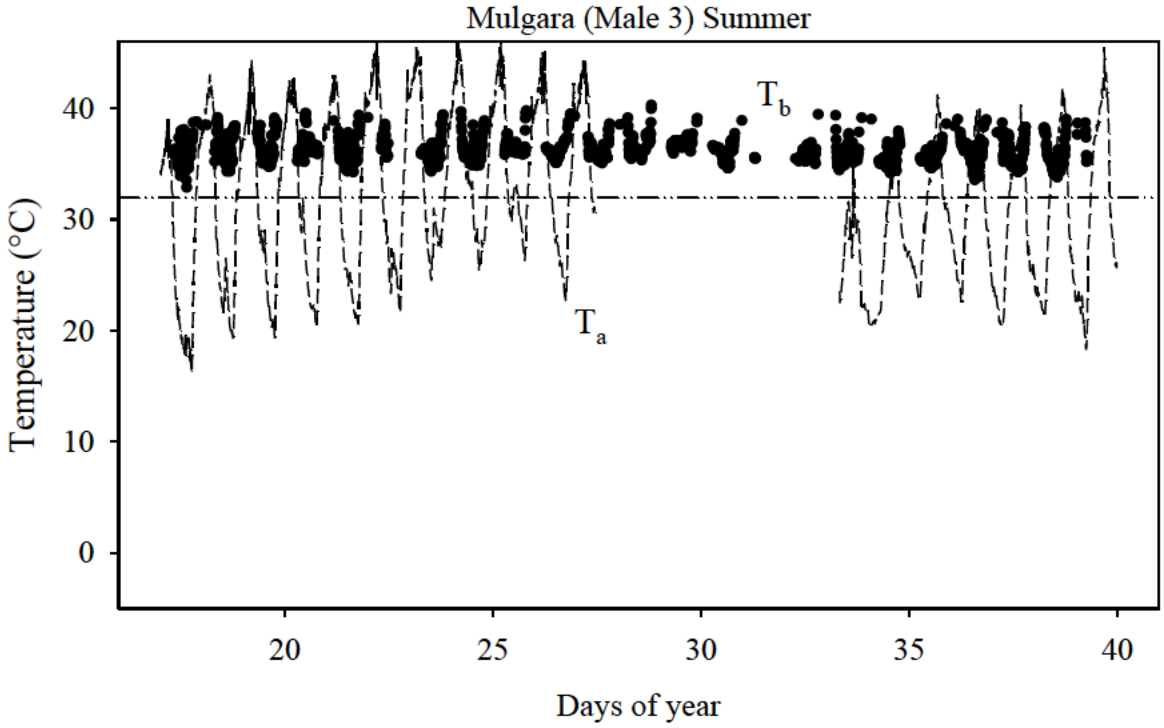

Figure 6. Fluctuations of T_b and T_a over three weeks in summer between 17 January (day 17) and 9 February (day 40). T_b did not fall lower than the torpor threshold for this individual throughout summer despite minimum T_a falling below 20°C.

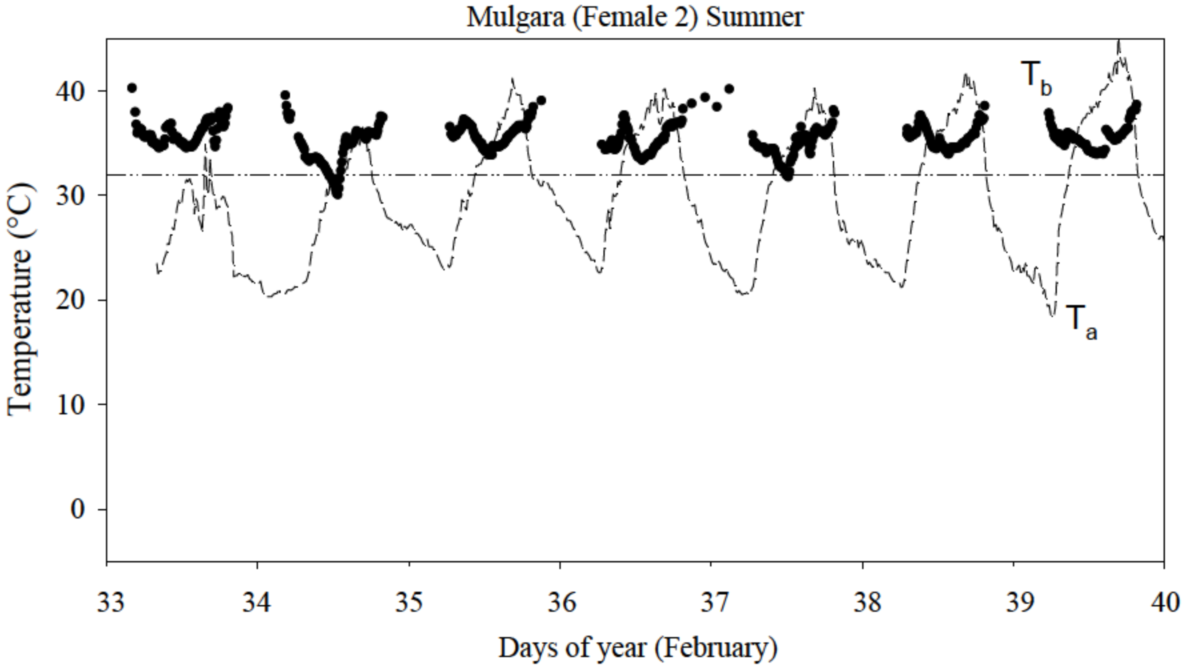

Figure 7. T_a and T_b of a female mulgara over 7 days in summer. Two shallow bouts of torpor (T_b below 32°C) occurred 3 and 6 February 2018 (day 34 and day 37). Normothermic resting

values of ~33-35°C are displayed while in the burrow and active T_b values exceed 36°C and the highest T_b values correspond with arrival and departure from the burrow.

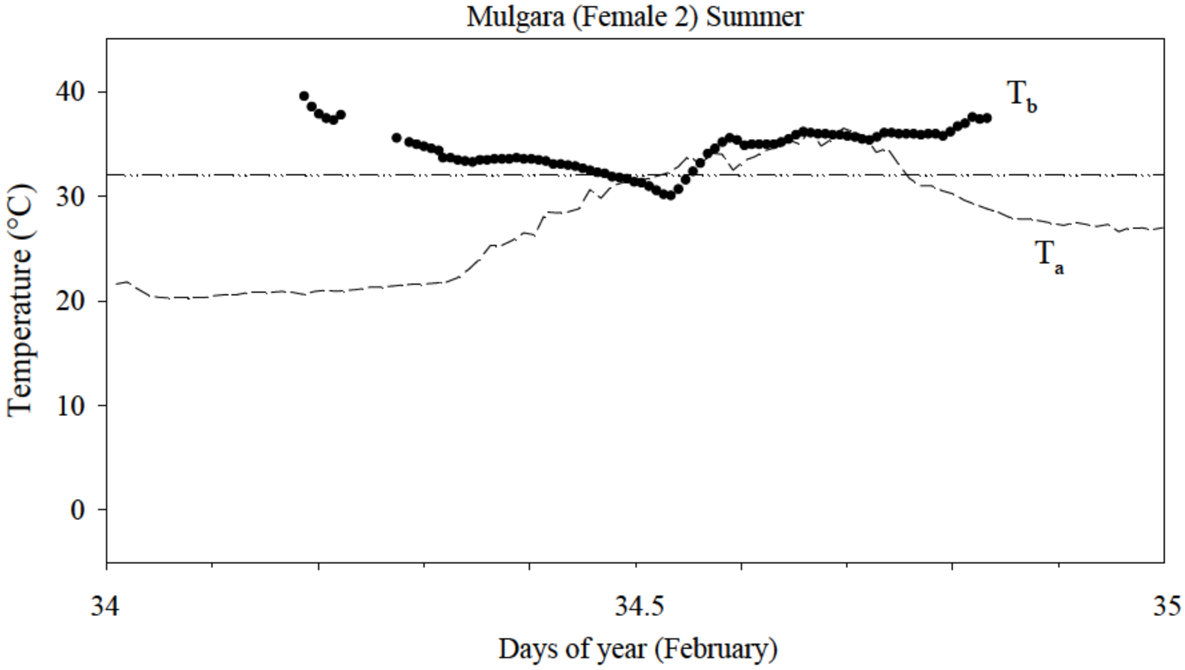

Figure 8. T_b and T_a on one day in summer (3 February 2018) at the Uluru-Kata Tjuta bore fields, NT. T_b decreased below the torpor threshold (32°C) but further cooling may have been restricted by rising T_a at mid-day (34.5).

We did not find an effect of sex on torpor bout frequency, possibly due to a low sample size for either sex during periods of monitoring, but season and average daily temperature were significant predictors of whether individuals used torpor. A one-way ANOVA showed that on days torpor occurred there was a statistically significant difference in use of torpor on days that torpor occurred between at summer (8 days/320; 2.5 ± 1.1%) and winter (264 days/301 days; 86.9 ± 8.1%, $F_{1, 11} = 784.3$, $P < 0.001$). When including multiple torpor bouts/day during winter, torpor was observed 295 occasions over 301 days (98.0 ± 4.8%). We also found the probability of torpor use was negatively correlated with T_a with individuals using torpor more frequently during colder weather (Figure 9).

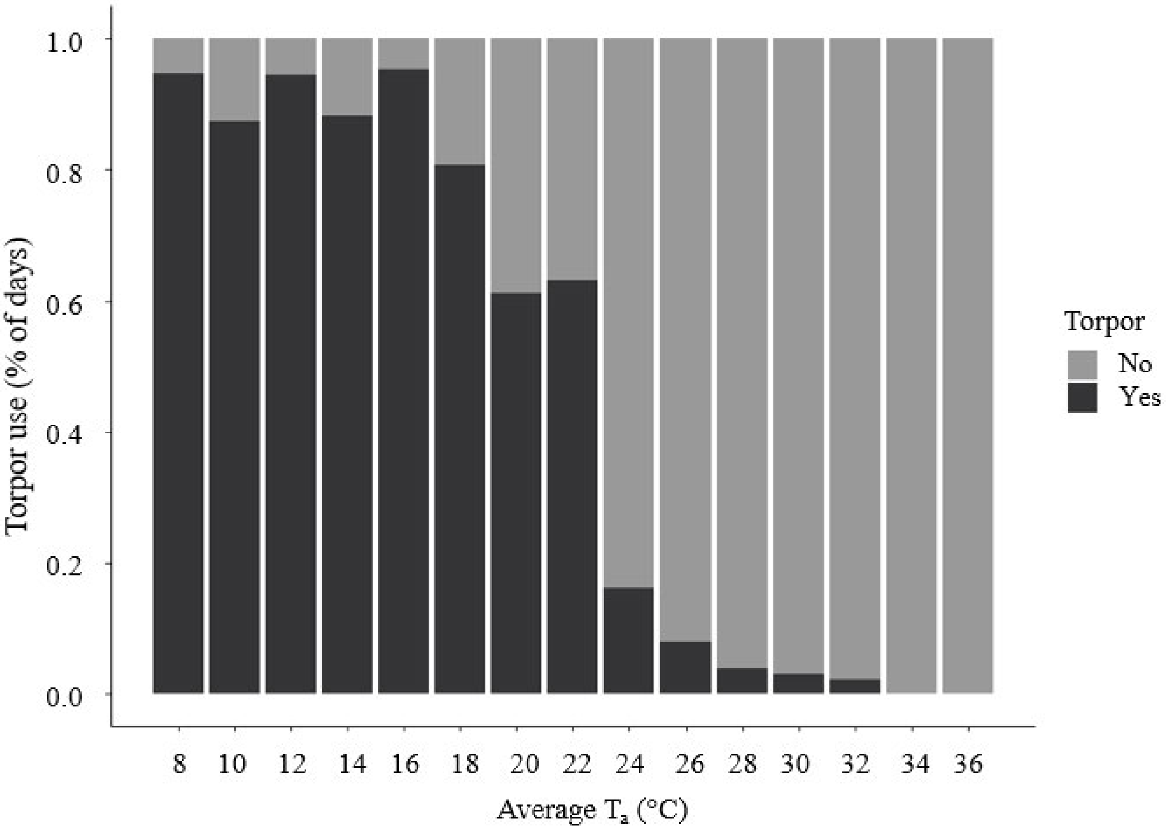

Figure 9. Use of torpor (% of days tracked) plotted against average T_a for both seasons and sexes for 5 mulgaras (*D. blythi*) during winter and 8 mulgaras during summer. Use of torpor occurred most frequently with average T_as between 8 and 16°C, were less frequent from 18 to 22°C and were least frequent at temperatures between 24 and 32°C.

Torpor bout duration

Summer torpor bout records were excluded from the analysis due to low number of records. Average summer torpor bout duration was however 61.8 ± 46.2 minutes ($n = 6$). In the winter dataset ($n = 122$), the interaction term "average ambient temperature : sex" was significant so we analysed each sex separately (Figure 10). For females there was a weak, but significant negative correlation between average temperature and torpor bout duration with longer torpor bouts associated with colder temperatures ($N = 50$, $n = 2$, $t = -3.80$, $P < 0.001$, df = 48.00). In contrast, there was no correlation between torpor bout duration and average temperature for males ($N = 78$, $n = 4$, $t = 0.248$, $P = 0.805$, df = 76.00). During winter, all but two torpor bouts (25.4 and 27.65 hrs) were less than 24 hours. Females generally exhibited longer torpor bouts than males (Table 1).

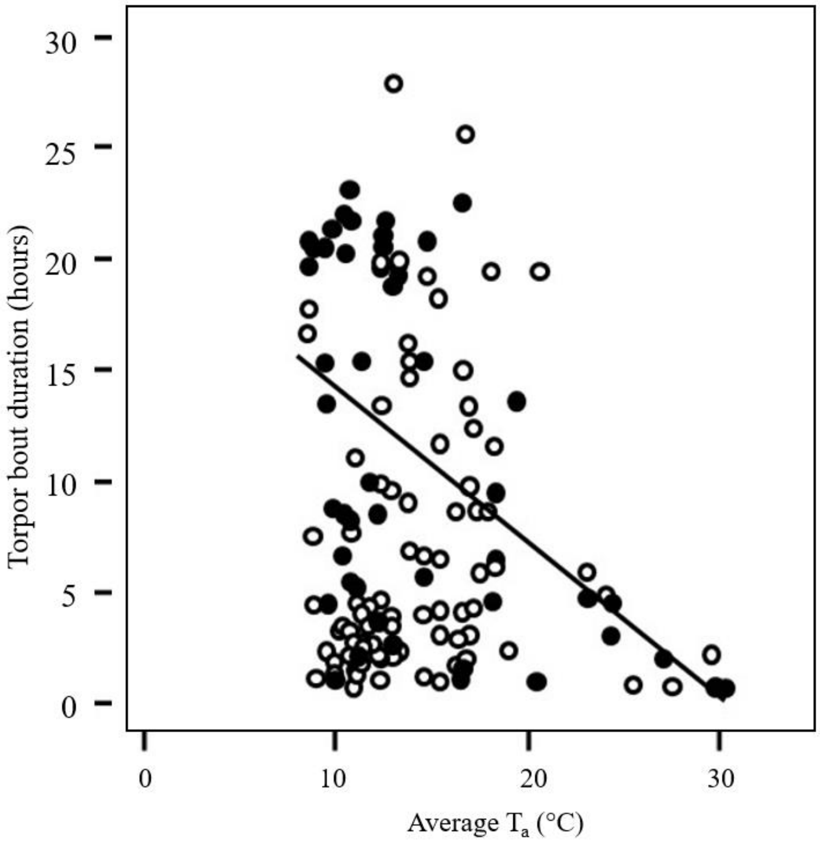

Figure 10. Torpor bout duration plotted against average T_a for males (white circles; torpor bouts = 78, individuals = 4) and female (black circles; torpor bouts = 50, individuals = 2 mulgaras (*D. blythi*) during winter. Solid line shows ordinary least square regression for females ($R^2 = 0.27$, $P < 0.01$), there was no correlation for males.

Table 1. Comparison between torpor bout length (minutes) of male and female mulgaras (*D. blythi*) captured during summer and winter. Estimated marginal means (emmeans) and SE values shown. Comparisons performed with Tukey HSD.

Sex	emmean	SE	df	Lower confidence interval	upper confidence interval
Female	671	62.8	3.26	480	862
Male	422	49.3	2.98	265	580
contrast	estimate	SE	df	*t*	*p*
Female – Male	249	79.9	3.15	3.116	0.0493

Activity

Mulgaras were largely nocturnal in summer and winter, but on a few occasions some were seen moving between burrows during the day in winter and departure from burrows occasionally occurred prior to sunset. The duration of activity differed between seasons in both sexes and also between sexes. In males the duration of activity was highly variable in winter ranging from 80 minutes to 760 minutes, but was not affected by T_a (Fig. 10). In summer, the duration of activity in males was 605 minutes on average and duration declined slightly with T_a. When statistically analysed, in the model of activity bout duration, the interaction term “Sex : Season” was significant so we analysed each sex separately (Figure 10; Table 2). For males, the interaction term “average temperature (T_a) : season” was significant so we analysed each season separately. In summer, there was a significant negative correlation between T_a and activity bout duration and males decreased their activity bouts with T_a (activity (min) = -7.67*T_a+ 846.3); $N = 32$, $n = 4$, $t = -3.1$, $P = 0.0051$, df = 27.4). In winter, T_a and activity bout duration and T_a were not correlated ($N = 24$, $n = 3$, $t = 0.71$, $P = 0.48$, df = 20.2).

For females, the duration of activity was low in winter, lasting between 30 and 670 minutes, and activity was positively affected by T_a (Figure 10). In summer, females were active for 575 minutes on average and activity duration showed a slight increase with T_a The interaction term “average T_a : season” was significant so we analysed each season separately. In summer, T_a and activity bout duration was positively correlated (activity(min) = 5.36*T_a+ 414.0); $N = 88$, $n = 4$, $t = 2.4$, $P = 0.02$, df = 83.3; Figure 10). In winter, the positive correlation between T_a and activity bout duration was strong (activity(min) = 31.16*T_a - 235.2; $N = 14$, $n = 2$, $t = 4.8$, $P < 0.001$, df = 12.0).

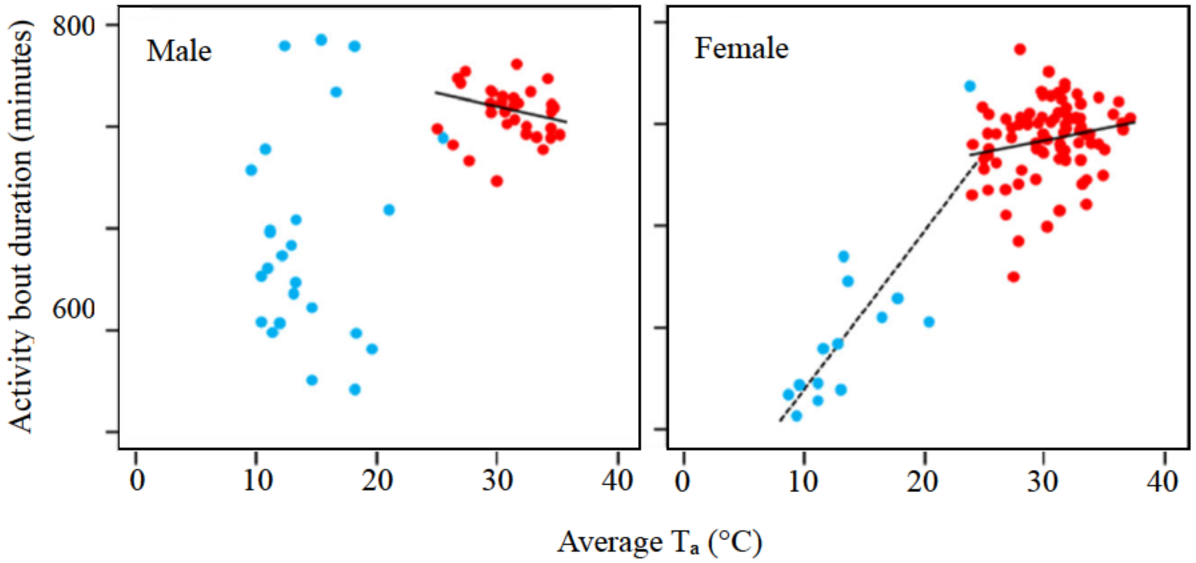

Figure 11. Activity bout duration (minutes) of male and female mulgaras (*D. blythi*) as a function of average daily T_a during winter (blue circles) and summer (red circles). The solid and dashed lines indicate significant linear regressions for summer and winter data, respectively. There was no significant effect of temperature on activity bout duration for males during winter.

Table 2. Final reduced linear mixed effects models of activity bout duration of male and female mulgaras (*D. blythi*) captured at the Uluru-Kata Tjuta NP bore fields during summer (13 January – 31 March 2018; 1 December - 12 January 2019) and winter (29 June – 30 September 2018). Numbers in brackets = (no. individuals, no. of observations).

		Estimate	SE	df	t	P
Activity bout length						
(8,158)	Season	-580.7	103.1	146.3	-5.6	<0.001
	Sex	657.8	168.7	146.2	3.9	<0.001
	Average T_a	5.8	3.0	145.7	2.0	`0.051
	Season : Sex	-230.7	98.7	148.7	-2.3	0.021
	Sex : Average T_a	-20.4	5.3	147.3	-3.9	<0.001
	Season : Average T_a	23.7	5.1	146.0	4.7	<0.001
Male (4, 56)	Season	-747.7	282.8	50.4	-2.6	0.011
	Average T_a	-12.9	8.5	50.5	-1.5	0.136
	Season : Average T_a	21.1	10.6	49.9	2.0	0.051
Male summer (4, 32)	Average T_a	-7.7	2.5	27.4	-3.1	0.005
Male winter (3, 24)	Average T_a	6.2	8.7	20.2	0.7	0.484
Female (4, 102)	Season	614.2	100.0	95.6	-6.1	<0.001
	Average T_a	5.4	2.5	95.4	2.2	0.031
	Season : Average T_a	25.4	5.2	95.1	4.9	<0.001
Female summer (4, 88)	Average T_a	5.4	2.3	83.3	2.4	0.020
Female winter (2, 14)	Average T_a	31.2	6.5	12.0	4.8	<0.001

We calculated the emmeans and compared the activity bout duration for each sex and season. In summer there was no difference in activity bout duration between sexes, but in winter, females had significantly shorter activity bout lengths than males. Both sexes had significantly shorter activity bout duration in winter compared to summer (Table 3).

Table 3. Comparison of mean activity bout duration (minutes) of male and female mulgaras (*D. blythi*), captured during summer and winter. Estimated marginal means (emmeans) and SE values shown. Comparisons performed with Tukey HSD.

Season	Sex	Activity bout length (minutes)	SE	df	95% confidence intervals
Summer	Female	575	28.7	5.27	502, 647
Winter	Female	228	39.8	17.83	144, 312
Summer	Male	605	32.6	8.45	531, 680
Winter	Male	376	36.2	10.93	296, 456

		Contrast	Estimate	SE	df	*t*	*p*
Season							
	Winter	Female – Male	-148.1	53.8	14.13	-2.75	0.015
	Summer	Female – Male	-30.6	43.4	6.78	-0.71	0.503
Sex							
	Female	Summer – Winter	347	30.7	152	11.31	<0.001
	Male	Summer – Winter	229	30.8	149	7.46	<0.001

Home range and burrow use

As we were not testing hypotheses about home range size and burrow use, we qualitatively describe them here. In general, males had larger home ranges than females and this was particularly evident during winter (Figure 11; Table 1). During summer, male home ranges overlapped with females but female home ranges did not overlap with each other. The result was similar in winter where some overlap between males occurred, and again female home ranges did not overlap (Figure 11).

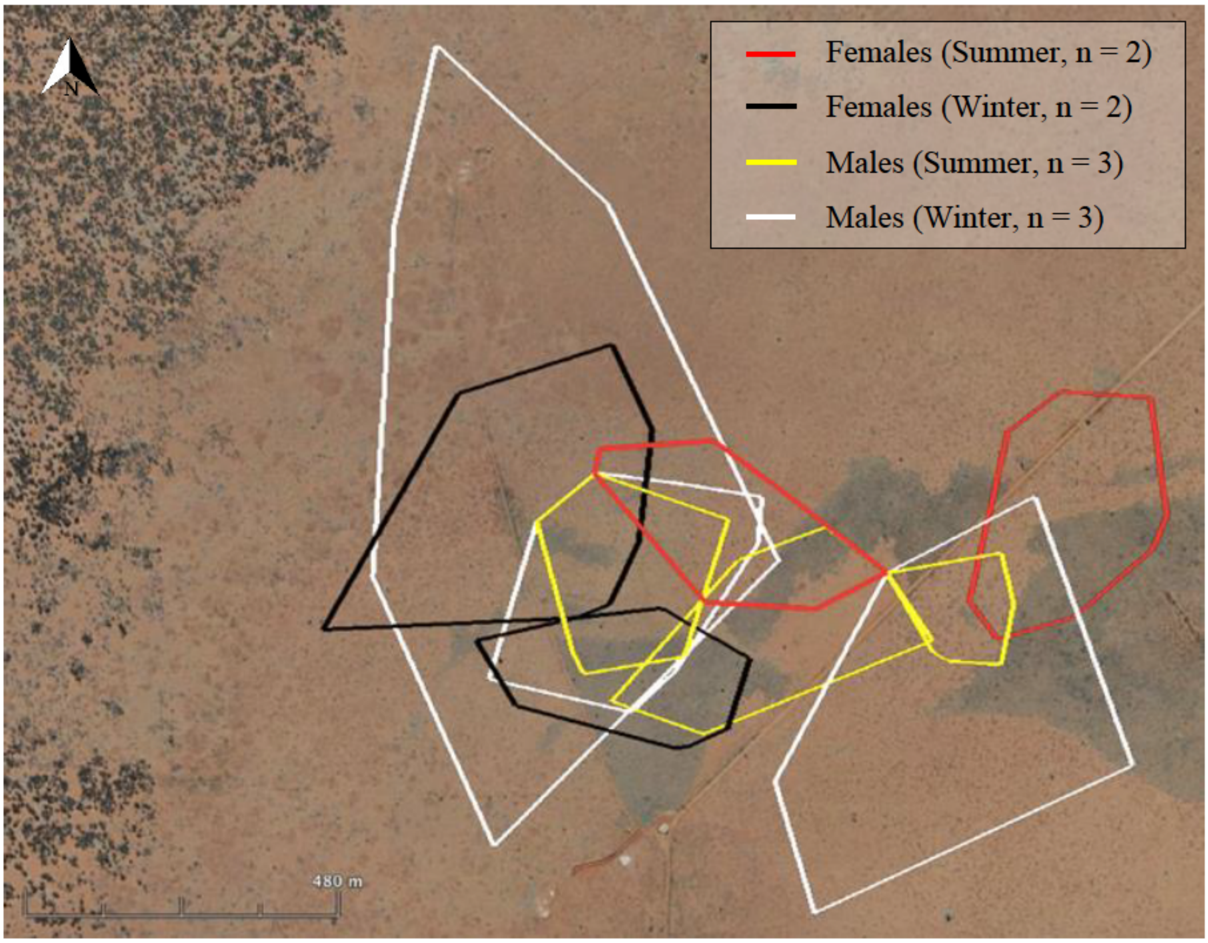

Figure 12. Minimum home range of male and female mulgaras (*D. blythi*) captured at the Uluru-Kata Tjuta NP bore fields during summer (13 January – 31 March 2018; 1 December - 12 January 2019) and winter (29 June – 30 September 2018). Polygons were created around radio-tracked burrows (*n* = 179) and night-time tracking locations (*n* = 29) using minimum convex polygons.

The maximum distance recorded for overnight movement from one burrow to another was 817 m by a male mulgara during winter. As the home ranges of males increased in winter so too did the number of burrows they occupied. However, although female home ranges in winter were smaller than males, the average number of burrows they used was greater than males. We recorded 179 different burrows used by all mulgaras over the course of the year (Table 4). 25 of those burrows were used by more than one individual on different days and 9 burrows were used by at least two mulgaras cohabitating simultaneously.

The number of times a single burrow was used by various individuals occurred more in winter than in summer (*N* = 35; *n* = 21). Of that number, members of the opposite sex were found to frequently use a shared burrow more often than mulgaras of the same sex in both summer and winter (N = 145, n = 115) (Table 5). Correspondingly, males and females were found cohabitating burrows simultaneously 8 of the 9 occurrences.

Table 4. MCP home range (ha), maximum distance moved between burrows and number of burrows used by individuals per season are listed. (M = male, F = female). Use of consecutive burrows provided insight into burrow use fidelity and the frequency of burrows shared informs the degree of social tolerance between individuals.

ID	Season	Home range (ha)	Maximum distance between burrows (m)	Burrows used per days tracked	Use of previous day's burrow per days tracked	Use of shared burrow per days tracked
M 1	Winter	19.6	477	28/69	22/69	2/69
M 2	Winter	10.1	500	13/36	20/36	9/36
M 3	Winter	43.4	817	21/68	24/68	3/68
M 1	Summer	2.3	200	10/68	16/68	42/68
M 2	Summer	6.1	226	10/57	12/57	9/57
M 3	Summer	8.1	464	10/56	2/56	23/56
M 4	Summer	*	118	3/9	4/9	0/0
F 1	Winter	6	334	28/86	21/86	23/86
F 2	Winter	14	432	27/84	30/84	14/84
F 1	Summer	8	376	12/57	10/57	9/57
F 2	Summer	6.5	358	14/47	10/47	22/47
F 3	Summer	*	100	2/33	30/33	0/0
F 4	Summer	*	0	1/32	28/32	0/0

* Indicates home range could not be calculated due to individuals either remaining in one burrow or using one-three burrows in a line rather than an area.

Table 5. Number of occasions burrow sharing occurred between season and males (M) and females (F).

Burrow sharing-Sex	Season	Number of shared burrows used	Number of times a shared burrow was used	Number of times simultaneous burrow cohabitating occurred
M-F	Summer	9	75	2
M-F	Winter	16	40	6
M-M	Summer	4	16	0
M-M	Winter	3	2	0
F-F	Summer	1	0	0
F-F	Winter	2	12	1
Summer total		14	91	2
Winter total		21	54	7

Discussion

The Australia desert environment is characterised by extreme temperatures, low rainfall and consequently periods of low food availability. The persistence of species such as heterothermic marsupials and bats through periods of fluctuating food and water availability is probably due to use of daily torpor as a means to conserve energy (Geiser, 2004). Our results confirmed that both male and female mulgaras (*D. blythi*) used multiday torpor frequently during winter when food supplies were likely restricted and infrequently during summer when ambient temperatures were higher (Figure 6 and 7). Overall, this study showed that season and average daily ambient temperature were significant predictors of whether individual mulgaras used torpor or not. During winter females typically exhibited longer torpor bouts than males, especially as temperatures became colder however, during winter average temperature did not appear to affect torpor bout duration for males. We also found that the activity of males and females responded differently to seasonal changes. Males in summer decreased duration of activity significantly with higher ambient temperatures but in winter ambient temperature fluctuations had no effect on activity duration for males. Females however became active for longer in summer as temperatures increased and even more so with high winter temperatures.

This is also the first research to record home ranges of male and female mulgaras during summer months. Home ranges were similar in size during summer but during winter males generally had noticeably larger home ranges than females (Körtner et al., 2007). Spatial overlap of home ranges occurred between both male and female mulgaras in both seasons including between males. While the home ranges of tracked females in this study did not overlap however, other females were trapped within the same area as the winter females. These were not used for tracking, but this indicates that female home ranges likely also overlap. During each season females used more burrows than males on average however, fewer burrows were used in summer than during winter by both sexes. Burrow fidelity occurred in both seasons but was higher in summer than winter.

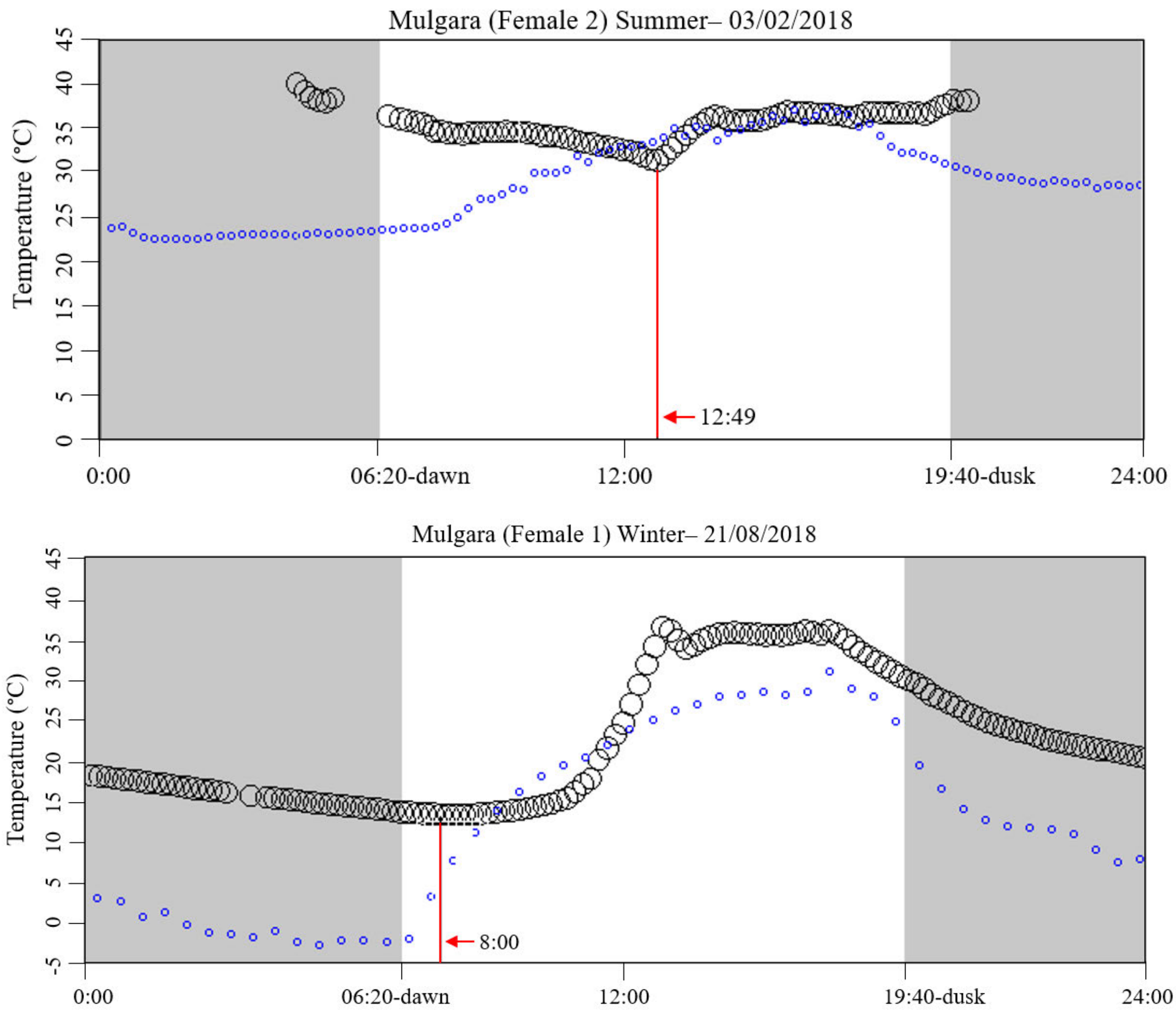

Figure 13. Examples of torpor use by two female mulgaras comparing minimum T_b during torpor in summer (top) and winter (bottom) at the Uluṟu-Kata Tjuṯa NP bore fields. The rise in T_b from minimum T_b shows rewarming to normothermia. Top; Shallow summer torpor was 30°C at 12:49 p.m. on 30 February 2018. Bottom; Deeper winter torpor reached 13.5°C at

8:00 a.m. on the 21 August 2018 but the overall minimum for the study was 11.7°C. The shaded area indicates mid-night to dawn (left), and dusk to mid-night (right). T_a (blue circles) are shown in relation to T_b (black circles) at 10-minute intervals.

Torpor Frequency

Use of torpor by mulgaras during this study in winter was frequent as per previous studies (Körtner et al., 2008a) and showed that torpor use by male and female mulgaras in winter was 97.4% of days tracked. In comparison to winter, torpor use by male and female mulgaras in summer was just 3.4% of days tracked with body temperatures during torpor ranging between 30.0°C to 31.8°C. Adult bats (*Myotis lucifugus*) were also found to significantly decrease torpor bout duration as ambient temperatures increased (Czenze et al., 2017). However, ambient temperature was found to influence torpor use in one species and not the other in studies on two related *Cercartetus sp.* (Turner et al., 2012a; Turner et. al., 2012b) which shows that ambient temperature cannot always be assumed to be the primary influence in use of torpor. Despite that, as hypothesised, we found that season and average daily ambient temperature had a significant effect on use of torpor by mulgaras.

Warmer summer ambient temperatures might have prevented mulgaras from being able to reduce their BMR to body temperatures below the torpor threshold. However, a lowered T_b, the only measure available during this study, is not necessarily a dependable criterium for torpor at high ambient temperatures. For example, in some species metabolic inhibition allows metabolic rate to be down regulated without a perceivable drop in T_b. As such, the Malagasy bat (*Macronycteris commersoni*) can use torpor during the warmest parts of the hot season in Madagascar with T_b reaching 42.9°C. So far, dasyurids have not been shown to perform similar feats, but then research into torpor at high ambient temperatures is still in its infancy. Although burrows provide protection from extreme summer temperatures, average mulgara burrow temperatures during this study in summer were 31.4°C which is close to the torpor threshold of 32°C. In contrast, mulgara burrows during winter can average 15.5°C at estimated depths of 25-30 cm (Körtner et al., 2007). This suggested that mulgaras can therefore benefit from relatively shallow burrows during winter as T_b can fall with decreasing T_a, facilitating the use of torpor and passive rewarming. High summer ambient and burrow temperatures however during this study in summer were not cool enough to facilitate regular use of torpor.

The infrequent use of torpor as an energy saving mechanism by mulgaras in summer should be expected if there were an abundance of food resources such as arthropods during the warmer months. Research on Common hamsters (*Cricetus cricetus*) also found that torpor use decreased where food was more readily available (Siutz & Millesi, 2017). Increased food availability allows the microbat (*Myotis lucifugus*) to increase body fat and therefore reduce thermoregulatory costs by offsetting the need to use torpor to conserve energy (Czenze et. al., 2017). We found that use of torpor by mulgaras during warmer months mostly occurred towards the end of summer which may be a result of decreasing ambient temperatures but also possibly due to decreasing food availability. Observations in a study on the eastern pygmy-possum (*C. nanus*) showed that torpor use during summer was strongly correlated with lack of food availability (Turner et. al., 2012b) and fat individuals under laboratory conditions where food was removed, and ambient temperature decreased could hibernate for up to a year (Geiser, 2007). Conversely, species such as blossom bats use torpor more readily in summer due to low nectar availability in winter (Geiser, 2020). This study found that bouts of summer torpor, albeit infrequent, occurred during the latter part of summer. The lower-than-average annual rainfall (147.6 mm vs mean = 316.6 mm) and possible subsequent reduction of insects could partly explain the use of torpor in summer by a predominantly insectivorous species.

Torpor duration

Female mulgaras entered torpor for longer periods than males during winter, and while the effect of ambient temperature on torpor duration of females was significant there was no correlation between ambient temperature and duration of torpor for males. Similar differences in torpor patterns between males and females in another study on mulgaras found that males showed only shallow and short torpor use during the mating season, but from mid-July, a transition to more frequent and deeper torpor resembled that of females which entered torpor almost daily between June and August, but from the end of the gestation period remained normothermic. (Körtner et al., 2008a). Mulgaras in our study displayed the same behaviour and females ceased use of torpor in September, presumably once parturition and lactation started (Körtner et al., 2008a).

Duration of torpor use in this study was generally less than 24 hours, similar to previous research on the thermal biology of mulgaras (Körtner et al., 2008a) and other species using daily torpor exclusively (Ruf & Geiser 2015). Our records generally consolidate these observations however males were observed exhibiting torpor which exceeded 24 hours on two occasions during winter (25.4 hrs and 27.7 hrs). In mulgaras longer torpor bouts can occur during rain or overcast periods in (Körtner et al., 2008a), but in the present study there was no rain on these two occasions and average ambient temperatures were not extreme. Torpor bouts exceeding 24 hours have been occasionally observed in other daily heterotherms such as stripe-faced dunnarts (*Sminthopsis macroura*) (Körtner, & Geiser 2009), and elephant shrews (*Elephantulus myurus*) (Mzilikazi & Lovegrove, 2004). As the 24h cycle of activity and rest is maintained irrespectively of the absolute length of a torpor bout these examples still fall within the definition of daily heterothermy (species using torpor for more than two days are defined as hibernators; Geiser, 2020).

Although torpor bout length during summer was not used for analysis due to low number of records it is interesting to note that torpor bouts ranged from just 30 minutes to 120 minutes. Summer torpor observed in the marsupial hibernator *C. nanus*, was also always relatively short and lasted about ~3.8 hours (Turner et. al., 2012b). In contrast average torpor duration of mulgaras during winter was about 9 hours for both male and female mulgaras. Whilst we found cooler ambient temperatures were a significant factor in enabling torpor use, reduced food availability and requirements for reproduction appear to be important factors influencing torpor duration (Geiser & Masters, 1994).

Activity bout duration

This research found that mulgara activity for both sexes was significantly shorter in winter than in summer. Use of torpor during summer was limited and as a result mulgaras possibly spent more time actively avoiding cycles of high ambient and soil temperatures within burrows. Additionally, availability of food resources during summer would be higher than in winter and this would initiate greater opportunities for foraging and thus, activity. Few studies however have specifically measured activity length in a daily heterotherm during winter and summer under field conditions. Similar findings have been recorded sugar gliders (*Petaurus breviceps*) which decrease activity and increase torpor use during colder periods when foraging becomes uneconomical (Körtner & Geiser, 2000), however it should be noted that these are arboreal species living in a different environment. In contrast to mulgaras, research on pygmy-possums (*C. nanus*) found that duration of activity in summer and winter were the same due to availability of food in both seasons (Turner et. al., 2012b) but these are also an arboreal species. For terrestrial mulgaras, sufficient levels of activity in winter therefore appear to be just enough to obtain sustenance for reproductive needs while also reducing exposure to predation when food availability is low.

In summer there was no difference in activity duration between sexes. This was expected because the survival needs for males and females are similar during the non-reproductive hotter months when increased temperatures reduce the ability to use torpor and food availability is higher. However, where females increased activity with higher ambient temperature in summer, males decreased activity with higher ambient temperature. Females of another dasyurid, the swamp antechinus (*Antechinus minimus maritimus*) were found to also be more active (move greater distances) during the non-breeding period (April) than males (Sale, 2009).

During winter females reduced duration of activity in response to cold temperatures and as a result were significantly less active than males in winter. Körtner and Geiser (2011) suggest that one reason females of the related *D. byrnei* reduce activity more than males during cold temperatures, could partly be due to smaller body size. Decreased activity for female mulgaras in winter is expected because breeding females need to conserve as much energy as possible during reproduction in preparation for lactation (Geiser & Masters, 1994). Despite this, where ambient temperatures did not appear to influence activity duration for males, higher ambient temperatures increased activity for females. Prior research on mulgaras during winter found that cooler temperatures can increase arousal time which in turn can increase duration of torpor and therefore decrease duration of activity (Körtner et al., 2008a). It stands to reason then that when higher winter temperatures occurred that females could increase activity in winter.

Throughout the winter breeding season, males used shallower torpor than females. This is likely due to males needing to arouse from torpor more frequently due to the selective pressure to find females. A study on kowaris and dunnarts also showed that males of both species were more active than females during winter (Körtner & Geiser, 2011). However, regular arousals from torpor can be brief and energetically costly so heterotherms must time arousals effectively to avoid squandering energy (Geiser, 2004; Thomas et al., 1990; Wang, 1989). Males therefore cannot afford to enter deep torpor as females do and this likely resulted in longer bouts of activity for males in winter.

Home range

The smaller average home ranges of mulgaras during summer (male 5.5 ha; female 7.3 ha) corresponded with the on average fewer number of burrows used by individuals (males 10; females 14). As summer transitioned into the winter breeding season, male home range increased almost four-fold on average to 24.4 ha compared to female mulgaras whose home ranges averaged 10.0 ha. Despite females having average winter home ranges less than half the size of average males, the average number of burrows used by females (n = 27.5) was higher than males (n = 20.7). Winter home ranges of mulgaras in another study were very similar to our results where the average home ranges of males (25.5 ha) were significantly larger than females (10.8 ha; Körtner et al., 2007). Spatial overlap between sexes occurred during both seasons which was similar to previous research (Körtner et al., 2007). However, the home ranges of female mulgaras in this study did not overlap in either season. Research on spotted-tailed quolls (*Dasyurus maculatus*) during winter and spring found males had significantly larger overlapping home ranges than females and, similar to our findings, female home ranges were exclusive of other females (Glen & Dickman, 2005). Another study on the southern ningaui (*Ningaui yvonneae*, Dasyuridae) found that home ranges of male and females were similar during non-breeding and breeding season but that the home ranges of males more than doubled during the breeding season (Bos & Carthew, 2007). This suggests that larger home ranges of males in these three species, particularly during the breeding season is due to the need for males to increase chances of reproduction by mating with multiple females, and perhaps to avoid inbreeding. Females likely remain within a smaller home range to support development of young during pregnancy and provide care for young after parturition.

The home range of two of the males in this study which occupied larger home ranges than females stretched across areas of reduced spinifex cover caused by previous fire scars. This may have contributed to one of these males occupying a very large area, also with the largest recorded maximum linear distance between consecutively used burrows for this study (Körtner et al., 2007). This distance however could be considered relatively small in comparison to the much smaller dasyurid *N. yvonneae,* which was found to move over 900 m (Bos & Carthew, 2007) and supports the suggestion that mulgaras are a relatively sedentary species (Masters, 1997). We found that one male occupied a smaller home range which corresponded to an area of dense cover. Male mulgaras in previous research that occupied home ranges within areas of denser spinifex cover also had home ranges smaller than the other males (Körtner et al., 2007). Larger home ranges during winter and increased burrow use compared to summer, appear to be a result of males being active for longer than females, and probably the result of their reproductive need to search for breeding females (Masters & Dickman, 2012).

Burrow use

The present study showed that burrow fidelity appeared to be higher during summer than in winter, particularly during the early stages of summer. Two female mulgaras each used one burrow for at least 26 and 28 consecutive days and one male mulgara used one burrow for at least eight consecutive days during the same period before monitoring ceased for that individual. Körtner et al. (2007) noted that mulgaras used a number of burrows throughout their home range but generally occupied one or two burrows for extended periods. Prior research on mulgaras also found they favoured one or two burrow systems throughout the year (Masters, 2003). Additionally, during summer, females used fewer burrows than in winter despite similar sized home ranges. Individuals may have been in poorer condition after the winter breeding season (Masters & Dickman, 2012) which may require conservation of energy by remaining more sedentary. Greater burrow fidelity during summer may have been facilitated by more readily available ectothermic food supply during warmer months while also reducing risk of predation by minimising movement between burrows.

During the winter period of this study, male mulgaras remained at the same burrow for up to 11 consecutive days and females up to four consecutive days possibly a result of prolonged mating (Michener, 1969). Female mulgaras were active for shorter periods than males and the number of burrows used was greater than in summer. Their brief periods of activity and increased use of burrows may be due to foraging demands during the resource poor winter, particularly due to the latter part of the night being too cold to find prey (Körtner et al., 2008a). The polygamous mating system of many dasyurids, including mulgaras, and the pressure for males to locate females across larger home ranges during winter probably explains their increased use of burrows compared to summer (Körtner et al., 2019).

Due to overlap of home ranges between male and female mulgaras, burrows were often used by multiple individuals. Burrow co-occupancy occurred occasionally throughout the year but predominantly in winter. This was similar to findings by Körtner et al. (2007)

where male-female pairs on 6 of 11 occasions during winter. Male and female co-occupancy of burrows during this study was considerably more common than by members of the same sex. These results are supported by Masters (2003) who found that male-female burrow sharing occurred on three occasions in May during the mating season.

In this study the male with the smallest home range during winter co-occupied burrows on three occasions with the two females with whom its home range overlapped. This suggests its reproductive and energetic needs were being met within a smaller home range in contrast to the other males. The home range of another male that overlapped both females also co-occupied burrows on two occasions with the same two females. This male however may have been healthier than the male with the smaller home range because that male died after the breeding season. Because the mating season can be variable by up to 3-4 months followed by a gestation period of 5-6 weeks (Masters and Dickman, 2012) it is probable that the winter breeding period for mulgaras during this study (probably July) coincided with when six of the nine occurrences of burrow co-occupancy took place. Because mating is a prolonged affair in dasyurids and can last for hours it appears that the main purpose for burrow sharing could be for breeding rather than to reduce the costs of thermoregulation during winter via huddling.

Conclusion

Data on seasonal torpor expression in free-living heterotherms are scarce (Geiser 2020). The present study is the first field study to determine torpor use and activity in free ranging mulgaras during summer. Ambient temperature was found to be a significant influence on use of torpor during both seasons. Torpor use and activity during summer was similar between sexes but differed between sexes during winter. Male torpor bouts were shallower than females during winter and correspondingly females were less active than males during the same period. The selective pressure on males to mate with several females during the breeding season likely resulted in longer bouts of activity and larger home ranges. The need for females to conserve energy for reproduction resulted in them limiting activity, entering deeper states of torpor and having smaller home ranges.

Further studies on specific torpor use patterns using a larger pool of mulgaras and other dasyurid species during summer months would provide further insights into energy conservation where torpor use is restricted by high ambient temperatures. Undertaking specific research to compare periods of higher rainfall (La Niña) with periods of drought (El

Niño) could determine the extent water and food availability has on torpor use during summer extremes.

Although findings on home range and burrow use in this study contribute the current pool of knowledge, they were mainly observational and highlight similarities and differences between populations in other studies. This study did not focus on basking behaviour by mulgaras however more targeted research could be specifically undertaken using motion/time-lapse sensor cameras at burrows to confirm the frequency of basking during winter. Lastly, new technology in small GPS devices may allow tracking of individuals during the activity phase that would provide further information about behavioural patterns and thermal biology that cannot be collected using radio telemetry.

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Appendices

Table A1. Mean, minimum and maximum ambient temperature records for summer and winter periods (Note- the winter tracking period for mulgaras commenced at the end of June).

Dec-18	MinT$_a$	MaxT$_a$	AvT$_a$
Mean	21.9	39.5	30.8
SD	3.9	4.1	3.9
Range	17.5	13.4	13.6
Min	12.5	32.7	24.0
Max	30.0	46.1	37.6
Sum	680.2	1223.2	955.6
Count	31	31	31

Jan-18	MinT$_a$	MaxT$_a$	AvT$_a$
Mean	23.2	40.3	31.9
SD	2.3	3.9	3.3
Range	8.9	15.2	12.3
Min	19.1	31.6	24.8
Max	28.0	46.8	37.1
Sum	718.9	1247.8	990.2
Count	31	31	31

Feb-18	MinT$_a$	MaxT$_a$	AvT$_a$
Mean	22.7	38.0	30.2
SD	2.2	2.8	2.1
Range	7.8	12.1	8.8
Min	18.3	30.5	25.2
Max	26.1	42.6	34.0
Sum	634.9	1064.7	844.5
Count	28	28	28

Mar-18	MinT$_a$	MaxT$_a$	AvT$_a$
Mean	18.8	35.8	27.5
SD	2.9	3.3	2.2
Range	12.6	14.0	9.5
Min	13.1	26.4	22.2
Max	25.7	40.4	31.7
Sum	584.0	1111.0	853.6
Count	31	31	31

Jun-18	MinT$_a$	MaxT$_a$	AvT$_a$
Mean	3.7	21.5	12.6
SD	4.5	3.3	3.5
Range	18.7	13.8	13.1
Min	-2.7	17.9	8.9
Max	16.0	31.7	22.0
Sum	111.6	644.3	377.3
Count	30	30	30

Jul-18	MinT$_a$	MaxT$_a$	AvT$_a$
Mean	2.7	23.5	12.9
SD	2.9	3.5	2.6
Range	12.2	11.1	9.4
Min	-2.0	18.7	8.8
Max	10.2	29.8	18.2
Sum	82.8	727.9	401.4
Count	31	31	31

Aug-18	MinT$_a$	MaxT$_a$	AvT$_a$

Sep-18	MinT$_a$	MaxT$_a$	AvT$_a$

Mean	4.5	23.9	14.1
SD	4.8	4.1	3.6
Range	21.7	14.3	13.8
Min	-2.3	17.2	8.6
Max	19.4	31.5	22.4
Sum	139.8	739.9	436.4
Count	31	31	31

Mean	10.5	28.9	19.8
SD	3.0	4.1	2.9
Range	13.2	15.1	10.2
Min	5.2	20.7	15.2
Max	18.4	35.8	25.4
Sum	313.9	866.8	592.5
Count	30	30	30

Table A2. Change in time between T_sMax - T_aMax (minutes) and change in time between T_sMin -T_aMin (minutes) across summer and winter. Soil temperatures at depths ≥ 50 cm remained constant (within 0.5 °C throughout the day) and were therefore not calculated (NA). Negative change in time values indicate that maximum T_s occurred before maximum T_a.

Time differences between T_s and T_a

Summer

	Change in time T_sMax - T_aMax (mins)	Change in time T_sMin - TaMin (mins)	Change in temp T_sMax - T_aMax (°C)	Change in temp T_sMin - T_aMin (°C)
	Summer- Tsoil 5 cm			
Mean	-54.3	69.4	3.9	4.5
SD	69.7	72.7	3.0	1.7
Range	330.0	285.0	12.2	6.2
Min	-246.0	-6.0	-5.4	1.5
Max	84.0	279.0	6.8	7.7
Count	19.0	19.0	19.0	19.0
	Summer- Tsoil 10 cm			
Mean	142.5	216.8	-4.2	10.5
SD	86.9	105.4	2.8	2.8
Range	390.0	412.0	10.2	11.2
Min	4.0	72.0	-9.3	5.5
Max	394.0	484.0	0.9	16.7
Count	47	47	47	47
	Summer- Tsoil 20 cm			
Mean	334.7	378.3	-7.2	11.4
SD	123.8	221.1	3.2	2.9
Range	590.0	1447.0	12.1	12.0
Min	14.0	207.0	-13.2	6.2
Max	604.0	1654.0	-1.1	18.2
Count	45	46	45	46

Winter

	Change in time T_sMax - T_aMax (mins)	Change in time T_sMin - T_aMin (mins)	Change in temp T_sMax - T_aMax (°C)	Change in temp T_sMin - T_aMin (°C)
	Winter T soil 5 cm			
Mean	-12.3	59.2	1.1	5.3
SD	71.7	78.2	2.9	2.0
Range	459.0	471.0	13.3	10.2
Min	-151.0	-22.0	-5.7	-0.8
Max	308.0	449.0	7.6	9.4
Count	103	103	103	103
	Winter- Tsoil 10 cm			
Mean	188.3	194.4	-7.0	13.4
SD	95.2	136.7	3.2	2.8
Range	486.0	600.0	14.1	13.0
Min	26.0	2.0	-13.0	6.2
Max	512.0	602.0	1.1	19.2
Count	104	104	104	104
	Winter- Tsoil 20 cm			
Mean	333.5	351.1	-8.0	15.1
SD	144.8	283.7	3.5	3.9
Range	630.0	1951.0	12.7	21.7
Min	1.0	-97.0	-13.7	0.2
Max	631.0	1854.0	-1.0	21.9
Count	73	68	74	105

	Summer- Tsoil 35 cm				**Winter- Tsoil 35 cm**			
Mean	348.8	492.5	-8.8	11.0	507.0	568.1	-6.9	15.8
SD	151.4	93.6	3.7	3.1	45.3	145.9	4.0	4.1
Range	505.0	330.0	13.1	13.7	64.0	540.0	17.0	16.5
Min	99.0	304.0	-15.2	5.0	475.0	415.0	-14.3	6.2
Max	604.0	634.0	-2.1	18.7	539.0	955.0	2.7	22.7
Count	23	15	46	47	2	11	105	105
	Summer- Tsoil 50 cm				**Winter- Tsoil 50 cm**			
Mean	NA	NA	-10.6	10.1	NA	NA	-5.7	16.8
SD	NA	NA	3.7	3.2	NA	NA	4.5	5.0
Range	NA	NA	12.6	14.7	NA	NA	18.0	20.7
Min	NA	NA	-17.2	3.0	NA	NA	-15.3	5.7
Max	NA	NA	-4.6	17.7	NA	NA	2.7	26.4
Count	NA	NA	43	43	NA	NA	84	84
	Summer- Tsoil 80 cm				**Winter- Tsoil 80 cm**			
Mean	NA	NA	-11.5	9.1	NA	NA	-5.7	17.5
SD	NA	NA	3.7	3.1	NA	NA	4.5	5.0
Range	NA	NA	13.9	14.7	NA	NA	17.8	21.7
Min	NA	NA	-18.3	2.0	NA	NA	-15.3	5.2
Max	NA	NA	-4.4	16.7	NA	NA	2.5	26.9
Count	NA	NA	54	54	NA	NA	105	106
	Summer- Tsoil 100 cm				**Winter- Tsoil 100 cm**			
Mean	NA	NA	-11.5	9.1	NA	NA	-5.8	17.4
SD	NA	NA	3.7	3.1	NA	NA	4.5	5.1
Range	NA	NA	13.9	14.7	NA	NA	17.8	21.8
Min	NA	NA	-18.3	2.0	NA	NA	-15.3	5.1
Max	NA	NA	-4.4	16.7	NA	NA	2.5	26.9
Count	NA	NA	54	54	NA	NA	106	107

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STATEMENT OF AUTHORS' CONTRIBUTION

(To appear at the end of each thesis chapter submitted as an article/paper)

We, the Research Master/PhD candidate and the candidate's Principal Supervisor, certify that all co-authors have consented to their work being included in the thesis and they have accepted the candidate's contribution as indicated in the *Statement of Originality*.

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Conclusion

It is clear that endemic species surviving in the harsh arid interior of Australia have evolved to cope with extreme daily and seasonal T_a fluctuations and periods with limited water and food supply. In addition to many invertebrates, a large number of vertebrates have been able to successfully occupy arid areas, but this required behavioural and physiological adaptations. In Australian deserts the groups that are especially successful are the ectothermic reptilian skinks and the endothermic dasyurid marsupials (Morton, 1982; Pianka, 1996). Due to their enormous differences in energy requirements, some aspects of their approach to life in the arid zone differ substantially whereas others are rather similar.

The ectothermic great desert skink (*Liopholis kintorei*), and the heterothermic brush-tailed mulgara (*Dasycercus blythi*), are two arid zone species which survive in patchy distributions within spinifex sand plains of the Great Sandy Desert. They are often sympatric, and populations of both species have suffered range declines due to direct and indirect ecological pressures such as habitat fragmentation, introduced herbivores and predators, diseases, and climate change.

The low energy requirements of reptiles allow them to conserve large amounts of energy by spending substantial portions of time inactive (Moore et al., 2018). By analysing the T_b of *L. kintorei* we confirmed they often remained inactive daily within their burrows for long periods each day but could also that they can estivate from several days at a time to over a month during summer, and brumate for three months during winter. During brumation *L. kintorei* remained in relatively shallow hibernacula up to ~225 m from their main burrows with body temperatures falling to minima of 7.8°C (mean = 14.2 ± 3.5°C). Within their hibernacula, which were at a depth of ~11cm, they were both protected from freezing temperatures yet sufficiently warmed during the hottest parts of winter days. As such, it can be assumed that this exposure to daily temperature fluctuations plays an important role in the timing of final emergence from brumation.

Cold months in the Australian arid zone are typically resource poor and non-hibernating species must still forage to survive. Freezing temperatures permit heterothermic dasyurids such as *D. blythi* to conserve energy by using deep and prolonged daily torpor within the protection of their burrows, lowering their T_bs on occasion to below 12°C. Torpor was interrupted with bouts of daily nocturnal activity to forage and seek mates for breeding.

Whilst ambient temperature was a good predictor of torpor use, male *D. blythi* used shallower torpor bouts during winter than females with T_bs generally falling to about 20°C. Summer temperatures however restricted the ability of *D. blythi* to lower their T_b below the torpor threshold (32°C) and so during hotter months they only used torpor occasionally for about one hour.

Selective pressure during the breeding seasons for both species (*D. blythi* ~June-September; *L. kintorei* ~September -November) brought about increased activity. The movement between burrows by both male and female *D. blythi* during winter roughly doubled compared to summer. Male *D. blythi* were more active than females during winter despite cold temperatures, probably due to the desire to locate breeding partners. The typically nocturnal *D. blythi* were observed on occasions moving between burrows and tussocks of spinifex during the day in winter, possibly disturbed when basking at burrow entrances. *Liopholis kintorei* activity was greatest immediately after winter brumation during their spring breeding season. They used predominantly one main burrow throughout the year, switching occasionally between several other burrows. The number of burrows used however increased between spring and summer whilst movement between burrows increased seven-fold. The home ranges of both species therefore increased during their breeding season.

The activity patterns of *L. kintorei* are known to be predominantly bimodal and crepuscular. However, throughout the year *L. kintorei* displayed greater levels of unimodal-diurnal activity than previously suggested. Activity either side of dawn and dusk was greater during hotter months when animals typically avoid dangerously hot day-time temperatures, however during cooler months unimodal activity was more common, evidently so they could warm up during the hotter parts of cool days. Diurnal activity was therefore maintained during cooler months, largely through basking, before *L. kintorei* were triggered into brumation by the rapid fall in T_a and photoperiod approaching the winter solstice in mid-June.

Male *L. kintorei* are likely more active than females as they move between more burrows and have greater home ranges (McAlpin et al., 2011; Dennison, 2015) but because determining sex was difficult, future research could also analyse differences of activity and behavioural patterns between the sexes including before, during and after the brumation period. Monitoring the timing of ingress into and egress from brumation across years could provide useful information on seasonal variation in behaviour as a response to climate change. Using arrays of sensor cameras positioned around whole burrow systems before and after brumation could improve our understanding of *L. kintorei* activity either side of this period. This may also inform us about how younger *L. kintorei* respond to winter temperatures. Additionally future studies on *L. kintorei* could attempt to confirm length of time individuals estivate during summer and autumn using a larger sample size, including recording the differences between age and sex when estivating.

Remarkably, small heterothermic endotherms such as *D. blythi* have persisted in arid regions when most marsupials > 250 g have disappeared (Geiser & Turbill 2009; Hanna & Cardillo, 2014). The persistence of such species is likely a combination of their behavioural and physiological regulation of T_b and a semi-fossorial existence. Further studies on summer torpor may therefore provide important information about how *D. blythi* and other dasyurid species conserve energy during warmer periods when torpor use is restricted. Additional research comparing periods of high food and water availability during La Niña with drought periods typically brought on by El Niño may provide novel understandings of torpor use by desert heterotherms. Basking behaviour of *D. blythi* in the field has never been quantified, and a targeted study could be undertaken using motion/time-lapse sensor cameras at burrows to confirm the frequency of basking during winter. Lastly, new technology in small GPS devices may allow continuous tracking of individuals during the activity phase that would provide fascinating information about behavioural patterns.

Because both *L. kintorei* and *D. blythi* are often sympatric, further research on interspecific interactions, especially the extent to which predator-prey interactions occur is of interest. Some data during this study were recorded on burrow use of *L. kintorei* by *D. blythi* and vice versa however this was outside the scope of this study and not included for analysis. Such information may be of use when considering combined threats to either species. We predict that *D. blythi* likely prey on juvenile *L. kintorei* both when they are active during warmer months and also during winter by potentially being able to locate juvenile or younger *L. kintorei* within their burrows when they are brumating. Although this is a natural phenomenon that may have always occurred, any additional predation pressure on remnant *L. kintorei* populations already diminished by impacts of introduced predators and altered fire regimes, could potentially result in localised population declines and extinctions.

The current project has identified similarities and differences on the thermal biology of two burrowing arid zone species: the ectothermic *L. kintorei* and the endothermic *D. blythi*. An endothermic mammal can maintain a high metabolic rate and T_b, however, as *D. blythi* is a heterothermic endotherm it can also employ daily torpor to conserve energy. The ectotherm with its low metabolic rate uses behavioural thermoregulation to balance its energy requirements in the active season but can conserve energy by remaining inactive within its burrow for a significant part of each day. They can further conserve energy by estivating for longer periods in a secluded underground chamber during summer, or brumate at low T_bs for a quarter of the year. Both species live a semi-fossorial existence and become active to obtain food or reproduce, but otherwise remain inactive underground to conserve energy and reduce unnecessary risk of predation.

Analysing the thermal biology of free-living species across seasons provides valuable information about how they respond to changing temperatures. The finding that *D. blythi* uses torpor in summer on occasion has contributed to the broader pool of information on this relatively large and sedentary arid zone dasyurid however, further research is required to quantify the use of torpor by terrestrial mammals during warm periods. The new information on seasonal patterns in activity and inactivity displayed by *L. kintorei* could be used to inform survey and monitoring methodology. Continuing to explore behavioural responses to changing temperatures over several years would contribute to better understanding of how climate change effects behaviour. Monitoring estivation and brumation patterns in ectotherms and torpor and activity patterns in heterotherms across several years could show interesting patterns reflecting the broader effects of changes in climate. Management actions should aim to protect and replenish the habitat shared by both species to reduce the risk of wildfires and increased likelihood of predation in the face of potentially shorter winters and hotter summers.

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