Interspecific Interactions: A Case Study using the Tuatara-Fairy Prion Association

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All animals are equal but some animals are more equal than others.
George Orwell
Animal Farm.

Abstract

Some of the key relationships in the life of an organism are interactions with individuals of other species within the community, for example, negative interactions such as predation and competition are well known to shape natural communities. Positive interactions also have well documented influences, such as intertidal seaweed canopies extending the distribution of many organisms to higher tidal heights, by reducing thermal and desiccation stresses. However, investigating interactions and measuring their significance for fitness is notoriously difficult. For example, several groups of fish are known to 'clean' other fish species by feeding on their ectoparasites, a mutually beneficial arrangement. However, foraging by cleaners can damage scales of their hosts and this interaction can become parasitic in times of low ectoparasite abundance. Using both field and laboratory data, I investigated factors that influenced the dynamics of an unusual vertebrate association, the cohabitation of tuatara and fairy prions in a burrow. The end goal was to contribute to the understanding of the classification of this association. The fairy prion is a seabird that comes to land only for the breeding season and the tuatara is a burrowing reptile, active primarily at night in a temperate climate. Specifically, I measured the effects that this association had on tuatara thermoregulation, and demonstrated the difficulty in applying that information to categorize a complex interaction. Investigations into the temporal and spatial habitat of the tuatara, and the degree to which this influenced thermal opportunities, revealed that mean tuatara body temperatures were always within mean environmental temperatures. Males and females did not differ in mean body temperature or effectiveness of thermoregulation. Body size did not predict body temperature or cooling rates, but heating rates were influenced, with larger animals heating faster than smaller individuals. The presence of a fairy prion in a burrow increased humidity within the burrow, and tuatara that occupied burrows containing a fairy prion were able to maintain up to 1.8°C higher body temperatures through the night during the austral summer months. Thus, burrow use behaviour and burrow selection had greater influences on tuatara body temperature than an individual's sex or size. Experimental evidence revealed that tuatara are capable of adjusting their habitat selection behaviour in response to different humidity constraints. More time was spent outside the burrows and tuatara were more active under humid laboratory conditions. Use of the burrow by tuatara almost halved the time that fairy prions spent at the burrow with their chick, indicating that tuatara were having a negative effect on fairy prions' use of their burrow. There

was no evidence to support the fact that fairy prions were gaining any fitness benefits from their association with tuatara. Thus, we cannot call this interaction a commensalism or a mutualism. In certain instances, it may be that this interaction is best classed as a parasitism with the tuatara benefitting from burrow use and easy predation opportunities, to the detriment of the lifetime reproductive success of the fairy prion. In other instances it may simply be a case of competition for a limited resource (a burrow) with the outcome varying depending on the individuals and the circumstances involved. Being able to categorize interactions between species of high conservation value or at least to have an understanding of the costs and benefits associated with the interaction is desirable for conservation purposes, as failure to consider the ecological network within which a threatened species is embedded, may lead to counterproductive management measures. Further, these results can be used to develop future research into how climatic changes in temperature and rainfall may interact with habitat availability to influence the full range of natural outcomes of the tuatara-fairy prion association.

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wrapper from my hand and seeing my first giant weta, by far the largest insect I'd ever seen! I think I was hooked on New Zealand ecology after that trip! Thank you Monica Awasthy for giving me my first paid ecology job, introducing me to New Zealand birds and making me learn New Zealand trees!

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CHAPTER ONE

Interspecific interactions: A case study using the tuatara-fairy prion association

1.1 Introduction

No individual exists in isolation within an ecosystem, and an individual's neighbours can have significant effects on survival and reproduction. Neighbours can include members of the same species (intra-specific interactions) or members of another species (inter-specific interactions). Many species will interact with countless other species over a lifetime, and a large body of work has developed around understanding the evolution of interspecific interactions. Vertebrates exhibit dynamic, positive interactions that form and dissolve under different circumstances, usually with multiple species as participants (Machicote et al., 2004). Interspecific associations range from closely related species, to species from different orders, and occur across a wide range of taxa (Stensland et al., 2003). They have been observed in fish (Barlow, 1974, Wolf, 1985), birds (Berner & Grubb Jr, 1985, Graves & Gotelli, 1993, Develey & Stouffer, 2001) and mammals (reviewed in Stensland et al., 2003). Many of these interspecific associations are thought to have adaptive functions, and many of these adaptive explanations mirror explanations for why animals live in monospecific groups (Chapman & Chapman, 2000). In contrast to obligate mutualisms, such as between some fungi and green alga (lichens), or fungi and gardening ants, associations between species of terrestrial vertebrates are not permanent, but may last for periods of a few minutes to several months (Dickman, 1992). In many species, associations among individuals may be favoured if they increase per capita feeding success, increase access to favourable habitats, or reduce per capita risk of predation (Pulliam & Caraco, 1984, Dickman, 1992). Mixed-species associations may similarly profit, but can also benefit from unique advantages that are not available as a result of interactions with conspecifics. Such advantages include access to food resources, an increase in the range of food types or habitats that are able to be exploited, greater vigilance against potential predators, and the reduction of ectoparasite loads (Dickman, 1992). An advantage of mixed-species associations includes a likely reduced resources use overlap, relative to single-species groups, perhaps reducing competition (Dickman, 1992).

Some key relationships in the life of an organism are the interactions with individuals of other species within the community. This is particularly true when an individual has to share living space, for example a burrow or retreat site, with another species, and when one species has a disproportionate effect on that living space, for example, by altering the structure or the microclimate of that retreat site. Under circumstances where the measurable change occurs as the result of the interaction, the association between the individuals of two species can have implications for fitness for one or both of the species.

1.2 Categorizing interspecific interactions

Ecologists regularly need to describe interactions and to judge their importance for the problem they are studying, whether their primary focus is on individuals; e.g., does a mixed species group increase individual foraging success?, populations; e.g., is predation density dependent?, or communities; e.g., does competition shape community structure? (Bronstein, 1994b). This is no easy task, as the significance of certain interactions is notoriously difficult to measure (Connell, 1983), and even their definitions are subject to debate (Lewis, 1985, Abrams, 1987, Saffo, 1993). For convenience, the diversity of interactions between species was often compressed into the familiar "interactions grid" (Fig. 1). Arising from their positive (+), neutral (0), or negative (-) effects on their partner species, interspecific interactions are differentiated into six discrete forms based on the pairwise signs (+, 0, -) of their interaction outcomes, termed mutualism, commensalism, amensalism, neutralism, competition and predation/parasitism (Holland & DeAngelis, 2009).

Species 2

| | + | - | 0 |

Species 1

+ Mutualism

- Predation/Parasitism   Competition

0 Commensalism   Amensalism   Neutralism
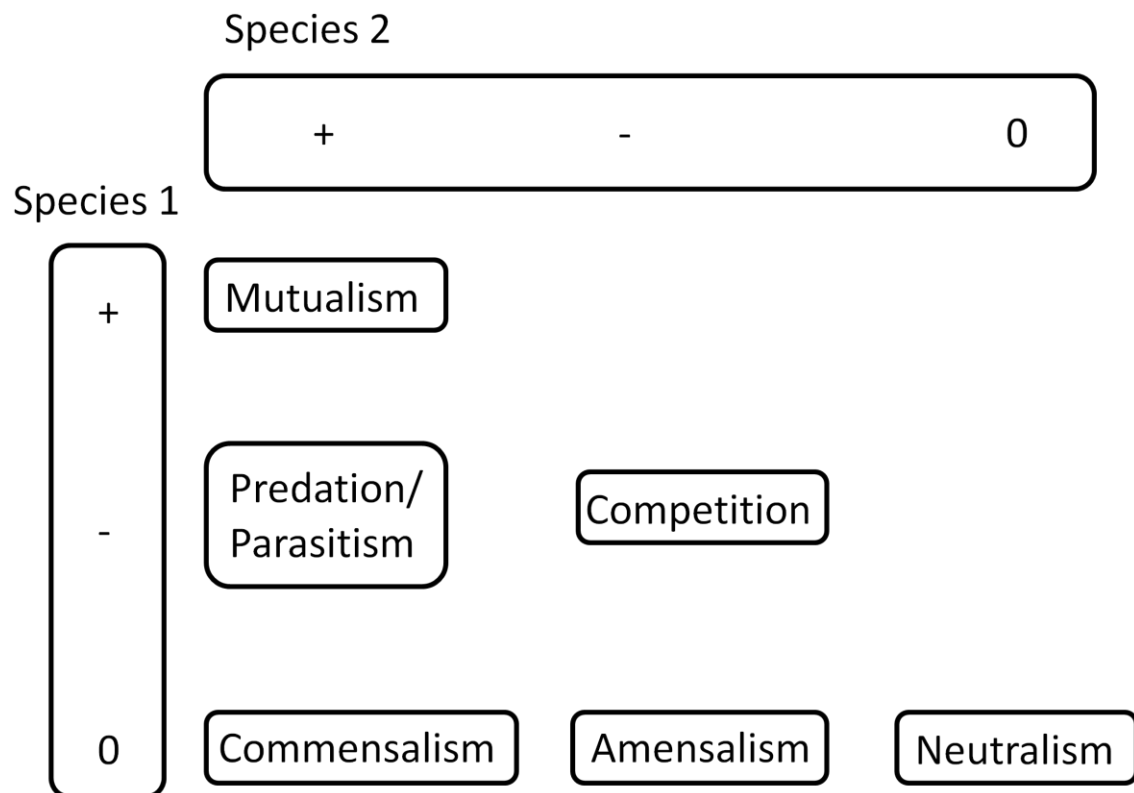
Figure 1. Interactions grid depicting the traditional approach to describe forms of interspecific interaction. Adapted from (Bronstein, 1994a).

The presentation of the static typology of the interactions grid has been heavily criticised. It placed interactions that occur by very different mechanisms into a single compartment, such as, predation, parasitism and disease (Abrams, 1987, Arthur & Mitchell, 1989), and simultaneously obscured ecological and evolutionary links between certain segregated interactions (Lewis, 1985, Ewald, 1987, Cushman & Addicott, 1991, Price, 1991). In reality, interactions occupy different quadrants of the grid at different places or times. They also vary in intensity (Bronstein, 1994a). However, like many other typologies in ecology, the interactions grid has served as a valuable heuristic tool (Bronstein, 1994b). In particular, when interactions are viewed this way, it becomes clearer that our current understanding of the different forms of interactions is distinctly unbalanced. Antagonistic ("minus") interactions, for example, competition and predation, have been extensively studied, and have been indisputably crucial in shaping modern ecological thought. In addition, a large body of information has now accumulated around mutualisms. However, studies with the specific goal of generalising patterns of beneficial interactions are rare, with the majority revealing case study information. In contrast, there has never been any appreciable interest in studying the ecology or evolution of commensalism,

amensalism, or neutralism, interactions that have no net effect on one or both partners (Bronstein, 1994b). These relationships apparently have been considered rare, difficult to document, or perhaps simply uninteresting (Bronstein, 1994b).

More recently, direct effects have been more accurately portrayed as an interaction compass (Fig. 2) (Holland & DeAngelis, 2009). Interactions occupy different sections of the compass at different places or times. The interaction compass describes continuous transitions and shifts back and forth between the six basic forms of species interaction. Now recognised as a key area of study to advance population and community ecology (Agrawal *et al.*, 2007), context dependency (or conditionality) refers to a change in the outcome of an interspecific interaction through the sign (+, 0, -) of one or both species due to variation in the local biotic or abiotic conditions of the community (Holland & DeAngelis, 2009).
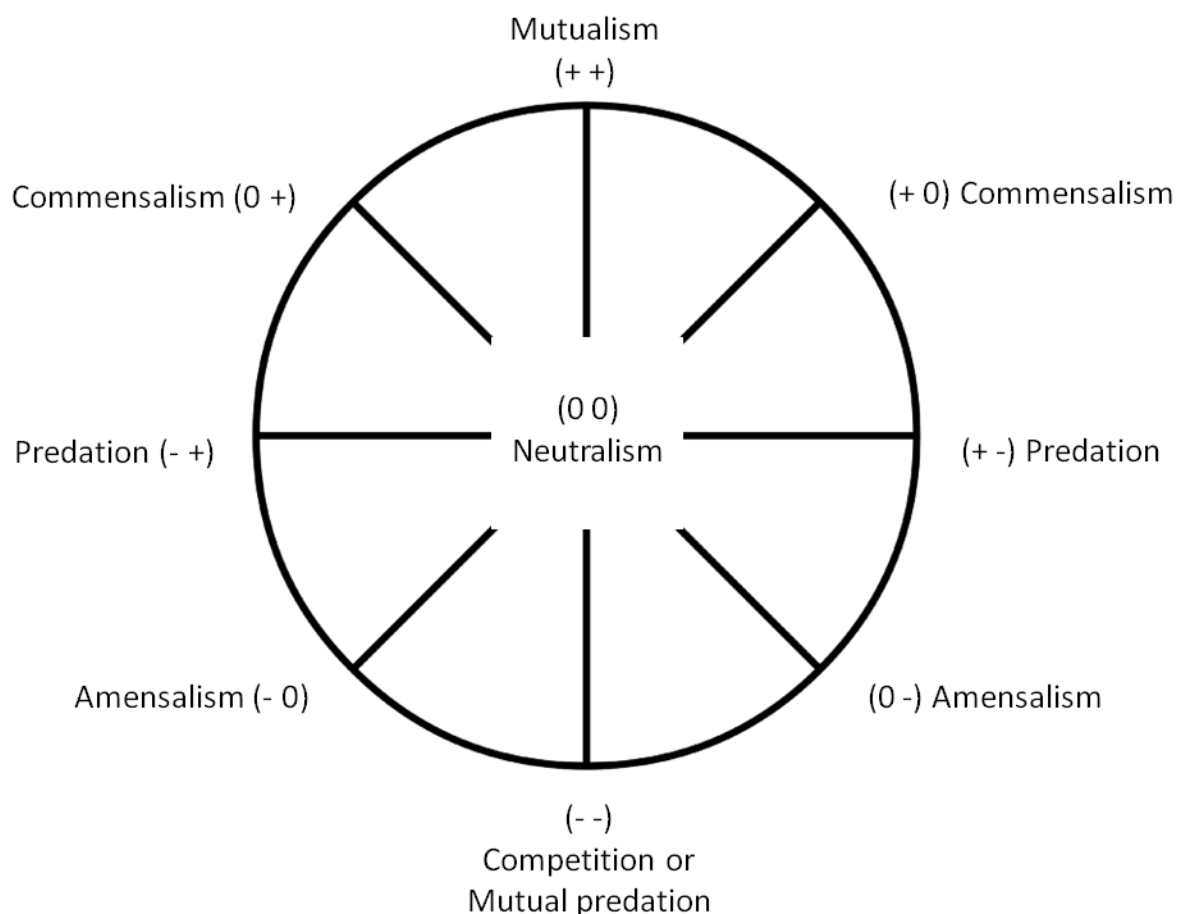
Figure 2. Unlike the discrete characterisation of interspecific interactions by the interaction grid, the interaction compass depicts how interactions between individuals reflects a continuum of transitions among the six basic forms of interspecific interaction. Interaction outcomes with (+ -) signs are termed predation here, but also include parasitism, herbivory, etc.

1.3 Retreat selection

Shelters, nests, and burrows constructed by many species of terrestrial vertebrates are often co-utilized by heterospecifics, and permit exploitation of environments that would otherwise be inaccessible. These associations are usually commensal. Rats (*Rattus rattus* and *R. norvegicus*) and house mice (*Mus domesticus* and *M. musculus*) have perhaps benefitted most conspicuously by using structures built by humans. The brown rat is mostly known as a commensal animal, found almost worldwide in human settlements (Traweger *et al.*, 2006). These rodents achieve their highest densities in urban or agricultural situations in many parts of the world, e.g. on the mainland of Britain, house mice are almost entirely restricted to urban habitats (Pocock *et al.*, 2004). Other associations involving use of rodent runways by shrews and weasels,(e.g. King, 1989) or use of owl burrows by small mammals are well known (Machicote *et al.*, 2004). However, benefits to the commensal species and possible costs or advantages to hosts in these situations have been poorly studied (Dickman, 1992).

An important component of the behavioural repertoire of many terrestrial reptiles is burrow use. Animals can use underground burrows as general shelter, as hibernacula, and as nesting sites. Moreover, burrows are often the site of social interactions among individuals, including courtship and aggression. Knowledge of patterns of burrow use is therefore important for understanding both habitat use and social structure (Bulova, 1994). Nests and burrows can reduce the hazards of external daily and seasonal temperature fluctuations, for example, many nocturnal desert rodents, such as kangaroo rats, live in areas of high environmental temperatures but apparently survive by using diurnal retreats (Walsberg, 2000). Similar to desert mammals, many temperate zone reptiles spend only a few hours a day above ground, and thus spend most of the day under rocks or in other retreats (Avery, 1976, Huey, 1982). Ectotherms can sometimes thermoregulate more effectively in retreats than in the open (Huey et al., 1989). Depending on the thermal properties of their retreat site, sequestered ectotherms may have different opportunities for thermoregulation, by experiencing different body temperatures from those associated with above ground activity (Christian et al., 1984, Peterson, 1987). Consequently, the retreat sites selected by ectotherms may have a profound impact on energy budgets and growth of individuals as well as the evolution of the thermal sensitivity of physiological performance and development (Huey, 1982).

1.4 Physiological ecology

Recently the role of the thermal environment has received increased attention due to the current threat of global warming. Altered thermal environments have numerous impacts on ecology. They can alter the potential range of a species resulting in range contractions or expansions, for example, observations of range shifts in parallel with climate change have been particularly rich in northern European countries, where observational records for many birds, butterflies, herbs, and trees date back to the mid-1700s (Parmesan, 2006).There have been impacts on the phenology and timing of prey species, and altered food webs (Visser & Both, 2005), with reproduction affected as a direct result of altered food availability or habitat change. For example, in North America four species of frogs are now calling 10–13 days earlier than at the start of the 20th century (Gibbs & Breisch, 2001). While the thermal environment has impacts on all species whether terrestrial or aquatic, vertebrate or invertebrate, it has a more immediate effect on the group of organisms termed ectotherms, as their internal body temperature is dependent on that of the environment. Biologists first began to recognize that reptiles employ behaviour to interact with their thermal environments as a means to regulate their body temperatures with the paradigm-shifting article by Cowles and Bogert (1944). Two decades of field and laboratory studies subsequent to the article by Cowles and Bogert gave birth to the field of animal physiological ecology and to an expanding literature documenting how some reptiles regulate body temperature by behaviourally and physiologically exploiting diverse thermal environments (Christian & Tracy, 2006).

The thermal environment changes perpetually on a geological timescale, seasonally and daily (Glanville & Seebacher, 2006). Hence, all organisms have evolved with thermal variability as a selection pressure, and environments that provide a constant thermal signal are rare (Osborn & Briffa, 2006, Glanville & Seebacher, 2006). Evolutionary responses to thermally variable environments range from regulation of internal body temperature to a constant or near constant level (thermoregulators), to letting body temperature fluctuate proportionally to environmental fluctuations (thermoconformers), while compensating cellular functions for the thermodynamic effect on reaction rates (Guderley, 2004, Lovegrove, 2005). Animals may attempt to regulate their body temperature to a particular 'set-point' temperature that coincides with the ideal or optimal temperature for organism function (Cabanac, 2006) and the behavioural mechanisms of thermoregulation to achieve this range are similar among terrestrial ectotherms (Somero, 1995, Seebacher, 1999, Samietz et al., 2005). However, actual body

temperature at which an organism can function is determined by the thermal sensitivities of the biochemical components, particularly enzyme activities (Somero, 1995).

Intraspecific interactions for thermal benefits are well documented, for example, huddling in birds, e.g., common bushtits, *Psaltriparus minimus* (Chaplin, 1982) and Emperor penguins (*Aptenodytes forsteri*) (Gilbert et al., 2006). Some bat species form small, loosely packed clusters, while other species cluster in compact groups (Brack, 2007) containing up to several thousand individuals (McNab, 1974, Clawson *et al.*, 1980) to reduce heat loss. The body temperatures of sun-exposed toads, *Rhinella spinulosa* averaged 2.3 °C higher when in aggregations than when solitary (Espinoza & Quinteros, 2008). Positive interactions can occur between species when one organism makes the local environment more favourable by reducing thermal stress via shading or decreasing wind stress via baffling (Stachowicz, 2001). However, studies on interspecies interactions between vertebrates based on thermal benefits are poorly represented in the literature. Moreover, ecologists know little about how different positive interactions ameliorate different stresses across the range of a single species, or about the evolutionary consequences of being involved in many such interactions. Thus, as a hybrid field integrating physiology and ecology, physiological ecology should have two primary goals: to understand how the interaction of organism and environment determines the characteristics of individuals that are relevant to ecology (e.g., age-specific fecundity and mortality, movement patterns, foraging, etc.); and to understand how these individual characteristics affect population and interspecific dynamics (Kingsolver, 1989).

1.5 Tuatara and seabird ecology

The tuatara is a medium-sized, long lived reptile (*c*. 100 years; Gaze, 2001) that is endemic to New Zealand, and is the sole, extant representative of the once diverse, ancient reptilian order Rhynchocephalia (*sensu* Gauthier et al., 1988). Although once widespread throughout the main and outlying islands (Holdaway & Worthy, 1997), natural populations are now restricted to small offshore islands, primarily due to predation from introduced mammalian predators. Tuatara are a diurno-nocturnal, burrowing species. They forage mainly at night when air temperatures are typically low (Walls, 1983) and are active at temperatures as low as 5.2 to 11.2°C (Thompson & Daugherty, 1998), but they also bask and feed during the day, attaining body temperatures up to 30°C when the opportunities arise (Walls, 1981, Barwick, 1982). Occupied burrows can be shared

occasionally with other individuals and nesting seabirds, and underground burrow systems are dynamic and can be extensive (Newman, 1987). These underground burrows are used as general shelter and are also often the site of basking and social interactions among individuals, including territorial behaviour and aggression. Tuatara differ from most lizards in that they are long-lived, and breeding intervals are prolonged for females (i.e. asynchorous reproduction occurs every 2-5 years, with 8-10 months from insemination to oviposition (Cree et al., 1992)). During late summer tuatara are physically most active and tuatara courtship begins in late January and continues throughout February (Gillingham et al., 1995). Mating peaks in March (Austral autumn) (Moore et al., 2009a). Approximately 8 – 10 months after mating, female tuatara migrate to nesting rookeries and lay eggs. Tuatara can live in very dense populations of up to ~2700 individuals/ha (Moore et al., 2009b) but the relatively simple spatial structure of tuatara populations is highly stable over years, possibly decades, and they can maintain particular burrows for long periods of time (Moore et al., 2009b), despite the potential availability of many other burrows. For example, on Stephens Island there are many more burrows than there are tuatara, as most burrows are excavated by fairy prions (*Pachyptila turtur*), and there are greater numbers of seabirds than tuatara (approximately 1,000,000: 40,000).

The close ecological relationship between tuatara and petrels has been noted since the 1800's (Mair, 1871, Reischek, 1881, Ramstad et al., 2007). In the past, the whole New Zealand coastline, and many inland areas, were honeycombed with burrows of hundreds of millions of petrels, prions, penguins, and shearwaters (Worthy et al., 2002). Despite a long awareness of their coexistance, the exact nature of the symbiotic relationship between tuatara and seabirds such as fairy prions is still unclear. However, there is sufficient evidence to suggest that tuatara benefit greatly from living within the same burrow alongside seabirds such as petrels, prions and shearwaters. Usually the birds dig the burrows providing the tuatara with a home (Newman, 1987), and the birds' eggs and chicks may provide an easy meal for larger males and important nutrients at an energy demanding time of year as they approach the mating season (Crook, 1975, Walls, 1978, Walls, 1981). Seabirds also deplete the understory vegetation in forested areas and increase the invertebrate biomass by nutrient addition (East et al., 1995). The increase in prey items potentially allows higher densities of tuatara to occur in an area, as is seen on Stephens Island where greater tuatara numbers are found in areas with more fairy prions (Markwell, 1998), up until high densities of prions (>2 burrows/m^2) when tuatara numbers are reduced (Newman, 1987). Despite predation on the eggs, chicks and even adults, the prion population as a whole is not significantly decreased by tuatara (Markwell, 1998).

Birds are one of the most diverse groups of ecosystem service providers, whose ecological functions range from creating soil in polar regions (see Heine & Speir, 1989) to shaping primate behaviour (Sekercioglu, 2006). Seabirds (order Procellariiformes) play significant roles in determining structure and function of New Zealand offshore island ecosystems (Atkinson & Bell, 1973). Although seabirds may return to their colonies at different times of the year, they are usually present in large numbers only during their breeding season. At the beginning of the breeding season, seabirds return to their colonies (Ovenden et al., 1991) and clear out an existing burrow or dig a new one (Richdale, 1945). Burrows are dug with the beak and feet, and can reach up to 3m underground, depending on the size of the bird and terrain. In dense colonies, many burrows anastomose to form a complex lattice under the fragile soil.

One seabird with which the tuatara is commonly found cohabiting is the fairy prion (*Pachyptila turtur*), a small Procellariid seabird (length 25cm, weight 90 – 175g). Fairy prions display high levels of philopatry, exhibiting natal philotropy and site fidelity, choosing to breed close to the site of their own hatching (Greenwood & Harvey, 1982). They have a lifespan of at least 15 years, can possibly fly 322km in a single day while foraging (Harper, 1976) and they feed entirely out at sea (Marchant & Higgins, 1990). Fairy prions form relatively stable pair bonds (Harper, 1976); lay only one egg, and both adults share in the incubation of the egg and the feeding of the chick. Following breeding, adult prions depart their colonies and spend the winter at sea in the Southern hemisphere. The fairy prion is present in large numbers at their colonies only over the breeding season from October to January (Falla, 1993). In September the birds begin prospecting and clearing out their burrows. In October the fairy prions lay eggs and incubate them for approximately 55 days. This coincides with a period of high metabolic demand for the tuatara, when moisture starts to become scarce (Walls, 1981), and when tuatara lay their eggs. The chicks hatch in January and during this period are left alone in their burrow during the day, with the adult fairy prions only visiting the island for short periods during the night (Marchant & Higgins, 1990). Most chicks are fledged by the end of February (Walls, 1978), and there are almost no fairy prions on the island in March when mating occurs between tuatara.

Stephens Island (also known by its Maori name *Takapourewa*), is inhabited by the largest and most well studied population of tuatara with total numbers estimated between 30,000 to 50,000 (Newman, 1987) and an estimated one million fairy prions use the island as a breeding ground (Harper, 1985), and this is the focal island for the research for this thesis. Stephens

Island is a 150 ha island with a history of human habitation and intensive habitat modification (Brown, 2000). Due to intensive farming, grazing and burning that began with the construction of a lighthouse in the late 1800's, an estimated 80% of the island had been deforested (Dieffenbach, 1843, Brown, 2000). My research was conducted in an area called Keepers Bush, which consists of a mix of degraded original forest and regenerating coastal forest. Canopy height is approximately 3-5m (Newman, 1987). Soils are either clay and shallow, or where burrowing seabird activity is greatest, very deep, acidic and friable (Ward, 1961). The only other seabird present in notable numbers at any time of year is approximately 1,000 sooty shearwaters (*Puffinus griseus*) (Markwell, 1997), although little blue penguins (*Eudyptula minor*) are also seen regularly, especially during the breeding season (pers. obs.).

The seabird-reptile association is an ideal model to study interspecies interactions in vertebrates as seabirds are an ephemeral presence in tuatara habitats, and when present not all individuals of both species associate to the same degree. Both tuatara and fairy prions, in particular, are conspicuous to a trained observer, and can occur at high enough densities (e.g. on Stephens Island) to conduct robust behavioural studies. Reptiles are also excellent models to advance thermophysiology, as many species are amenable to studies in both the wild and the laboratory. Thermophysiology and habitat use of squamates (snakes and lizards) are relatively well understood but understanding the thermophysiology and ecology of the tuatara may help to shed light on possible phylogenetic patterns of habitat use and thermoregulation in reptiles, as tuatara represent a distinct lineage of reptiles that diverged from their sister group (the squamates) approximately 230mya (Rest et al., 2003). Tuatara are ecologically similar to insectivorous lizards but they also have many morphological and physiological differences. Tuatara are unusual amongst modern reptiles in being active at very low temperatures (Barwick, 1982, Walls, 1983, Thompson & Daugherty, 1998). Therefore, predictions about the thermal requirements can only be based on evolutionarily distant and ecologically similar relatives (i.e., squamate lizards). The potential role that cohabitation with a seabird may have in terms of thermoregulation for tuatara, remains an enigma.

1.6 Key questions, thesis outline and style

The aim of this thesis is to advance current understanding of the relationship between tuatara and fairy prions, and to evaluate the impacts for tuatara thermal ecology. The findings will

enhance the current knowledge of interspecific interactions and improve conservation efforts for both species.

1.6.1 KEY QUESTIONS

• *How is the body temperature of tuatara influenced by its environment and by its behaviour?*

• *Do tuatara use thermal cues for retreat site selection?*

• *Can the presence of a heterospecific such as a seabird provide a thermal opportunity which is exploited by tuatara?*

• *Does tuatara behaviour or use of the burrow have any effect on the burrowing behaviour of fairy prions?*

1.6.2 THESIS OUTLINE AND STYLE

This thesis comprises four research chapters that are formatted for submission to peer reviewed journals. This style inevitably results in some repetition, especially in introductory sections, descriptions of species, and methods. However, the advantage of this style is the production of separate studies whilst addressing the overall hypotheses and research questions. This study is the first to look at tuatara body temperatures over extended periods of time with the specific goal of determining what impacts seabirds are having on tuatara thermoregulation. Understanding the potential impacts that a seabird may have on a tuatara's body temperature first requires knowledge of the physical attributes of the burrow and environmental variables across seasons. Thus, I investigated thermoregulation of tuatara, with the use of dataloggers and observed behavioural data (chapter two).

To investigate factors influencing burrow selection by tuatara, I conducted a series of laboratory experiments (chapter three). I explored traditional hypotheses that have been used to explain temperature selection on a thermal gradient and applied them to attempt to elucidate some of the factors underlying burrow choice, that is, time of day, humidity and digestive state.

In chapter four, I investigated the potential impacts of cohabitation with tuatara for fairy prion behaviour using a novel monitoring technique. An automated monitoring system was placed at the entrance to burrows to evaluate seabird visitation patterns at burrows in response to tuatara, specifically the amount of time the seabird spends in the burrow and thus the amount of time spent attending to it's egg and chick.

Not all tuatara are found in burrows occupied by fairy prions, thus I investigated the thermal effects that this association may have for tuatara. In chapter five, I compare tuatara body temperatures of individuals in both occupied and unoccupied fairy prion burrows across different periods of burrow occupancy by the seabirds, specifically during the egg laying and chick rearing periods.

In chapter six I provide a synthesis of the main findings of this thesis, and discuss implications for tuatara and seabird conservation, and opportunities for future research.

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CHAPTER TWO

Behaviour not morphology determines thermophysiology

2.1 Abstract

The body temperatures of reptiles depend essentially on that of their environment. Reptiles can exploit their thermal environment to a certain extent, but they are ultimately limited by the availability of a heat source. The aim of the current study was to better understand the temporal and spatial habitat of the tuatara, and the degree to which this influences thermal opportunities. The environment on Stephens Island, which is the location for the largest population of tuatara, only permits a tuatara's preferred body temperature to be reached in Austral spring and summer. Tuatara are not precise thermoregulators for much of the day or year, as mean body temperature for tuatara on Stephens Island was always within 1°C of mean environmental temperature. When operative environmental temperatures (T_e) enabled preferred body temperature to be reached, the majority of tuatara (62.4%) did not exploit their thermal environment. Males and females did not differ in mean body temperature or effectiveness of thermoregulation, and body size did not predict body temperature or cooling rates (although heating rates were influenced by body size). Burrow location and depth influenced burrow temperature, with deeper burrows maintaining more stable temperatures, and burrows in more open areas warmer than those in the shade. Variation among individuals in timing of burrow use also affected body temperature. Tuatara which remained in their burrows in the afternoon were on average 2-3°C cooler than those outside, with the reverse occurring in early morning. Individuals within their burrows between 2 - 4am were warmer than those outside their burrows. The presence of a seabird within a burrow increased both humidity of the burrow and the body temperature of tuatara. Thus, burrow use behaviour and burrow selection had greater influences on tuatara body temperature than an individual's sex or size. This has implications for habitat conservation and potential translocations. Although physiology is the ultimate controller of an organism's ability to achieve or maintain certain temperatures, within these physiological constraints it may actually be behaviour and the availability of suitable burrows that has more ecological relevance.

2.2 Introduction

Body temperature could be the single most important ecophysiological variable affecting the performance of ectotherms (Angilletta et al., 2002, Robert et al., 2006). Virtually all aspects of the behaviour and physiology of ectotherms are sensitive to body temperature (Huey & Stevenson, 1979, Huey, 1982), including locomotion (Weinstein, 1998, Forsman, 1999b, Ojanguren & Brana, 2000), immune function (Mondal & Rai, 2001), foraging ability (Ayers & Shine, 1997), courtship (Wilson, 2005), and rates of feeding and growth (Kingsolver, 2000). As all squamate reptiles are ectothermic, variation in their body temperature (T_b) affects their developmental, physiological, and behavioural processes (Schieffelin & de Queiroz, 1991, Keogh & DeSerto, 1994). The 'warmer is better' hypothesis is based on the finding that the catalytic efficiency of enzymes is higher generally at high than at low temperature, and predicts a positive correlation between maximum rate of performance and temperature at which performance is at its maximum (Forsman, 1999b).

In general, a higher body temperature means that internal processes are likely to happen at a faster rate (Cree *et al.*, 1991, Cartland & Grimmond, 1994) up to an upper threshold, beyond which is lethal, recorded as 34.5-40.0°C in the tuatara (Dawbin, 1962, Wilson & Lee, 1970). At a suboptimal temperature, any increase in a reptile's body temperature, however slight, could therefore have significant consequences in terms of fitness; the ability to survive and reproduce. If some individuals within a population could occupy higher quality habitats in terms of thermoregulatory opportunities, then that could lead to a fitness advantage for those individuals, for example, increased reproductive frequency, growth and/or survival. In the pygmy grasshopper, *Tetrix subulata*, different colour morphs exhibit different reproductive strategies which may reflect different thermoregulatory capabilities (Forsman, 1999a). Experimental studies have revealed that increased thermoregulation leads to increased growth rates in the lizard, *Eublepharis macularis* (Autumn & De Nardo, 1995).

The body temperature of reptiles is largely dependent on that of their environment (Saint Girons, 1980). Usually the capacity for thermoregulation is linked to the availability of solar radiation, which varies temporally and spatially (Angilletta et al., 2002). Reptiles can exploit their thermal environment to a certain extent either behaviourally, morphologically or physiologically, but are ultimately limited by the availability of a heat source. Optimal body temperatures can be attained behaviourally through the selection of microenvironments or orientation to heat sources and sinks (Tracy & Christian, 1986). Each animal must secure a habitat with very specific

thermal attributes (Huey, 1982, Downes & Shine, 1998), and this may be particularly important for ectotherms. The thermal opportunities within a habitat can be viewed as an environmental resource, thus animals might compete for habitats with suitable basking sites or thermal refugia. Habitat selection by animals is dependent on various constraints such as the physical structure of the environment, the physiology of the animal, food availability and protection from predators (Ward & Lubin, 1993, Reaney & Whiting, 2003). Retreat site selection may have a profound impact on an ectotherm's physiology and ecology (Huey, 1991). There are two extreme strategies of thermoregulation: thermoconformity (lack of behavioural regulation) and accurate thermoregulation (Herczeg et al., 2003). Thermoconformers are animals which do not attempt to thermoregulate and their body temperature closely tracks that of the environment at all times. A perfect thermoregulator would maintain their preferred body temperature regardless of environmental temperatures (Soulé, 1963).

The tuatara, *Sphenodon puctatus*, is a burrowing reptile endemic to New Zealand. It was once widespread throughout the main and outlying islands (Holdaway & Worthy, 1997), but by the early 19th century was extirpated on the two main islands, presumably as a result of habitat modification and introduction of rodents (*Rattus exulans*) by human settlers (~750ya; Anderson, 1996). It is the only surviving species of its order Rhynchocephalia (*sensu* Gauthier et al., 1988), and is therefore of particular interest in the study of thermophysiology in reptiles. Tuatara occupy burrows with other individuals and nesting seabirds, and the underground burrow systems can be dynamic and complex (Newman, 1987).

Tuatara thermophysiology has been investigated numerous times in laboratory studies. Early work on thermal gradients demonstrated that tuatara use temperatures between 3.5 – 27.9 °C with a mean of 18.3 °C (Stebbins, 1958). Laboratory work then revealed that tuatara tolerate, but do not prefer, low temperatures, and that over the course of a 24 hour period, males are on average more active than females (Garrick, 1969). More recently, it has been found that tuatara in poorer quality habitats (less basking opportunities) thermoregulate more accurately and maintain higher body temperatures than those in a higher quality habitats (Besson & Cree, 2010). Hughes (1968) discovered that there are three main environmental factors which control emergence of tuatara from burrows: light, temperature and humidity. He found that when ambient temperatures were in the range of 20-25 °C, emergence from burrows was 30-45 minutes earlier than when temperature was around 15 °C. Regulation of head temperature may

be more important than that of the body, and the panting threshold for tuatara was found to be at a head temperature of 33.0 °C (Heatwole, 1982).

The investigation of tuatara body temperatures in natural conditions (Bogert, 1953) found that the mean night-time body temperature in April is 11 °C and in November is 10.6 °C, and tuatara are generally about 0.8 °C cooler than the surrounding air. Tuatara forage at night between 10.5 – 12.5 °C (Werner & Whitaker, 1978). The temperatures of tuatara on windier nights was also found to be more uniform than when the weather is clearer and calm (Bogert, 1953). Saint Giron *et al*. (1980) found that the body temperatures of tuatara in the forest were identical to air temperature. However, in the middle of the afternoon body temperatures (measured with a cloacal mercury thermometer) of tuatara sitting in filtered sunlight varied over 19.4-23.1 °C, and in full sunlight ranged from 27.0 – 40.8 °C (Saint Girons *et al.*, 1980). Barwick (1982) investigated active thermoregulation in the tuatara on Stephens Island. He used cloacal probes and obtained 24hr observations over a period of 3-9 days. The highest body temperature he recorded was 30.1 °C, and he concluded that water loss may be the over-riding factor which governs the number of days that an animal can bask. However, there has been some controversy in the past over whether tuatara actively thermoregulate or not. For example, Walls (1983) looked at the relationship of tuatara body temperature and activity to ambient air temperature and weather conditions, and concluded that they actively thermoregulate by following sun spots. However, Thompson & Daugherty (1998) found no evidence of active thermoregulation in tuatara. Tuatara may also thermoregulate to different degrees depending on the amount of food they had consumed the night before (Saint Girons, 1980). Investigations into the physical conditions of tuatara among islands revealed that those animals cohabiting with various species of petrels were warmer than other individuals (Tyrell, 2000, Besson, 2009) suggesting that birds may increase the thermal quality of a burrow.

Any increase in temperature within the burrow would increase metabolic rate and possibly lead to higher growth rates for tuatara. Higher temperatures on Lady Alice Island mean that tuatara reach the inferred size of maturity about 2-3 years earlier than on the colder, more southern Stephens Island (Castanet *et al.*, 1988). Thermal benefits for the tuatara could also have reproductive implications. Tuatara take at least ten years to reach sexual maturity and have a low reproductive output. Tuatara eggs have a soft, parchment-like shell. It takes the females between one and three years to provision eggs with yolk, and up to seven months to form the shell. It then takes between 11 and 16 months from the time the eggs are laid to the time they

hatch. The rate of reproduction in tuatara is the lowest of any reptile (Cree et al., 1992). Mating occurs in February/March and nesting intervals from two up to nine years have been recorded (Cree et al., 1992, Mitchell et al., 2010). The reasons for the variance in nesting frequency between females are unclear, but are possibly linked to their thermal environment and available resources such as food, and the interaction between these, for example, the conversion of energy into reproductive output.

From laboratory studies, it is now known that tuatara can adjust their thermoregulatory strategy in response to the thermal quality of their habitat (Besson & Cree, 2010). However, there are costs to thermoregulation, such as exposure to predation when basking, and the most obvious of which is time, because time spent thermoregulating may not be used for other activities such as foraging or mating (Avery, 1982). When the thermal quality of the habitat decreases, individuals need more time and energy to thermoregulate more efficiently, and thermoregulation becomes more costly (Besson & Cree, 2010). Conversely, if the thermal quality of the habitat increases, i.e. moves closer to the tuatara's preferred temperature range, as may be the case when a bird moves into a tuatara burrow, an individual may save time and energy on thermoregulatory activity.

Another cost of thermoregulating at higher temperatures may be water loss. Temperature and humidity are both important environmental variables for reptiles, and are strongly linked as relative humidity changes with respect to temperature. The body temperature of a terrestrial reptile may be lowered by the loss of heat from the evaporation of body fluids (Bogert, 1949). In addition, the time available to bask and raise body temperatures may be limited by loss of water (Barwick, 1982). A 400g tuatara held in captivity for 4 hours at 25°C and at 70% relative humidity may lose 400mg of water, compared with a loss of 140mg at 15°C and 100% relative humidity (Hill; pers comm. in Barwick, 1982). These temperatures and humidity values are comparable to tuatara body temperatures when basking and in the burrow respectively, which suggests that water loss may increase by a factor of 2.7 when a tuatara is basking in the sun. Tuatara are also particularly vulnerable to water loss, as many of the offshore islands they inhabit are without permanent sources of freshwater. They therefore obtain all their water requirements from their food, dew or mist. Since body temperature has a profound effect on the performance of ectotherms (Angilletta *et al.*, 2002), they therefore need an effective means of dealing with spatial and temporal heterogeneity in both their thermal and hydric environment. If burrows differ in their capacity for providing a thermal and hydric refuge, daily and seasonal movements

among burrows may be influenced by variation in burrow microclimate (Bulova, 2002). Seabird burrows are more humid than ambient air (Towns, 1992), and thus may provide a burrow microclimate more conducive to the minimisation of water loss.

To my knowledge, only limited long term data are available for tuatara body temperatures in their natural surroundings. Hence it remains largely unknown how weather conditions, burrow microclimate and conspecifics affect body temperature over extended periods of time. The extent to which bird-inhabited burrows affect tuatara thermoregulation is also poorly understood, with tuatara facing potential tradeoffs between enhanced burrow conditions while at the same time coping with increased disturbance at the burrow. When investigating the predominant influences on tuatara body temperature, I analysed morphological factors of each animal, temporal changes, environmental factors, presence of a bird in the burrow and behavioural use of the burrow. My aim was to better understand both the temporal and spatial habitat of the tuatara, and the degree to which this influences tuatara thermal opportunities. Specifically, I asked the question, which plays the larger influence on determining body temperature: morphology, behaviour or habitat?

2.3 Methods

Study area and species

This study was conducted on Stephens Island (also known by its Māori name, Takapourewa), a 150-ha island located in Cook Strait, New Zealand (40°40′S, 174°00′E). It was conducted over three successive field seasons (October 2008 – March 2011) in an area called Keepers Bush, which consisted of regenerating coastal forest. Canopy height is approximately 3-5m (Newman, 1987), and the dominant species consist of *Coprosma repens, Melicytus ramiflorus, Dysoxylum spectabile, Hedycarya arborea*, with a sparse undergrowth of *Macropiper excelsum, Urtica ferox* and *Solanum nigrium* (Markwell, 1999). There were a total of 10 fieldtrips, each covering a two to three week period in Austral spring; September (n=1), October/November (n=3), summer; January (n=3) and autumn; March (n=3). These periods were selected because they are biologically important months for tuatara reproduction.

The tuatara, is a medium sized reptile, up to 450mm total length and 500g in females, and up to 600mm total length and 1kg in males (Dawbin, 1982a). Stephens Island is home to the largest

population of tuatara, with estimated densities of up to 2700/ha in Keepers Bush (Moore et al., 2007), and total numbers estimated between 30,000 to 50,000 (Newman, 1982). Tuatara inhabiting forested areas are active throughout a 24 hour period (Gillingham & Miller, 1991). On Stephens Island, the tuatara share their burrows with fairy prions (*Pachyptila turtur*), a small Procellarid seabird (length 25cm, weight 90 – 175g). The fairy prion is present in large numbers on Stephens Island only over the breeding season from October to January (Falla, 1993). In September the birds begin prospecting and clearing out their burrows. In October the fairy prions lay eggs and incubate them for approximately 55 days. This coincides with a period of high metabolic demand for the tuatara, when moisture starts to become scarce (Walls, 1981), and when tuatara lay their eggs. The chicks hatch in January and during this period are left alone in their burrow during the day, with the adult fairy prions only visiting the island for short periods during the night. Most chicks are fledged by the end of February (Walls, 1978), and there are almost no fairy prions on the island in March when mating occurs between tuatara.

2.3.1 Thermal quality of habitats

The possible values of body temperatures (T_b) available to an ectotherm in the field are referred to as the operative environmental temperatures (T_e) (Blouin-Demers & Weatherhead, 2001). To record operative environmental temperatures, temperature dataloggers (Hobo Tidbit®; reported accuracy ± 0.2°C Onset Computer Corporation, Massachusetts, USA) were positioned in the field in both areas of full shade and full sun (just outside the forest). A datalogger was placed on the ground surface and covered with leaf litter and twigs in both areas and one was tied to the trunk of a tree at the height of 1m in the forest. These were left in the habitat for 2.5 years (October 2008 - March 2011) and the dataloggers recorded temperature every hour. This method did not capture every nuance of habitat variability but it elucidated the general thermal properties of the two extremes available in the operative thermal environment: full shade versus full sun. It was assumed that animals could achieve any value of T_b in between the two extremes by selecting areas in partial shade, such as filtered sun through the tree canopy. To obtain a measure of the average operative temperature available to tuatara, a mean of the T_e measurements of both full sun habitat and full shade habitat was calculated. At each hour the temperatures recorded at ground level in the forest (shade) and temperatures recorded at ground level out of the forest (open) were averaged to get one hourly temperature to represent T_e values, as it was decided that this measurement best reflected the range of temperatures experienced by the tuatara. This method of calculating mean T_e assumes that each tuatara was aware of, and had access to both shade and sun. This assumption is based on home range size

(30.6 ± 3.9m² (males) to 13.9 ± 2.8m² (females) (Moore *et al.*, 2008)) and the fact that Keepers Bush consists of coastal scrub, intersected with paths, which provides ample open space for full sun.

2.3.2 Body temperatures

On each field trip between 20 and 32 tuatara were caught by hand, and weighed and measured (snout-to-vent length, vent-to-tail length and regenerated tail (new growth)). The majority of individuals were identified by a unique bead tag on their nuchal crests, and tuatara that were not bead tagged were marked with a number on their left side using a non-toxic marker. A datalogger (Thermochron iButton DS1921G, reported accuracy ± 1°C; Dallas Semiconductor, TX, USA), set to record temperature every 15 minutes, was attached to the base of the tail of each tuatara with surgical tape (mass: 3.3g, size: 17.5mm x 6mm). When taped down, each iButton's thermistor was in direct contact with the tuatara's tail surface, and the tape also helped to reduce the effect of sunlight heating the surface directly. The tape was camouflaged by rubbing damp soil over it (Fig. 1) and the iButtons remained attached for a period of 5-10 days.

Most recent studies using iButtons in reptiles (also used in birds and mammals) obtain body temperatures by surgically implanting an iButton into the intraperitoneal cavity (described in: Lovegrove, 2009), but this was not feasible in the current study due to the large sample size and the protection accorded to tuatara, making the technique unlikely to gain permitting approval. Temperatures obtained using iButtons attached externally can also accurately represent a reptile's internal body temperature (Shine et al., 2003), (see Appendix 1.) and while there may be a greater margin of error than with an internal thermocouple, an iButton is more practical in the field. This method permits sequential temperature monitoring to be related to behaviour and is less invasive than a rectal thermometer or thermocouple which can become easily detached. In addition, rectal thermometers or thermocouples can only really be used on individuals who take refuge in accessible areas or under captive conditions, since there is always the danger that wires can become caught. The use of iButtons also reduces the risk of measuring body temperatures which are elevated from handling or changing behaviour from recapturing the same individuals.

Figure 1. Female tuatara with datalogger attached to tail (circled, under camouflaged surgical tape). F1 (written with non-toxic marker) is a unique ID. This tuatara is above average size for females in the present study. Snout-to-vent length = 215mm (mean for females: 197 ± 2 mm) and mass= 355g (mean for females: 270 ± 8g).

Thermoregulation was analysed using the terminology and symbols introduced by Hertz et al (1993), subsequently used by most researchers, and described in the pictogram below (Fig. 2). T_b is the symbol for tuatara body temperature, T_e stands for environmental temperature or ambient temperature in the tuatara habitat, T_{set} is the tuatara's preferred temperature range, d_b is the deviation of T_b from T_{set}, and d_e is the deviation of T_e from T_{set}. Besson and Cree (2010) used a thermal gradient ranging from 10-12°C at the cold end up to 30-32°C, and determined the range of preferred body temperatures (T_{set}) of adult tuatara to be 19.5 – 23.1°C. This range was therefore used for T_{set} in all subsequent analyses.

Unless otherwise specified, data for males and females were separately analysed. Series of T_b values recorded from a single individual are not independent. Therefore, all analyses using the full data set were performed on data (T_b, d_e- d_b or E_x) averaged for each individual over the period appropriate for the specific analysis (year, month, hour), thereby avoiding pseudoreplication (Shine & Madsen, 1996). The data set did not consist of complete T_b data for

most individual tuatara for the three years, as logistical constraints meant tuatara had to be caught opportunistically; therefore it was not practical to use a repeated-measure design on individuals for most of the analyses. However, to investigate within individual fieldtrips repeated-measures analyses were used. To determine whether body temperature differed between the sexes, mean T_b was used as the response variable in a two-way ANCOVA where mean monthly T_e, sex, month and the interaction between sex and month were included as predictor variables. Mean monthly T_e was entered as a factor in the analysis to control for the potential effect of measuring T_b on different individuals under different climatic conditions.

2.3.3 Effectiveness of thermoregulation

Thermoregulation indices developed in recent years compare the extent to which a study animal is within its preferred range of body temperatures (T_{set}) to the extent to which the habitat in which it lives allows body temperature (T_b) within the T_{set} to be reached (the thermal quality of the habitat). The accuracy of T_b was measured as the mean of the deviations of individual T_b measurements from T_{set} (individual deviation, d_b) (Hertz *et al.*, 1993, Blouin-Demers & Weatherhead, 2001). If a tuatara's T_b is below the preferred range at any given time, then d_b is the difference between the lower bound of T_{set} and T_b, and if T_b is above T_{set}, d_b is the difference between T_b and the upper bound of T_{set} (see Fig. 2). Similarly, the thermal quality of each habitat was measured by the mean of the deviations of T_e from T_{set} (individual deviation, d_e) in each habitat. If T_e is below the set point range, d_e is the difference between the lower bound of T_{set} and T_e, and if T_e is above T_{set}, d_e is the difference between T_e and the upper bound of T_{set}. However, because T_e values never exceeded the upper bound of T_{set} in the shade (see Results), tuatara could always use the shaded areas to provide a refuge from high temperatures in full sun. Therefore, to calculate d_e, only instances where the lower bound of T_{set} could not be reached in either the shade or full sun, were considered. Hence, d_e was assigned a value greater than zero only when T_e in both areas was less than the lower bound of T_{set}.

To quantify the extent of thermoregulation (departure from perfect thermoconformity) the index $d_e - d_b$ was used (Blouin-Demers & Weatherhead, 2001). If animals thermoregulate precisely then $d_e - d_b$ will be a positive number, if animals select habitats randomly with respect to T_e then this index will be close to zero and if animals actively avoid habitats in their T_{set} range $d_e - d_b$ will be a negative number (Fig. 2). The magnitude of the difference is a measure of how much an animal departs from thermoconformity.

An additional index of thermoregulation (E_x) which determines the extent to which animals exploit the thermal environment was also calculated (Christian & Weavers, 1996). E_x is defined as the amount of time an animal spends within its T_{set}, expressed as a percentage of the time that it was possible for the animal to do so (as indicated by the T_e data). Therefore, E_x was calculated as a proportion of T_b measurements that fell within T_{set} for times when d_e = 0 in either the shade or sun (when T_e fell within the preferred range, T_{set}, (Fig. 2)). Following Brown and Weatherhead (2000), the index was modified slightly to calculate the proportions of T_b measurements that fell below ($T_b < T_{set}$) and above T_{set} ($T_b > T_{set}$) when d_e = 0 in at least one habitat (when T_b values within T_{set} could be achieved).

A two-way ANOVA was used to determine whether females and males differed in their effectiveness of thermoregulation, and if there was a seasonal component to any difference. Effective thermoregulation was calculated for each individual in each month of each year using the mean monthly d_b of an individual and the mean monthly d_e for that month, and these values were the response variables. Month, sex and the interaction of these two factors were included as predictor variables. The same analysis was conducted separately for each year and for day (0700 -1800) and night (1900 – 0600).

Two-way ANOVAs were used to determine if females and males differed in their thermal exploitation indices ($T_b = T_{set}$, $T_b > T_{set}$, and $T_b < T_{set}$), and whether there was a seasonal component to any difference. The three thermal exploitation indices were calculated for each individual in each month of each year using the mean monthly d_b of an individual and the mean monthly d_e for that month and these values were then each used as the response variables. Month, sex and the interaction of these two factors were used as predictor variables.

2.3.4 Heating and cooling rates

A subset of the data (January 2009; largest range in temperatures, 10-34.4°C) was examined to investigate the rate of heating and cooling among individual tuatara. Body temperature, T_b values were analysed every 15 minutes and the difference between successive T_b values was taken as the change in temperature over a 15 minute period.. To test for heating and cooling rates based on size, the 25% smallest (n = 8) and 25% largest (n = 7) tuatara by SVL, were separated into two binary categories: small and large. Repeated measures generalized linear models were conducted to test for differences in both heating and cooling rates between the two size classes.
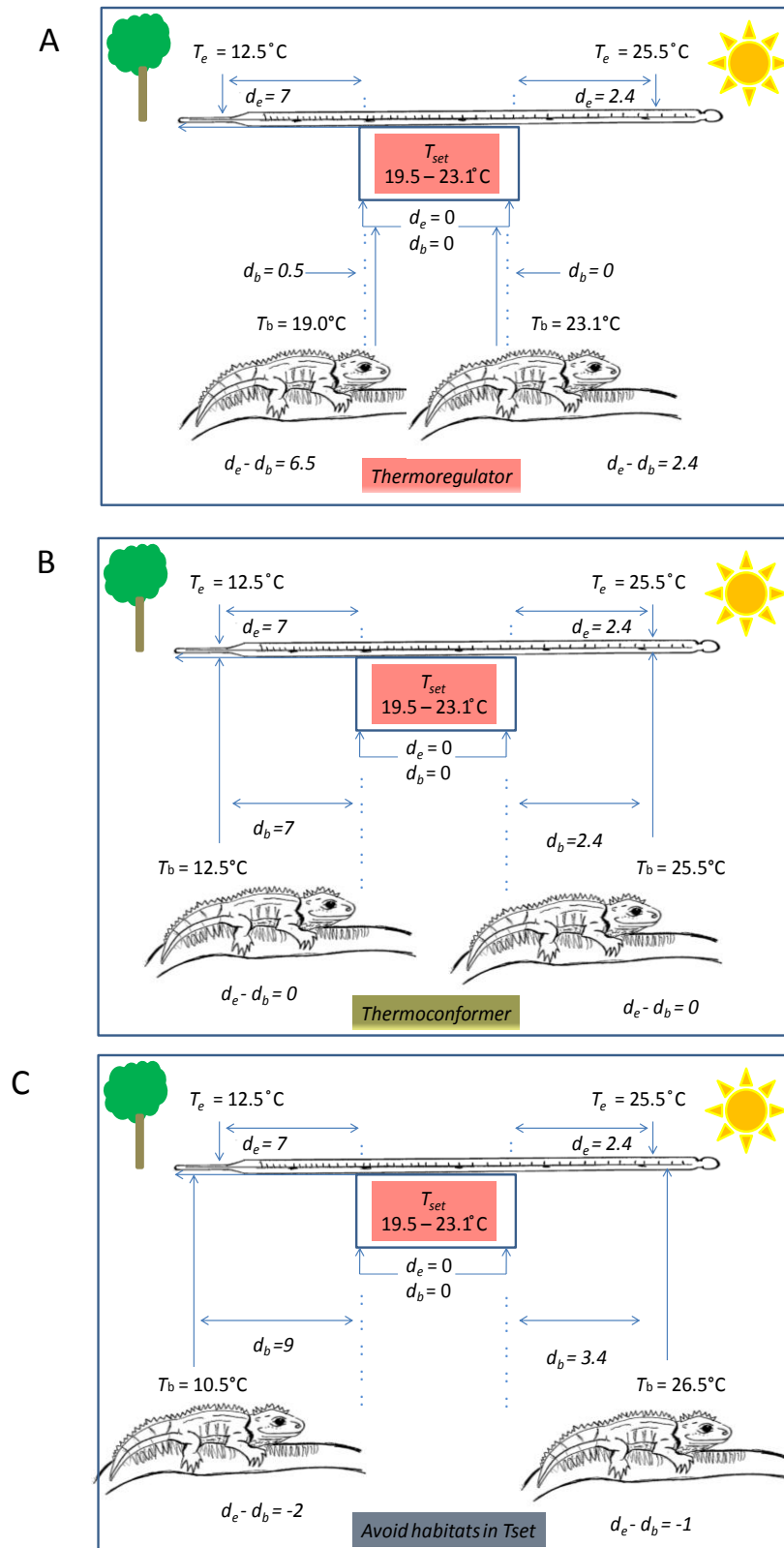
Figure 2. Terminology and symbols used in all analyses of tuatara thermoregulation. T_e = environmental temperature, T_b = tuatara body temperature, T_{set} = range of preferred body temperatures, d_b = deviation of T_b from T_{set}, d_e =deviation of T_e from T_{set}. If animals thermoregulate precisely then $d_e - d_b$ will be a positive number (a), if animals select habitats randomly with respect to T_e then this index will be close to zero (b) and if animals actively avoid habitats in their T_{set} range $d_e - d_b$ will be a negative number (c). A, B and C provide examples of body temperatures of tuatara that would indicate each of these behaviours, under representative T_e (see results section)

2.3.5 Morphology and body temperature

Tuatara were measured by taking snout-to-vent length (SVL) and mass, and these were used to create a body condition index. Body condition was defined as the residuals from a regression of log-transformed mass/log-transformed SVL. The first record for each individual caught was used in an ANOVA to confirm for size differences between males and females in the sampled individuals, as tuatara are sexually dimorphic (Dawbin, 1982b). Potential correlations between an individual's mean monthly T_b and SVL, mass, and condition were tested respectively using Spearman rank-order correlation. This is the non-parametric equivalent of the Pearson product-moment correlation and produces a statistic, r_s. The analyses were conducted separately for each month, for day and night and for males and females. Only the three months from season one and the first capture of each individual were used to avoid repeat sampling of the same individuals. The same analyses were repeated but with mean monthly index d_e - d_b and E_x instead of T_b.

2.3.6 Burrow use

The amount of time a tuatara spends within its burrow was investigated to understand the extent to which behaviour of an individual influences body temperature. Observations were made from a distance (sufficient to prevent startling animals) at 1400, 1600, 2200, 2400 and 0200 hours every day and occasionally 1200 and 0400 hours, to record the locations of all tuatara with temperature dataloggers attached. Recordings were carried out over the 20 minutes it took to walk a circuit through the forest past all marked burrows. A repeated measures generalized linear model was used to determine if tuatara differed in their T_b values when inside versus outside their burrows at 1200, 1400, 1600, 2200, 2400, 0200 and 0400. The mean monthly T_b of an individual at the above set time points throughout the day were used as the response variable.

A PIT tag (Passive Integrated Transponder) scanner was used to monitor the burrow use of a total of 20 tuatara in March 2010 (n= 10) and 2011 (n = 10). This method of monitoring animals marked with a PIT tag is described in chapter 4. Briefly, it consists of an aerial placed around the entrance to a burrow, through which a tuatara has to pass. The aerial is connected to a logger which records the tuatara's unique PIT number and the time at which it passes through the entrance.

2.3.7 Burrow conditions

A burrow can differ from another burrow in an almost infinite number of ways and these differences will vary in importance depending on the immediate requirements of the individual, such as food, shelter and access to mates. However, for the purposes of this study on tuatara body temperatures, burrows were categorised in two major ways: a) location, a burrow could be located in the open or under shade and it could be at different depths and b) its occupancy, some burrows on Stephens Island were occupied by fairy prions.

A series of loggers (Hobo Tidbit®;) were buried at depths of 0.1m, 0.2m, 0.3m and 0.4m (fairy prion burrows can be from 20 to 70cm deep; Markwell, 1997), in the forest in the shade and in an open, grassy area to investigate differences among soil temperatures. Dataloggers (temperature: Thermochron iButton DS1921G, reported accuracy ± 1°C, humidty: Thermochron iButton DS1923, reported accuracy ± 0.5°C, 0.6% RH; Dallas Semiconductor, TX, USA) were deployed to record both temperature and humidity in burrows (n varied from 2 to 10 on each trip). These were taped to a length of string, tied to a small twig and were inserted ~0.75m into the burrow and the twig wedged into the ceiling of the burrow so the datalogger dangled into the burrow interior.

To investigate whether thermoregulation was affected by the presence of the birds, burrows of all tuatara with attached dataloggers were inspected with a burrowscope. The mean hourly T_b, mean maximum T_b and mean minimum T_b of those tuatara that shared a burrow with a bird and those without were analysed. Mean T_b was used as the response variable in a repeated measures general linear model. The presence of bird, year, sex and the interactions were included as predictor variables. Each month was analysed separately and repeat individuals were removed from subsequent years.

2.3.8 Data analysis

Data were analysed using the statistical software SPSS, version 18.0 (SPSS Inc.) and R, version 2.11.1 (R Development Core Team, 2007). Data were tested for normality and data for some variables were transformed as required to meet assumptions of normality. Significance was assumed at $P < 0.05$. A subsample of the data (October 2009), were analysed to investigate whether there were differences between T_b values averaged to give the mean temperature for each hour versus on the hour T_b values. There was no significant difference (Independent

Samples Mann-Whitney U test; P = 0.875), therefore, "on the hour" T_b values were used for all further analyses.

2.4 Results

During October 2008 - March 2011, a total of 207,399 body temperature (T_b) measurements were recorded from 114 individual tuatara (62 males, 52 females). To summarize general patterns within the data, these measurements were reduced to 36, 808 hourly T_b values that were then used as the basis for all analyses (except where otherwise stated): 18,247 (49.6%) were recorded during the day (0700-1800) and the remaining 18,561 (50.4%) during the night (1900-0600). Some individuals were sampled during just one fieldtrip while others were sampled up to seven times.

2.4.1 Thermal quality of habitats

Ambient temperatures recorded in the shade at the height of one metre in the forest, ranged from 4.5 - 24.4°C over the 2.5 years sampled. January was the warmest month of the year, with a mean monthly temperature of 14.3 to 19.5 °C. The coldest time of year was July with mean monthly temperatures of 7.5 to 10.1°C (Fig. 3). The greatest variance in temperature recorded over a single day was 18.4°C and occurred in October 2008, when temperatures fluctuated from 11.3°C at 2400 hours up to 29.7°C at 1500 hours. The most stable 24 hour temperature cycle occurred in January 2010, when temperatures fluctuated less than 1°C and stayed at 15 ± 1°C over the course of 24 hours.

The operative environmental temperatures (T_e values) for all analyses were based on temperatures recorded at ground level in the shade and in the open. For those months in which tuatara T_bs, (body temperature measurements) were recorded, temperatures at ground level in the open ranged from a minimum of 9.6°C (October), to a maximum of 43.5°C (January). Temperatures in the shade, ranged from 9.4°C (October) to 17.3°C (January). Mean temperatures in January in the open, fell into a tuatara's T_{set} (preferred temperature) range between 1200 and 1800. October mean temperatures were just within T_{set} from 1300 to 1500, and mean temperatures in September or March never reached T_{set} (Fig. 4). Temperatures at ground level in the shade were always below a tuatara's T_{set} range.
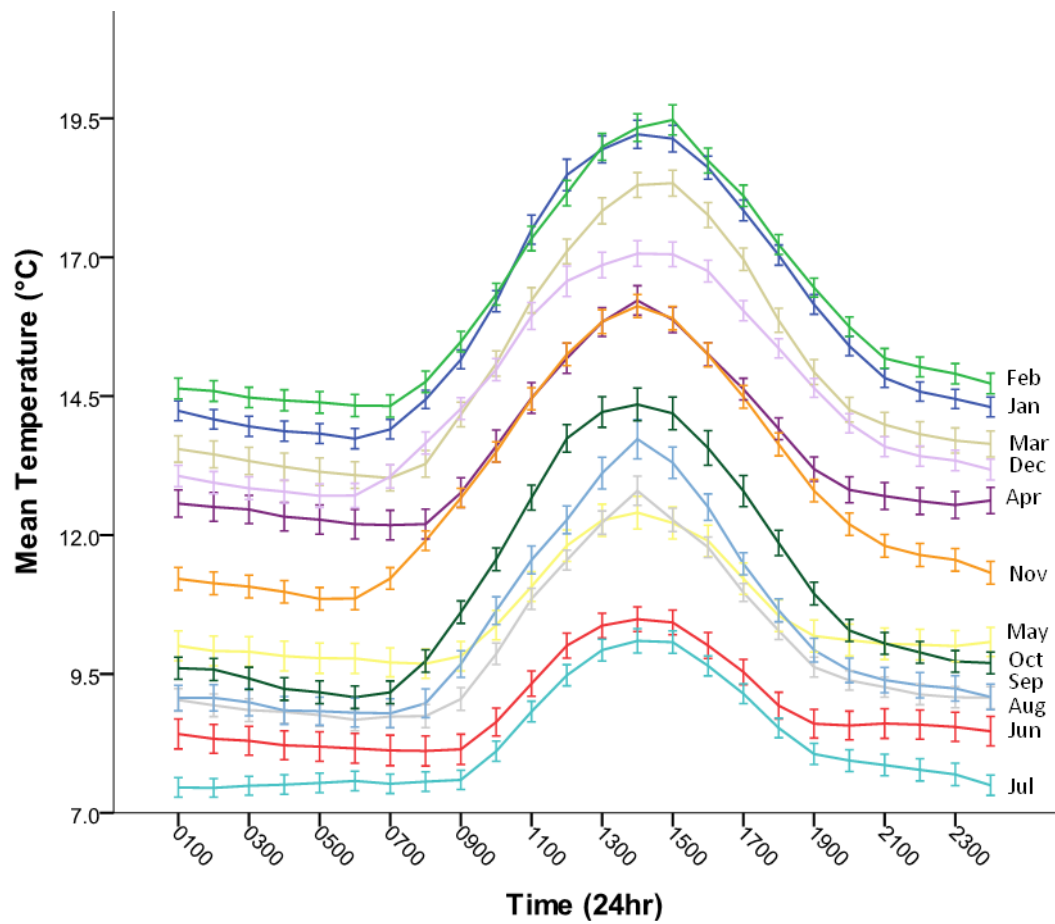
Figure 3. Mean hourly temperature ± 1 SE at 1 metre high in the shade, over a period from October 2008 to March 2011. July is the coldest month of the year, while February and January are the warmest.
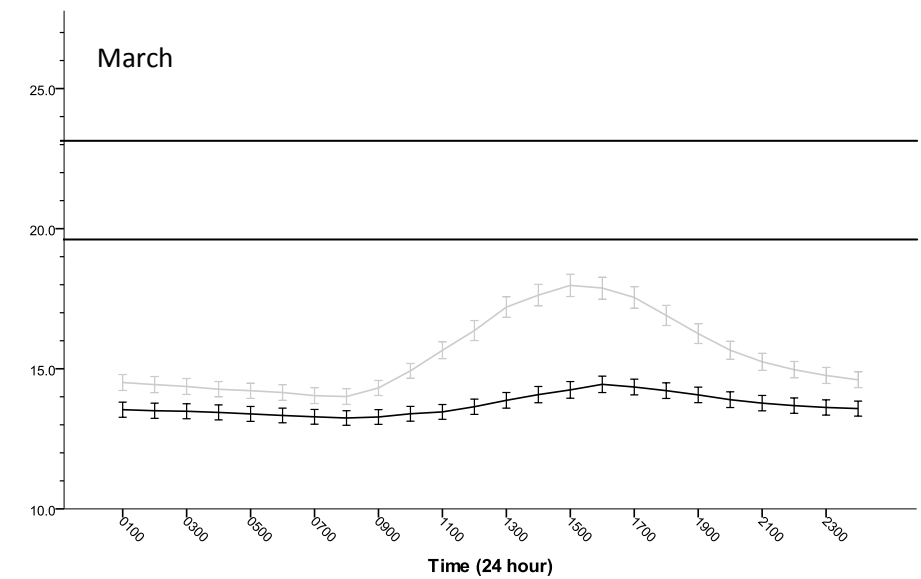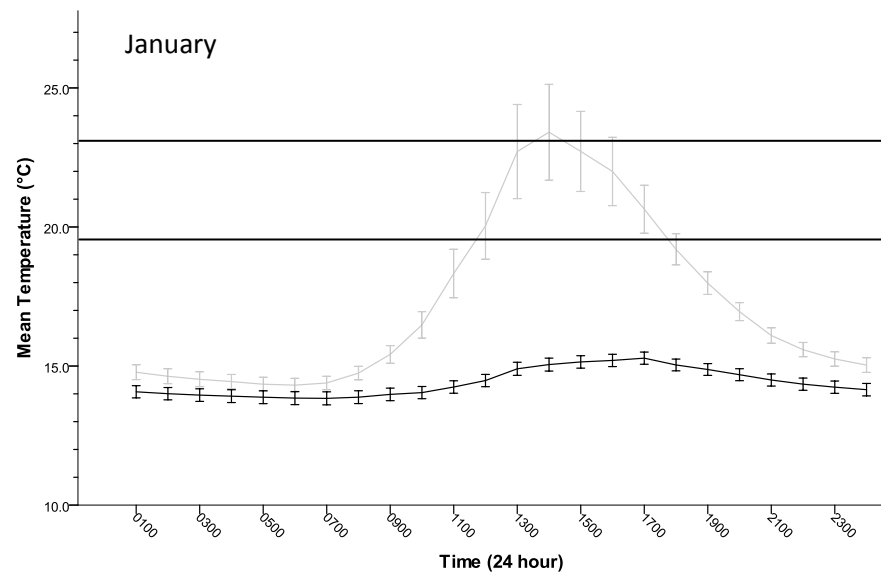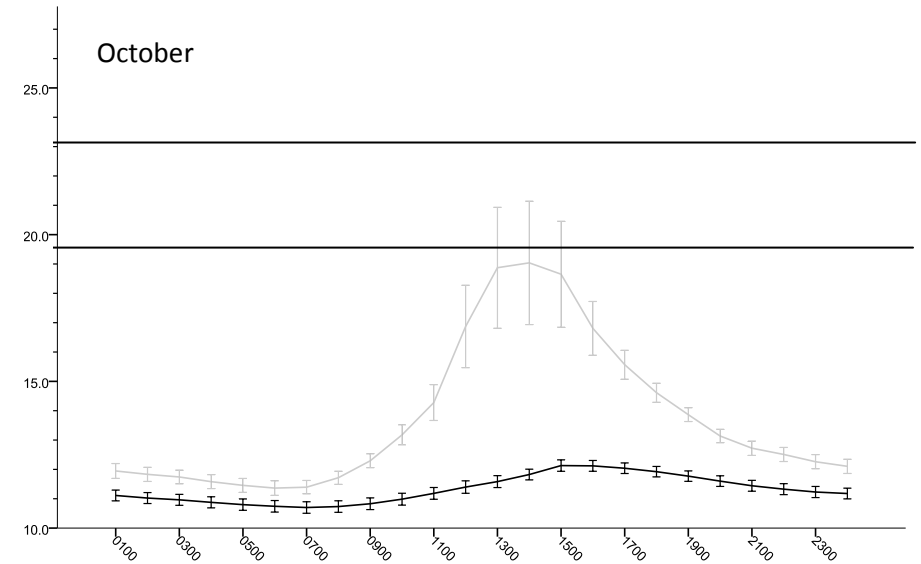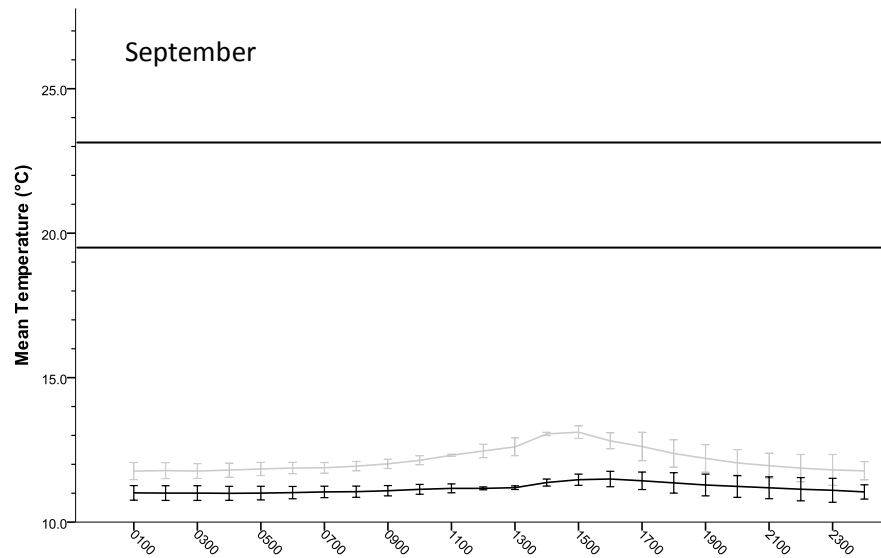
Figure 4. Mean hourly temperature ± 1 SE at ground level in the shade (black) and in the open (grey). Black bars indicate the upper and lower bounds of T_{set} (preferred temperature). In January, tuatara have the greatest number of potential hours to achieve T_{set} (1200-1800), and T_{set} is never possible to achieve in September or March.

2.4.2 Body temperatures

Mean monthly T_b (body temperatures of tuatara) were calculated in September, October, January and March. Mean monthly T_b was at a minimum in September (11.5°C), began to increase in October (12°C) to reach a peak in January (15.9°C) and decreased in March to 14.1°C. Body temperature extremes ranged up to 34.5°C (January 2009; 15 minutes) and down to 4.5°C (October 2009; 60 minutes) (Table. 1). Body temperatures of 28.5°C or above (highest 20%) were recorded only in January and October (n=45 hourly T_bs) but were usually sustained for less than 15 minutes (89.7%). There were only nine recorded instances of body temperatures maintained at or above 28.5°C for an hour or longer (n = 6 tuatara: 3 males and 3 females), and these were all recorded ~1300, with one exception, recorded between 1600 - 1700 hours. The highest temperature sustained for greater than one hour was 29.0 ± 1.0°C, over a 105 minute period in January 2009. Body temperatures of 7.5°C or lower (lowest 10%) were only recorded in October (n=37 hourly T_bs) but in contrast to the highest temperatures they were nearly always sustained (97.5%) for at least one hour. One tuatara (male) stayed at 7.5°C or below for over eight hours. The lowest temperature sustained for longer than one hour was 5.5 ± 1.0°C over a 255 minute period.

Table 1. Summary of tuatara body temperatures (T_b) over months sampled

Month	# T_bs	# Tuatara	Mean (°C)	S.E.	Min (°C)	Max (°C)	Range (°C)
September	1054	17	11.4	0.03	8.5	15.0	6.5
October	11832	57	11.9	0.02	4.5	30.0	25.5
January	14025	63	15.9	0.02	10.0	34.5	24.5
March	9897	47	14.1	0.02	9.0	28.0	19.0

Mean hourly T_b, minimum T_b, maximum T_b and mean T_e for each month sampled, indicated that for most of the day, tuatara were in habitats that allowed them to maintain T_b values close to the mean T_e. Mean T_b was always within 1°C of mean T_e (Fig. 5). Tuatara were never able to reach T_{set} in September and it was only during January that mean T_b ever fell within T_{set}. Maximum T_b often exceeded the T_{set} range during the day in October, January and March.
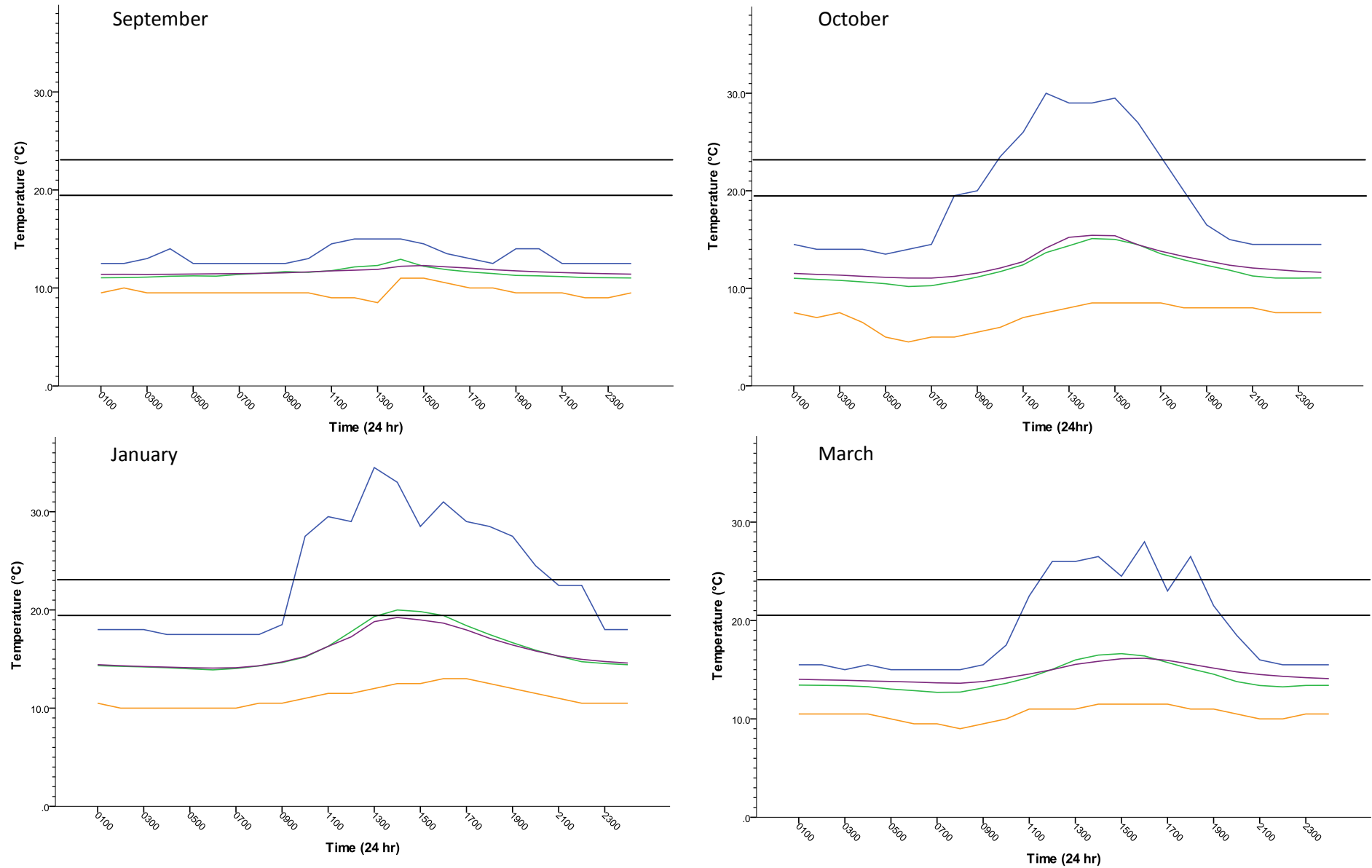
Figure 5. Mean hourly (green), minimum (orange) and maximum (blue) tuatara body temperatures (T_b) and mean hourly environmental temperatures (T_e) (purple) for September, October, January and March. T_e = average of sun and shade temperatures over an hour. Black horizontal bars indicate T_{set} range. Mean T_b was always within 1°C of mean T_e and tuatara were never able to reach T_{set} in September.

The mean monthly T_b data for each individual in each year was also used to determine if body temperature differed between the sexes, and/or whether differences varied seasonally. The same analyses were conducted separately for day T_bs (0700-1800) and night T_bs (1900 - 0600). Month had a significant effect on the T_b maintained by the tuatara, both during the day (F_3 = 118.296, P < 0.001) and during the night (F_3 = 14.542, P < 0.001). The effects of sex alone during the day (F_1 = 2.570, P = 0.110), during the night (F_1 = 0.014, P = 0.906), or as part of the interaction with month for day (F_3 = 0.456, P = 0.713) or night (F_3 = 0.550, P = 0.649) were not significant.

2.4.3 Effectiveness of thermoregulation

The extent to which an individual deviated from T_{set} at each hour (d_b) in each month of each year was calculated. This differed by 0 to 15°C, either above or below the range 19.5 − 23.1°C, and the mean d_b based on all the individual values was 5.7 ± 0.1°C. The degree to which the hourly temperature of the habitat (mean of shade and sun areas) deviated from from T_{set} (d_e) was also calculated. The mean d_e for the three years of the study was 5.4 ± 0.1°C. Over the sampled months, the mean d_b and mean d_e followed a similar pattern (Fig. 6).
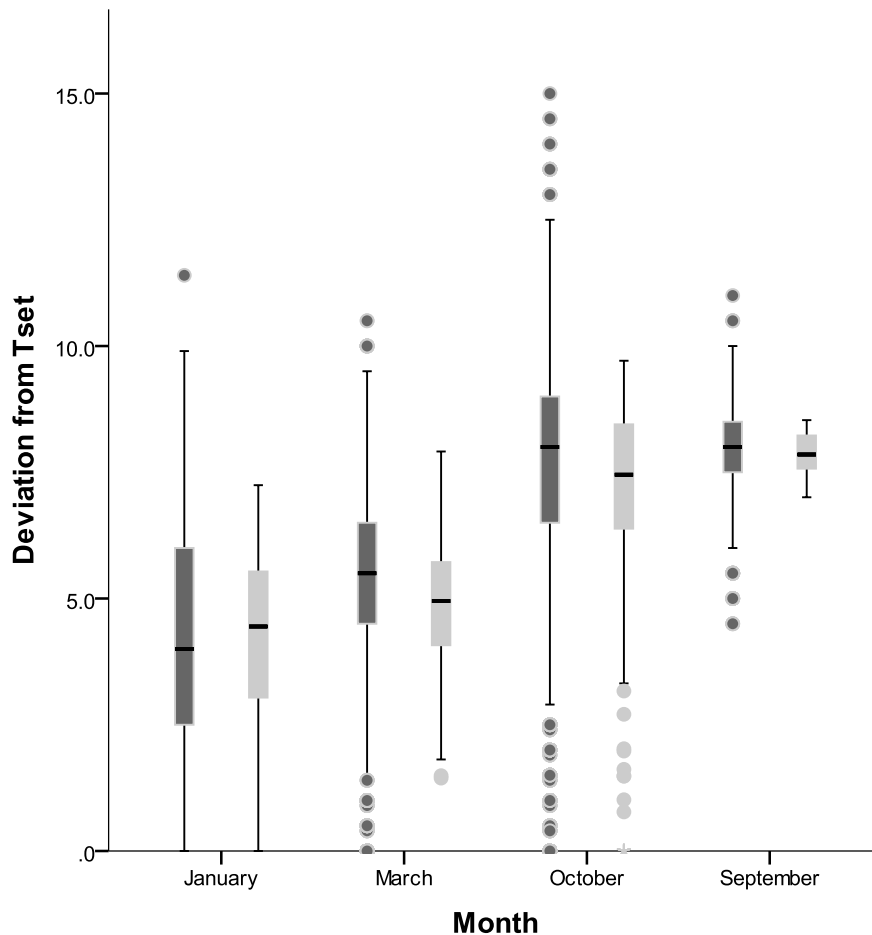
Figure 6. Box and whisker plot to display the mean accuracy of tuatara thermoregulation (d_b ± 1 SE) (dark grey) and thermal quality of the habitat (d_e ± 1 SE) (light grey) over three years.

Mean d_b and mean d_e values were lowest during January, which was the warmest month, increased in March, to reach their highest point in September, which was the coldest month, and then decreased again in October. To investigate variation in thermoregulation over the course of the day, the mean hourly d_b was calculated in each month of each year. Overall, mean d_b was higher than mean d_e during the course of the day (Fig. 7). Between 1100 and 1900 the T_bs of individual tuatara usually fell between the d_e in the open and d_e in the shade (Fig. 8).
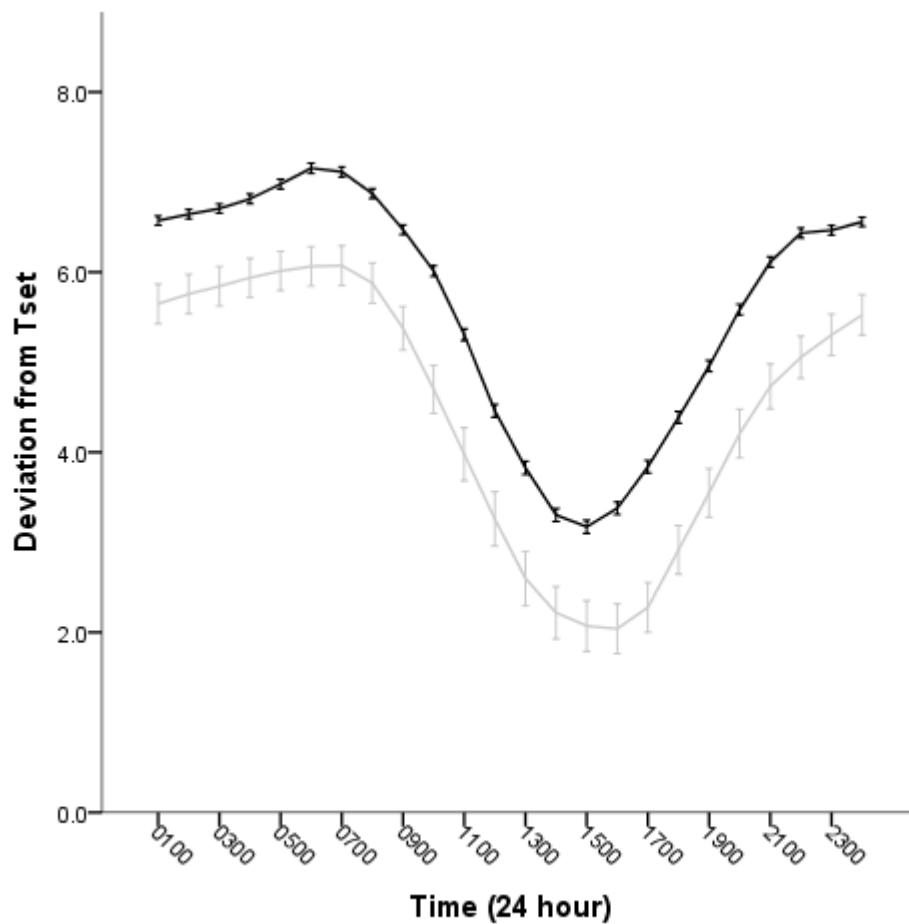
Figure 7. Mean hourly deviations of T_b from T_{set} (d_b) (black) and mean hourly deviations of T_e from T_{set} (d_e) (grey)
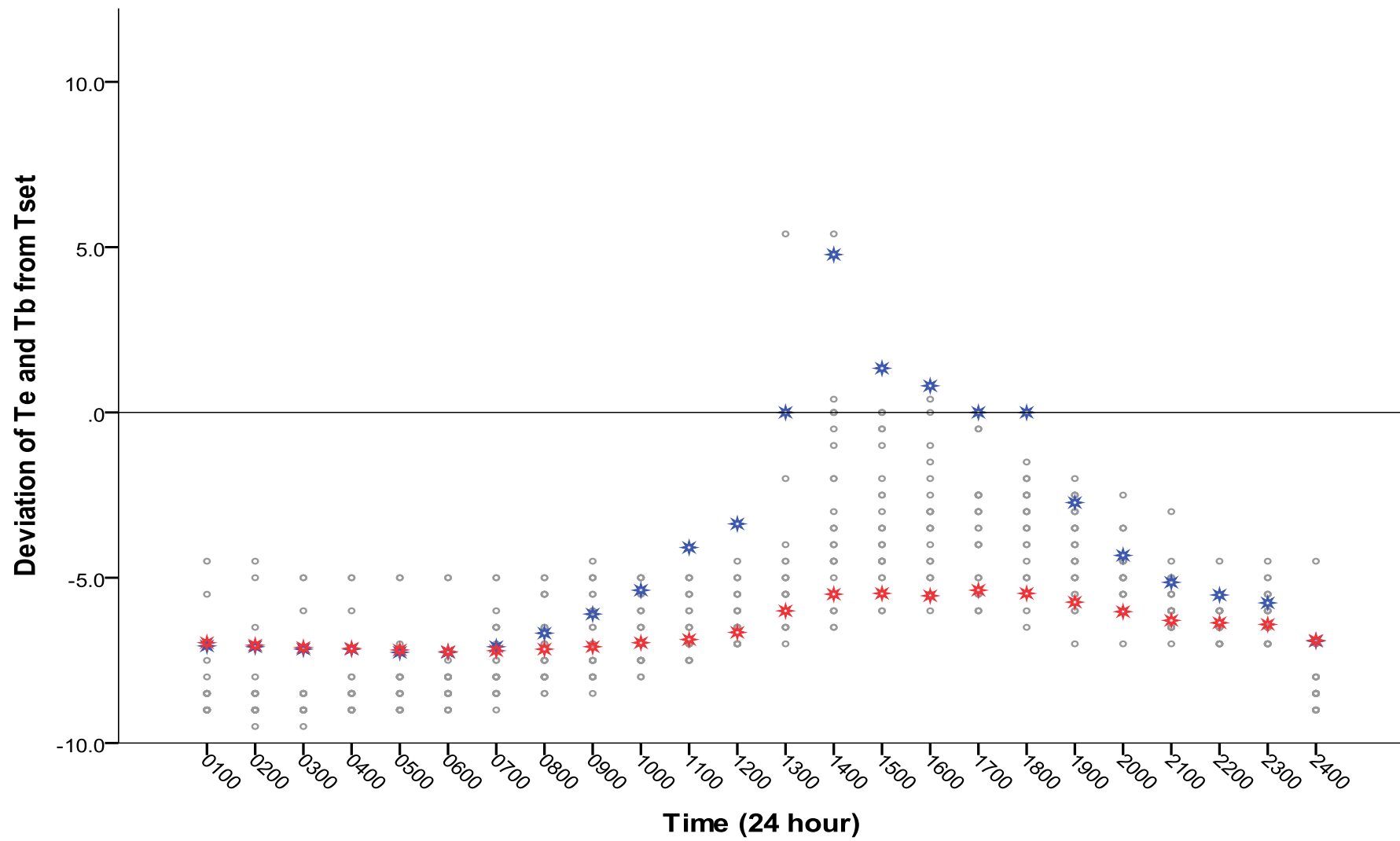
Figure 8. Deviation of T_e and T_b from T_{set} during one representative day in January 2009 (T_e = 12.3 to 20.9°C). Grey circles represent individual tuatara d_b, blue stars = $d_{e(open)}$, red stars = $d_{e(shade)}$. Tuatara are all below T_{set} except between 1300 -1800 hours.

The effectiveness of thermoregulation was calculated by subtracting d_b from the d_e for all individuals at every hour sampled. During the day 42.3% of (d_e - d_b) values were below zero, 28.3% were at zero (± 0.5°C), and 29.4% of values were above zero. During the night 49.4% of values were below zero, 36.9% at zero (± 0.5°C), and 13.7% above zero. Mean d_b was higher than mean d_e in every month except January, when it was 0.1°C lower, and the difference between d_b and d_e was greatest in March and October, months between the highest and lowest temperatures (Fig. 8). This plot reveals that most mean values are negative which means that animals are not thermoregulating and may even avoid habitats with T_e closer to their T_{set} range. Between 1200 to 1500 hours, mean d_e - d_b was positive but individual values ranged from -9.0°C to 7.6°C.
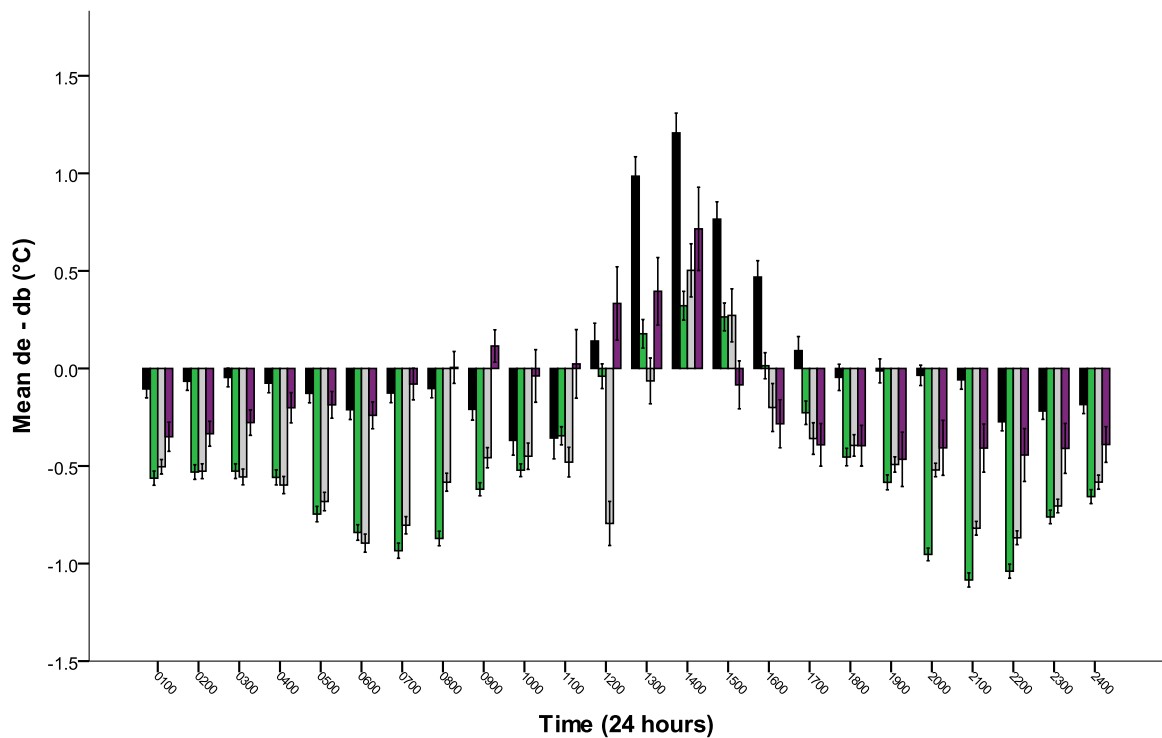
Figure 8. Mean d_b - d_e (°C) over 24 hours for all months sampled. Black bars = January, green = March, grey = October, purple = September.

Month had a significant effect on the effectiveness of thermoregulation in every case except during the day in year 2 (Table 2). As the data from year 2 only contained 2 months (October & January), this may explain the lack of a seasonal effect in this analysis. Males and females did not differ in their effectiveness of thermoregulation. Neither the effect of sex, nor the interaction between sex and month was significant during either day or night (Table 2).

Table 2: Summary results of the two-way ANOVAs for the effects of month and sex on effectiveness of thermoregulation (d_b - d_e) data for each individual.

Year	Predictor	F	df	P
1	**Day**			
	month x sex	2.070	2	0.133
	month	57.859	2	0.000
	sex	2.117	1	0.150
	Night			
	month x sex	1.099	2	0.338
	month	5.014	2	0.009
	sex	0.178	1	0.675
2	**Day**			
	month x sex	0.020	1	0.889
	month	0.658	1	0.422
	sex	2.669	1	0.110
	Night			
	month x sex	0.004	1	0.948
	month	9.721	2	0.003
	sex	0.031	1	0.862
3	**Day**			
	month x sex	0.119	3	0.949
	month	21.881	3	0.000
	sex	1.741	1	0.190
	Night			
	month x sex	0.159	3	0.924
	month	71.089	3	0.000
	sex	0.005	1	0.942

The three thermal exploitation indices were calculated for each individual each year. Over the three years T_e data were collected for every hour that tuatara T_b (n= 1539) were measured, and d_e was equal to zero in at least one area (shade or open) for 150 hours (8.4 % of the total time sampled), i.e. T_e was between 19.5 and 23.1°C in either the shade or open. Averaged across all individuals, the proportion of T_b within T_{set} (i.e., E_x) when it was possible was 29.6 %. The proportion of T_b above T_{set} was 7.9%, and the proportion below was 62.4%. The index of thermoregulation (E_x) reached its maximum in January (33.4%) and its lowest point in October (12.9%) (Fig. 9). January was also the month, in which the percentage of T_b values below T_{set} reached a minimum (57.7%), subsequently increasing to a maximum in October (81.6%). The percentage of T_b values above T_{set} was highest in January (8.9%) and lowest in March (1.9%), (Fig.

9). During the course of the day, T_{set} was only ever attainable between 0900 and 2000. E_x was at its peak at 1500 but outside the hours 1100 – 1900 during the day, mean T_b values were never within T_{set} range (Fig. 10). Mean T_b values were only ever over T_{set} during mid afternoon 1100 – 1800 and were at their maximum at 1400 (15.7%). The highest proportion (43 -100%) of T_b values fell below T_{set} right throughout the day.
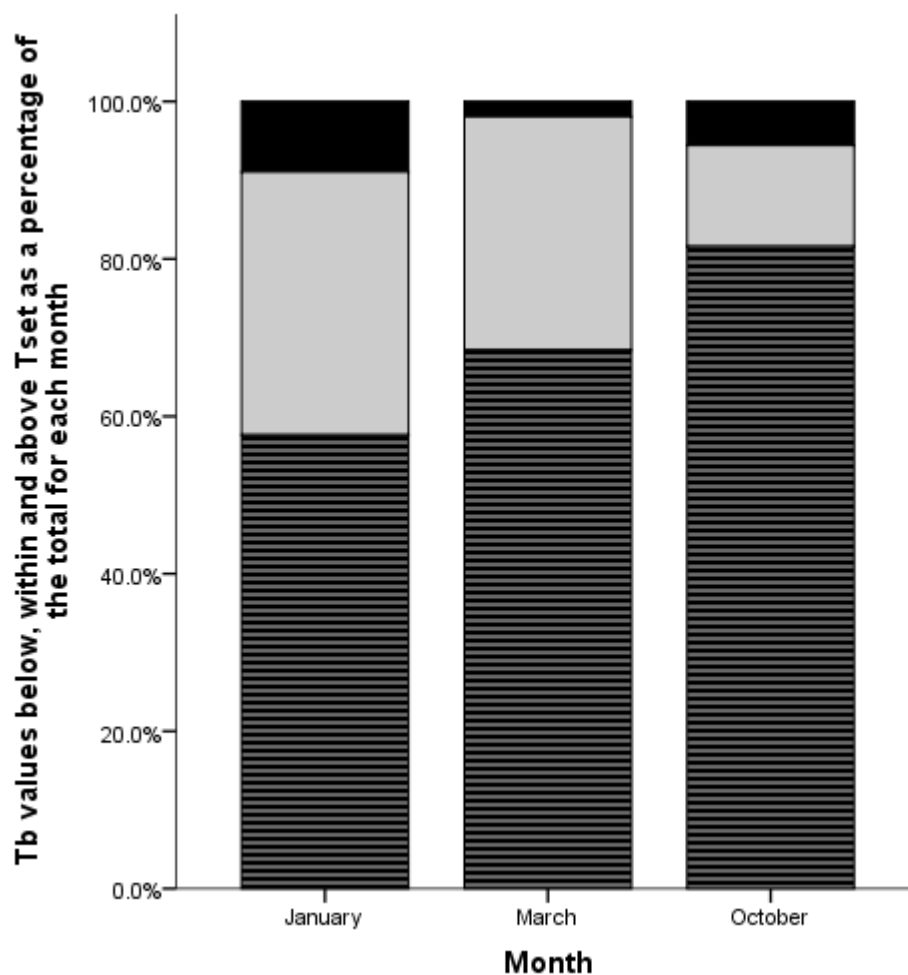
Figure 9. The percentage of tuatara body temperatures (T_b) that fell below (striped area), within (grey area) and above (black area) the preferred temperature range (T_{set}) across three months. The majority of T_b values are below T_{set} for all months.
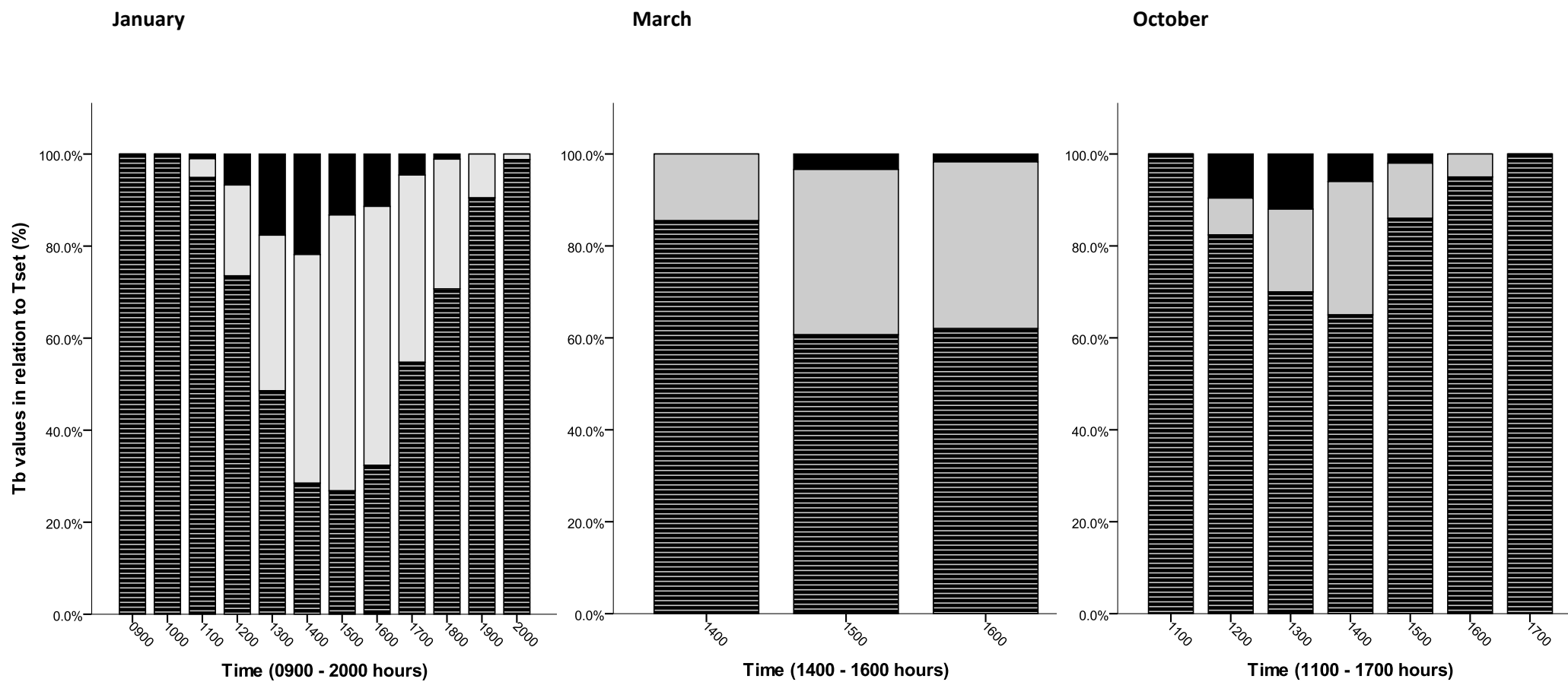
Figure 10. The percentage of tuatara body temperatures (T_b) that fell below (striped area), within (grey area) and above (black area) the preferred temperature range (T_{set}) at each hour across three months. X axis varies with month according to hours available for T_{set} to be achieved.

Males and females did not differ in their thermal exploitation indices in any month over the three years (Table 3). Day and night were not separated for this analysis as the data set only included values from 0900 to 2000 (T_e was never within T_{set} range between 2100 and 0800).

Table 3: Summary results of the one-way ANOVAs for the effects of sex on thermoregulation indices.

Period	Predictor	F	df	*P*
$T_b = T_{set}$ (E_x)				
Year 1 Jan	sex	0.179	1	0.676
Year 1 Mar	sex	3.325	1	0.079
Year 1 Oct	sex	1.967	1	0.174
Year 2 Jan	sex	0.277	1	0.603
Year 3 Jan	sex	1.767	1	0.196
Year 3 Mar	sex	0.709	1	0.408
$T_b > T_{set}$				
Year 1 Jan	sex	0.022	1	0.882
Year 1 Mar	sex	1.321	1	0.260
Year 1 Oct	sex	1.546	1	0.226
Year 2 Jan	sex	2.491	1	0.127
Year 3 Jan	sex	0.019	1	0.892
Year 3 Mar	sex	1.042	1	0.317
$T_b < T_{set}$				
Year 1 Jan	sex	0.052	1	0.822
Year 1 Mar	sex	3.505	1	0.071
Year 1 Oct	sex	2.212	1	0.151
Year 2 Jan	sex	2.008	1	0.162
Year 3 Jan	sex	1.101	1	0.304
Year 3 Mar	sex	0.177	1	0.677

2.4.4. Heating and cooling rates

Of the 25,760 T_b values, 69.2% (n = 17813) showed no change in temperature from one 15 minute record to the next, 18.2% of the total T_b values (n= 4694) had decreased from the last record and cooled between 0.5 – 8°C. The remainder of T_b values (12.6%, n = 3253) had increased since the last record and were warming up at rates of 0.5 – 12.5°C per 15 minute period. Most (89.6%) T_b changes were within 1°C. The largest increase in temperature for a 15 minute period was 12.5°C, giving a maximum heating rate of 0.8°C/min and the largest decrease was 8°C, that is, maximum decrease of 0.5°C/min.

There were no significant differences in cooling rates between small and large tuatara (Wald Chi-Square = 1.682, df = 1, *P* = 0.195); small and large animals cooled on average 0.7°C and 0.6°C over a 15 minute period, respectively. However, there were significant differences in heating rates (Wald Chi-Square = 11.068, df = 1, *P* = 0.001), with small animals heating at 0.4°C on average and large at 1.2°C over a 15 minute period.
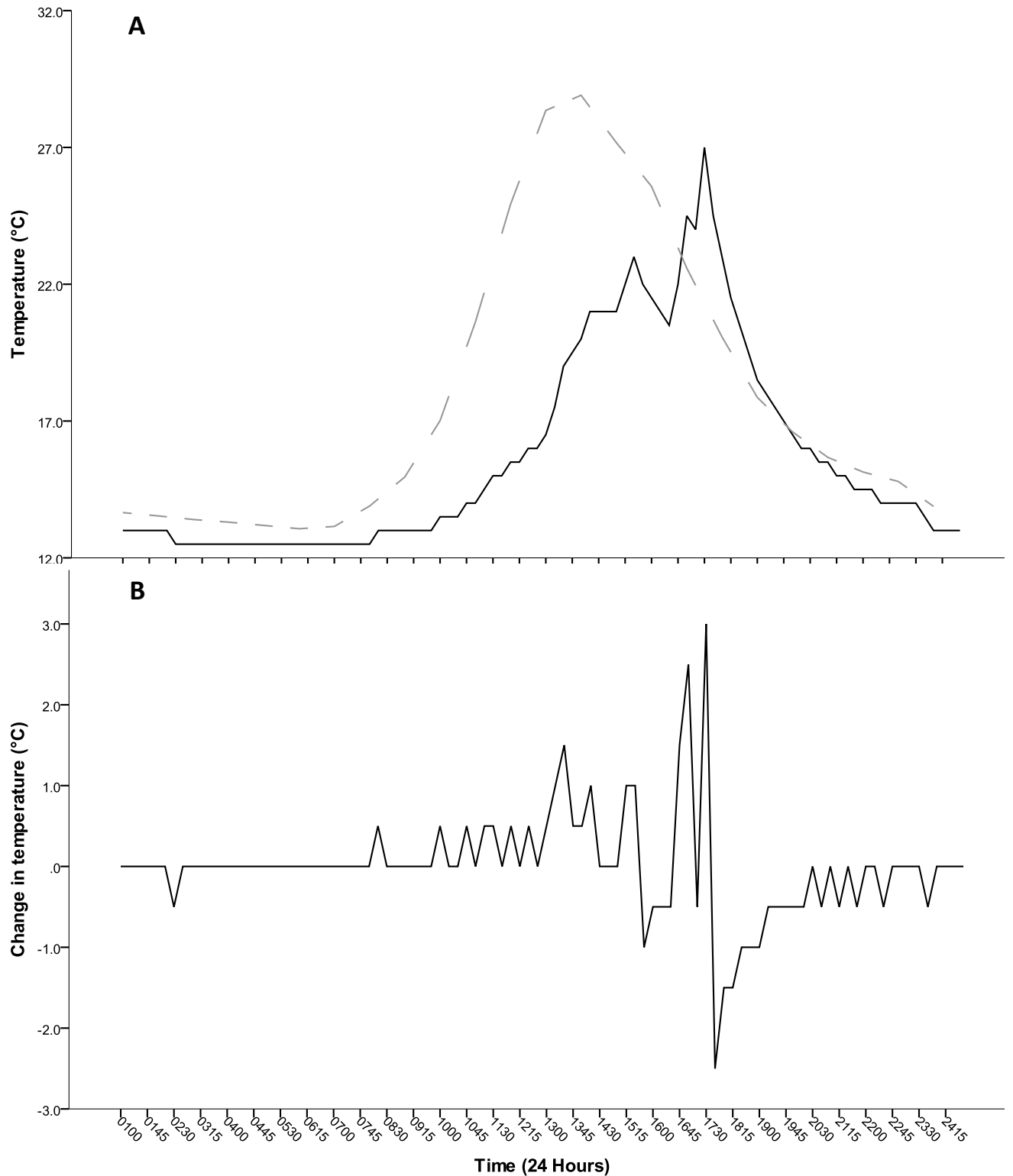
Figure 11. An example of a large (svl = 280mm, mass =700g) male tuatara T_b (black top line) with respect to hourly environmental temperature, T_e (grey dashed line) (A). Heating and cooling rates over a representative 24 hour period (January 2009) (B). Body temperature starts at 0100 hours at 13.0°C and end at 2445 at 13.0°C.

2.4.5 Morphology and body temperature

Snout-to-vent length ranged from 160 – 300mm (males: 160 - 300, females: 172 - 230), with a total mean for females of 197 ± 2mm, and for males 240 ± 3mm. Mass ranged from 150 – 770g (males; 150 - 770, females; 195 - 400), with a total mean for females of 269 ± 8g and males 503 ± 3g. Condition ranged from 0.99 – 1.20 (males; 0.99 - 1.20, females; 1.00 - 1.11), with a mean of 1.05 ± 0.00 for females and 1.13 ± 0.01 for males. There were significant differences between males and females for all measurements of body size; SVL (F_1= 120.294, $P < 0.001$), mass (F_1= 119.384, $P < 0.001$) and condition (F_1 = 107.036, $P < 0.001$), with the males on average larger than female tuatara.

There were no significant correlations for female tuatara between an individual's mean T_b and SVL, mean T_b and mass, or mean T_b and condition in any month sampled. However, in males, mean daytime T_b in January was correlated with condition (r_s = 0.261; P = 0.043; Fig. 12), males with higher condition indices having higher mean daytime T_bs. The same analyses were repeated but with mean monthly index d_e - d_b instead of T_b. There were no significant correlations for any of the interactions. The same analyses were again repeated with E_x index. There was a significant correlation between E_x and mass (r_s = 0.595, P = 0.05), and E_x and condition (r_s = 0.606, P = 0.05) for females in March.
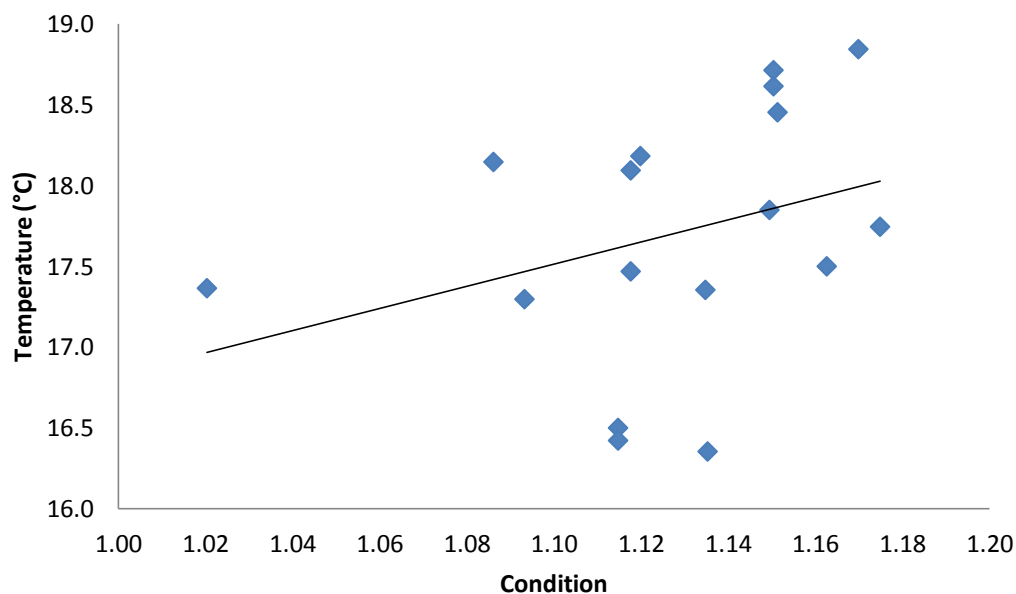
Figure 12. Mean T_b of males in January versus condition. Individuals with higher condition indices have higher mean daytime T_bs.

2.4.6 Burrow Use

The number of times that a tuatara was recorded at the entrance to its burrow provided additional information regarding its activity patterns. Tuatara could be found at their burrow entrance at any hour of the day. The lowest number of recordings was between the hours 2100 to 0100, when tuatara were often away from the burrow (confirmed with observations at 2200 and 2400), with another dip at 0800. The highest number of recordings was from 1600 - 1700 when tuatara are often sitting at the entrance to their burrows (Fig. 13).
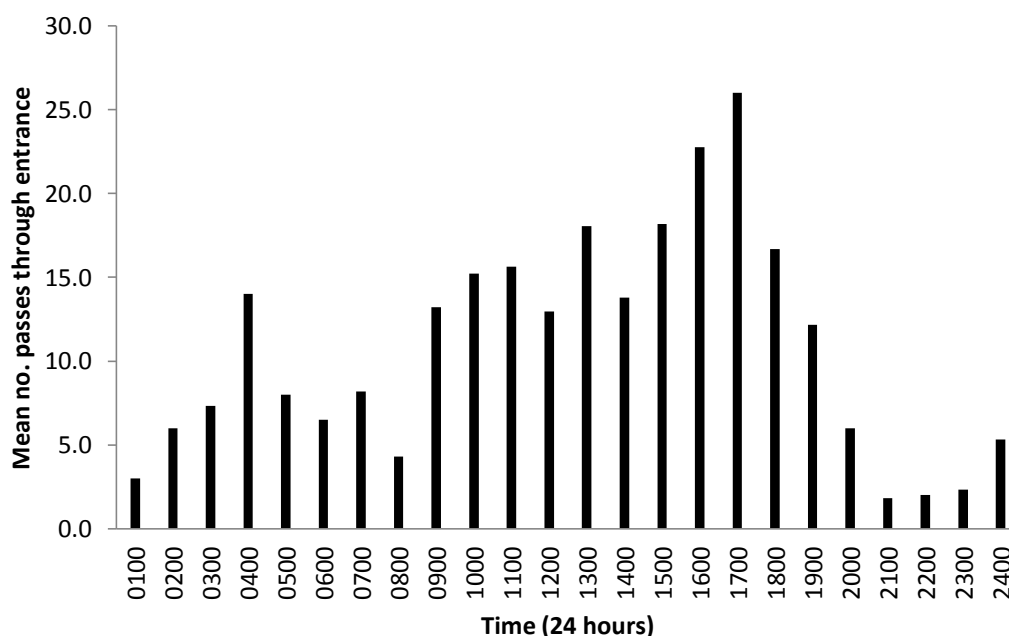
Figure 13. Mean number of times per hour a tuatara was recorded at the burrow entrance

At set points throughout the day and night, an individual was recorded as inside or outside its burrow. A model incorporating month and time significantly explained the differences between T_bs of individuals inside versus outside their burrows. (Wald Chi-Square = 60.770, df =14, $P <$ 0.001). The model's fit was not improved by adding in year (Wald Chi-Square = 2.591, df = 2, $P =$ 0.274).

At 1200, 1400 and 1600 the mean monthly T_b values were always warmer for those tuatara which were outside their burrows (2 - 3°C). At the start of the night, at 2200 and 2400, there was no obvious trend in mean T_b values for those tuatara that were inside their burrows versus those that were outside, despite the statistical difference for January and March. Early morning, at

0200, 0400, T_b values were higher for those inside the burrows versus outside but this was only significant for January and March (Table 4).

Table 4. Mean T_b ± 1 SE of tuatara inside burrows versus outside. A * represents significant differences in T_b between tuatara inside versus outside their burrows.

TIME (24 hr)	IN BURROW (mean *Tb*)	OUTSIDE (mean *Tb*)
September		
1400 *	12.3 ± 0.3	13.8 ± 0.3
1600 *	11.6 ± 0.2	11.8 ± 0.4
2200	11.0 ± 0.2	10.9 ± 0.4
2400	11.0 ± 0.2	10.7 ± 0.3
0200	10.4 ± 0.2	10.1 ± 0.2
October		
1200 *	12.6 ± 0.4	15.1 ± 0.4
1400 *	13.5 ± 0.3	16.5 ± 0.3
1600 *	13.4 ± 0.2	15.6 ± 0.2
2200	11.1 ± 0.1	11.1 ± 0.1
2400	11.0 ± 0.1	10.9 ± 0.1
0200	10.9 ± 0.1	10.8 ± 0.1
0400	10.7 ± 0.2	10.6 ± 0.4
January		
1200 *	16.2 ± 0.4	20.2 ± 0.4
1400 *	18.9 ± 0.3	21.3 ± 0.3
1600 *	18.5 ± 0.3	20.8 ± 0.2
2200 *	15.0 ± 0.1	15.3 ± 0.1
2400 *	14.8 ± 0.1	15.1 ± 0.1
0200 *	15.0 ± 0.1	15.4 ± 0.1
0400 *	13.3 ± 0.3	12.7 ± 0.3
March		
1400 *	15.1 ± 0.3	17.0 ± 0.2
1600 *	14.8 ± 0.2	17.2 ± 0.2
2200 *	13.0 ± 0.1	12.9 ± 0.1
2400 *	13.1 ± 0.1	13.2 ± 0.1
0200 *	13.2 ± 0.1	13.5 ± 0.2

2.4.7 Burrow Conditions (a)

Temperatures had a narrower range with greater depth (at 0.1m; 6.8 – 23.0°C, at 0.4m; 8.0 - 22.5°C). Even at 0.4m, temperatures in the open (13.9 ± 0.02°C) were warmer than in the shade (12.4 ± 0.01°C) (Fig. 14). In the coldest months, temperatures at 0.4m were warmer than at the surface and during the warmest months, temperatures were cooler at 0.4m than at the surface. July was the coldest month and February the warmest in terms of soil temperatures (Fig. 14). There was an obvious thermal diel trend with temperatures peaking from 1500 - 1700 and dipping from 0800 - 1000 (Fig. 14).

2.4.7 Burrow conditions (b)

In October, tuatara sharing a burrow with a bird (n = 24) had a higher mean T_b than those without a bird in their burrow (n = 33), (F_1=17.622, $P < 0.001$). This effect varied among years (F_2= 3.539, $P = 0.037$), in 2008 mean T_b for tuatara with a bird in their burrow was 12.8 ± 0.1°C (95% CI = 12.5 – 13.1°C) and T_b for those without a bird in their burrow was, 12.3 ± 0.1°C (95% CI = 12.1 – 12.6°C). In 2009, the mean T_bs for tuatara with and without a bird in their burrow were 11.5 ± 0.1°C (95% CI = 11.2 – 11.8°C) and 11.4 ± 0.1°C (95% CI = 11.2 – 11.6°C) respectively. And in 2010, mean T_bs were higher at 12.4 ± 0.1°C (95% CI = 12.0 – 12.8°C) for those with a bird in their burrow and 11.8 ± 0.1°C (95% CI = 11.5 – 12.0°C) for those without. The combined interaction of bird with sex and year (F_2 = 4.347, $P = 0.019$) was also significant, but the pattern was not consistent across years, with males having higher T_bs than females in the presence of a bird in 2008 and 2010 but not 2009. The interaction with sex alone was not significant (F_2 = 2.627, $P = 0.112$).

In January, there was no difference in mean T_b between tuatara with a bird in their burrow (n = 19) and those without (n = 43), (F_1 = 3.108, $P = 0.084$), and this did not change over the three years (F_2 = 0.001, $P = 0.999$) or when sex was included as an interaction with year (F_1 = 0.000, $P = 0.987$).

Humidity in burrows ranged from 64% relative humidity (RH) to 100% RH. Bird-occupied burrows had significantly higher levels of relative humidity than unoccupied burrows across all months sampled; October 2010 (F_1 = 14.660, $P < 0.001$), January 2010 (F_1= 18.991, $P < 0.001$) and January 2011 (F_1 = 2138.283, $P < 0.001$) (Fig. 15).
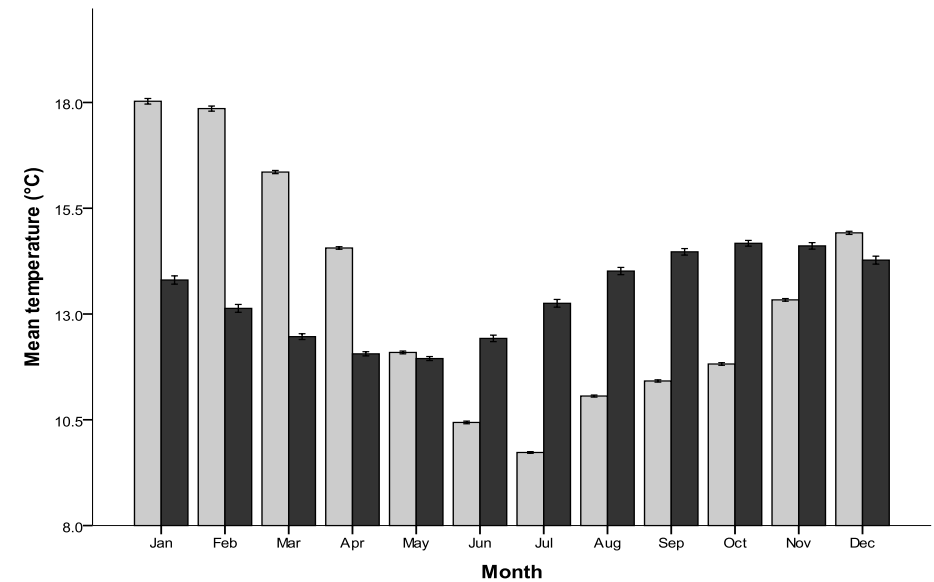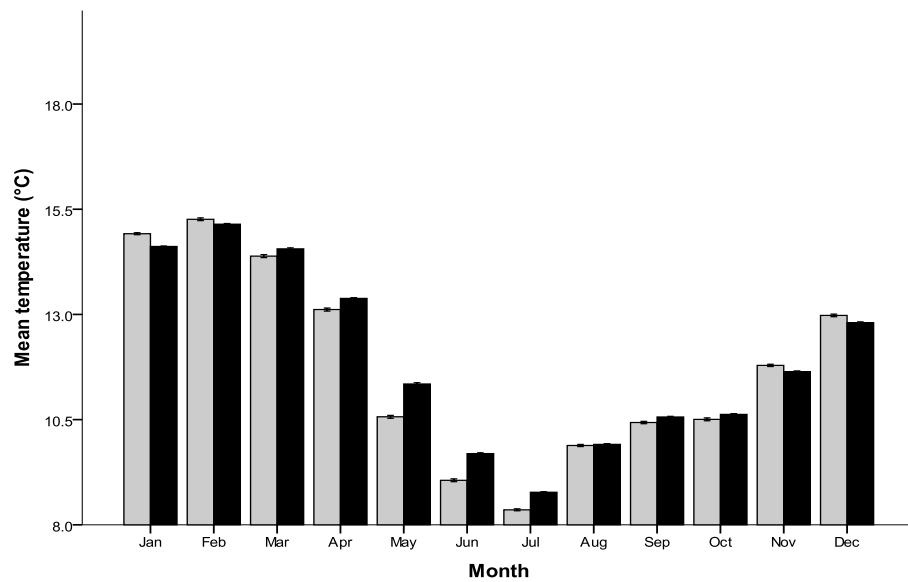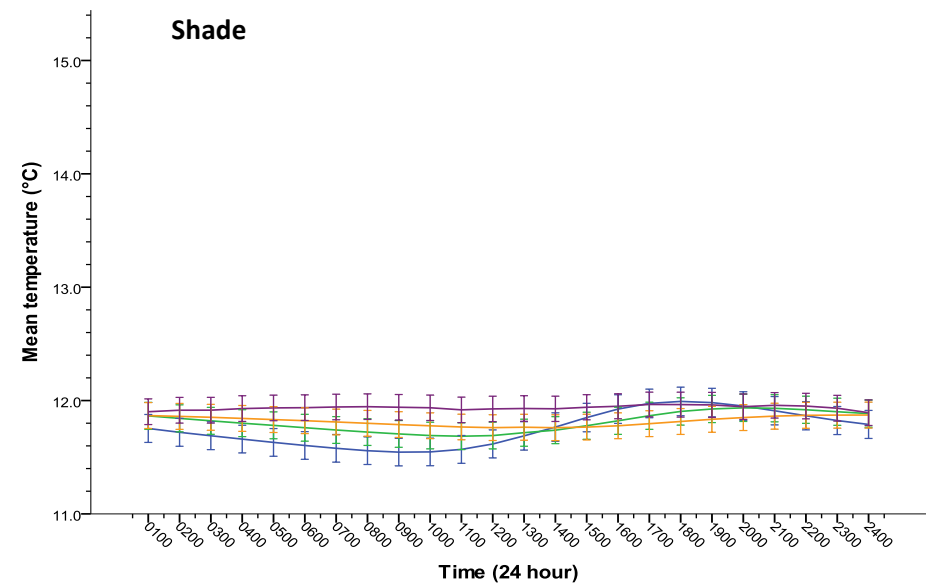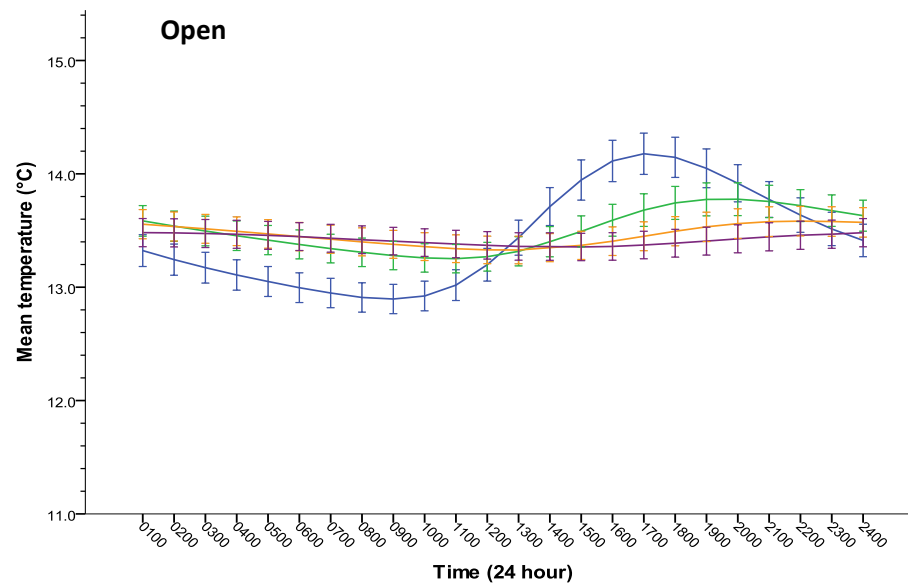
Figure 14. Top graphs display hourly ground temperatures at 100mm (blue), 200mm (green), 300mm (orange) and 400mm (purple) deep in the open and shade. Bottom graph displays monthly ground temperatures at 100mm (grey) and 400mm (black) soil depth in the open and shade.
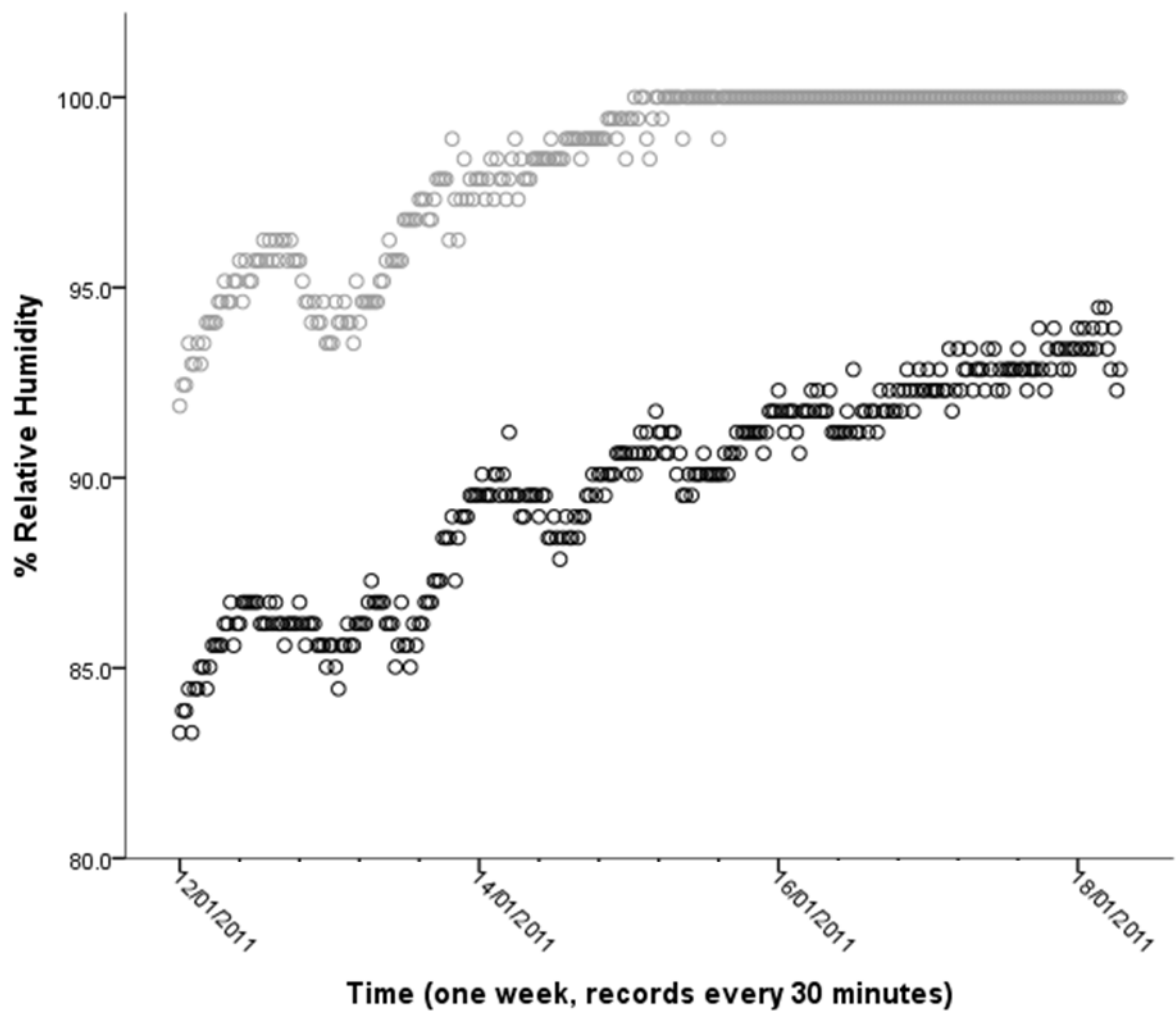
Figure 15. Relative humidity recorded every 30 minutes at a tuatara occupied burrow (black circles) and a bird occupied burrow (grey circles) over the course of a week in January 2011.

2.5 Discussion

Tuatara inhabit a thermally challenging environment. For example, on Stephens Island, home to the largest population of tuatara, tuatara body temperatures from spring 2008 to autumn 2011 reveal that on average, the environmental temperature is rarely warm enough to be within the preferred temperature range of tuatara. Thus, tuatara have to either survive under less than optimal temperatures and/or actively thermoregulate with behaviours such as seeking out sun spots to increase their body temperature. Maximum temperatures at ground level in the shade

were 17.3°C but in sun spots temperatures could reach 40°C. This difference in temperatures between shade and full sun meant that the thermal opportunities available to tuatara, at least during summer months in the middle of the day could be as great as 20°C. During the course of a day, temperatures in the forest can fluctuate through a range of more than 20°C so even within a 24 hour period, tuatara are confronted with temperatures both above and below their preferred body temperature.

The long-term body temperature measurements in this free ranging reptile revealed a distinct 24 hour daily cycle, with temperature peaks occurring between 1300 to 1500 hours. Overall, body temperatures of tuatara fluctuated through a range of 30°C from 4.5 to 34.5°C. As with all ectotherms, environmental temperatures have a huge influence on tuatara body temperatures and during colder days without sun, tuatara were unable to raise their body temperature much above ambient. Despite large variations among individual's T_b and environmental temperatures in the shade versus the sun, mean T_b was always within 1°C of mean T_e. In this population of tuatara, the mean d_b (5.7°C) was higher than the mean d_e (5.4°C) producing a negative value of d_e - d_b of -0.2°C. Values of d_e - d_b for lizards and snakes range from -0.33 to 8.4°C (summarized by Blouin-Demers & Nadeau, 2005). Compared with the documented range of d_e - d_b in other reptiles, the tuatara in this population can be classified as thermoconformers. E_x also indicated that tuatara are low thermoregulators. When operative environmental temperatures enabled preferred body temperature to be reached, the majority of tuatara (62.4%) did not exploit their thermal environment to reach preferred body temperature. About 29.6% of individuals were within their preferred body temperature range when climatic conditions permitted but there was high monthly variation in the percentage of tuatara which exploited the thermal options.

I am aware of only one previous study on captive individuals (Besson & Cree, 2010) that has applied the quantitative indices of thermoregulation developed by Hertz et al. (1993) to tuatara. According to Besson and Cree (2010), the index of thermoregulation, d_e – d_b, suggested that tuatara are active thermoregualtors regardless of habitat quality. However, a mean d_b of 5.6 ± 0.6°C in the present study was higher than those in the captive study (< 2.5 in both high and low quality habitats) and these results indicate that the majority of the population are only actively thermoregulating in January. They are also only actively thermoregulating between 1200 and 1500, and outside these times appear to neglect thermal opportunities, perhaps constrained more tightly by other factors. Despite the fact that preferred body temperature was attainable on occasion from 0900 through to 2000, it was only ever reached between 1100 and 1900. The

E_x index of 29.6% is consistent with that of Besson and Cree's (2010) study, where tuatara in medium and low quality habitats have an E_x index of 36% and 10.9% respectively. Therefore, although tuatara have the ability to adjust their thermoregulatory behaviour in response to thermal constraints there may be other factors that limit this behaviour in the wild.

When I explored body size as a possible predictor of body temperature, correlations were only significant for certain months. Mean individual daytime body temperature in January was significantly correlated with the condition of male tuatara, and male tuatara with a higher condition index also had a higher mean body temperature. This could also be due to behavioural differences, with larger males being more likely to maintain territories which allow for basking opportunities since they are better able to defend their territories (Moore *et al.*, 2008). However, I found that males and females did not differ in their mean T_b's or in their effectiveness of thermoregulation. It appears that size does not predict temperature at any time or cooling rates. However, larger animals did heat up faster and size may have some impact within each sex on overall thermoregulation. Female thermoregulation indices were correlated with both mass and condition in March. Females in higher condition, with more time spent in their preferred temperature range may be able to maintain higher levels of activity and may thus be more likely to mate at this time. Thermoregulation would facilitate a more active lifestyle so there would be good reason for breeding individuals or individuals intending to breed to thermoregulate and maintain a high T_b (Seebacher & Grigg, 1997). High levels of activity (Christian & Tracy, 1981) as well as testicular and ovarian development (Dawson, 1975) are facilitated by high temperatures. Warm temperatures have been shown to initiate ovarian growth and development in temperate zone lizards *Uta stansburiana* (Tinkle & Irwin, 1965) and *Sceloporus undulates* (Marion, 1970). The Carolina anole, *Anolis carolinensis* (Crews *et al.*, 1974, Licht, 1973) also requires high temperatures to induce ovarian growth. Additional body fat affects ovarian development in lizards (Hahn & Tinkle, 1965) and annual differences in nutritional levels affect reproductive output in *Urosaurus ornatus* (Ballinger, 1977). Hence, thermoregulation could increase breeding success, because more active individuals in a higher body condition may have an advantage during intraspecific struggles or in the case of females, more time in the preferred body temperature range may give them a head-start in egg production.

I found that heating and cooling in tuatara usually occurred in small incremental steps. Within a 15 minute period the vast majority of temperature changes were within 0.5 to 1.5°C. However changes of up to 12.5°C did occur. According to Barwick (1982), rapid increases in body temp of

6 - 9 °C occurred over the first 30 minutes of exposure each day when tuatara emerged from their burrows (approximately 0700 to 1000). This study found that rapid increases in temperature only occurred after midday and only a very gradual T_b increase occurred early morning, with the occasional initial decrease (0.5 - 1.0°C) suggesting that outside air temperatures are often still cooler than burrow temperatures before 1100 hours, even in the middle of summer. Because rates of heating and cooling decrease as size increases (Stevenson, 1985), large reptiles heat and cool more slowly than do smaller animals (Spotila et al., 1972, Spotila et al., 1973). However, I found that only the rate of heating differed between large and small tuatara, while cooling did not differ among individuals of different size classes. This may indicate that heating and cooling rates in tuatara may be due to behavioural effects more than physiological, for example they may be constrained by being unable to move too far from a burrow entrance in order to maintain possession of particular burrows or are prevented by conspecifics from basking in a particular sun patch, as has been described for crocodiles (Seebacher & Grigg, 1997). Crocodiles engaged in aggressive interactions often culminated in subordinate animals being chased from their basking sites.

Habitat selection is an important component of the thermal ecology of tuatara, especially as microhabitats can potentially vary considerably within an island ecosystem. Thermal constraints or opportunities may dictate retreat-site selection, for example, in garter snakes (*Thamnophis elegans*), the snakes select rocks of intermediate thickness to retreat under as these offer a variety of suitable thermoregulatory opportunities. Body temperature regulation is achieved by adjusting microhabitat selection and timing of activity (Patterson & Davies, 1982, Huey *et al.*, 1989, Krohmer, 1989). Tuatara are most often found basking at or very near to their burrow (pers. obs; Saint Girons et al., 1980), which means that their chosen burrow also affects basking opportunities. Depth of a burrow can have an impact on the temperatures maintained whilst not actively foraging. The deeper the burrow, the more stable the temperatures, at least up to 0.4m below the soil surface. Temperatures fluctuated less at 0.4m deep than at 0.1m deep, which resulted in warmer burrows than outside temperatures on cold days. Burrow location also determined burrow temperatures, with burrows in more open areas warmer even at 0.4m depth than those in more shaded areas.

No reptile is always active, and most spend very long periods in retreats (Huey, 1982). One way that tuatara can manage their body temperatures is by choosing when to remain in their burrows. If they stay in their burrows during the afternoon they miss out on basking

opportunities and are on average 2 - 3 °C cooler than those tuatara that are outside their burrows. The opposite is true in the early morning, (between 2am and 4am), when those tuatara that are outside their burrows are cooler than those inside. There was no difference in body temperatures between tuatara inside or outside their burrows at 10pm and at midnight. Therefore, to maintain higher body temperatures it would be thermally beneficial for tuatara to leave their burrows early in the evening and to complete their foraging expeditions before 2am and use their burrow as a refuge against the colder night time temperatures.

In addition to depth, one major way an individual burrow can differ thermally from another burrow is that it can be occupied by a pair of breeding seabirds such as fairy prions. The presence of a seabird within a burrow can alter the thermal and hydric environment of the burrow by increasing temperature and relative humidity levels. This is particularly pertinent for tuatara in October, when environmental temperatures are still low before summer (October temperatures are ~5°C cooler at 1m high in the shade at all hours compared to January). It has been previously noted that the presence of seabirds during this annual period provides tuatara with supplementary protein in the form of eggs and chicks, which particularly for breeding tuatara may have a direct survival value (pers. obs.,Walls, 1981). However, these results show for the first time that the presence of an endotherm within the burrow has direct transferrable thermal benefits to the tuatara. Further study into whether individuals occupying seabird burrows thermoregulate to different extents would further elucidate the importance of behaviour in thermophysiology. It may be that tuatara in humid, warmer burrows are more active and are more likely to bask during the hottest part of the day as they are less concerned with water conservation, and can therefore maintain body temperatures within their preferred body temperature range for longer periods (chapter 5).

Physiology is the ultimate controller of an organism's ability to achieve or maintain certain temperatures. However, within these physiological constraints it may actually be behaviour and habitat selection that has more ecological relevance. Research on captive tuatara has revealed much important information regarding tuatara thermobiology, but experimental evidence that a particular factor can influence behaviour may not mean that the factor influences behaviour in free-living animals, as its relevance may be context dependent. This study emphasises the importance of thermoregulatory data from wild, free ranging populations in forest habitats, especially when assessing both biotic and abiotic influences on the thermal environment. However, the current study was conducted in an extremely dense population, hence there may

be other over-riding factors to explain thermoregulatory behaviour, that do not apply in all natural sites. In summary, tuatara have the capacity for thermoregulation, but may be considered closer to thermoconformers for the majority of the time. It appears that tuatara maximally exploit their thermal environment only when thermal opportunities are most available. However, there is a great amount of variation among individuals in their effectiveness and amount of time spent thermoregulating. This variation may have less to do with an individuals' physiology/sex and more to do with behaviour and burrow use and conditions. This has implications for habitat conservation and potential translocations. Within the physiological constraints of tuatara, it may actually be behaviour within the context of the availability of suitable burrows, density and structure of populations, and the presence of seabirds, that has more ecological relevance for how a tuatara thermoregulates.

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CHAPTER THREE

Behavioural thermoregulation under hydric and digestive constraints in juvenile tuatara

3.1 Abstract

An important component of the behavioural repertoire of many terrestrial reptiles is burrow use. The availability and/or selection of suitable burrows within the environment may have consequences for fitness as retreat site selection can affect an animal's physiology and ecology. Tuatara, a medium sized reptile, use underground burrows as general shelter and are often found cohabiting with procellariiform seabirds. A number of microhabitat components were identified (structural, microclimatic, physiological) that might act as cues for burrow selection by tuatara. Captive tuatara were given a series of choices between burrows varying in temperature and humidity whilst in a fed or post-absorptive state, to test hypotheses that tuatara choose burrows based on temperature, humidity and digestive state. Juvenile tuatara exhibit a preference for warm temperatures regardless of digestive state, humidity or time of the day. However, there was a clear diel trend in thermoregulatory behaviour with tuatara selecting higher temperatures during the day. Tuatara were outside their burrows and moved about the gradient more often during the night. Under the dry treatment, tuatara selected higher temperatures on the gradient. However, tuatara were outside their burrows in greater numbers under the wet treatment compared to the dry. Digestive state had no discernable effect on either temperatures selected, or burrow use under captive conditions. This study provides experimental evidence that reptiles are capable of adjusting their habitat selection behaviour in response to different humidity constraints.

3.2 Introduction

Habitat selection by animals is dependent on various constraints such as the physical structure of the environment, the physiology of the animal, food availability, and protection from predators (Ward & Lubin, 1993, Reaney & Whiting, 2003). Physiological consequences of habitat

selection are ecologically important (Huey, 1991), and within any given habitat, the presence of suitable retreats for a particular species has consequences for fitness. Retreat site selection may have a profound impact on an animal's physiology and ecology (Huey, 1991). For example, naked mole rats (*Heterocephalus glaber*) which live permanently in the stable temperatures of their burrow systems have almost completely lost their capacity for physiological thermoregulation (McNab, 1966). However, animals use habitats in complex ways, and the reasons why particular habitat features are essential for particular taxa remain unclear in most cases (Simberloff, 1987, Webb & Shine, 1998).

Animals can use habitats in a multitude of ways, e.g. feeding and reproductive events, but those species that remain sequestered within retreat sites for periods of time such as burrowing animals, present an opportunity to quantify the attributes of habitat selection. Recent studies investigating the factors that govern retreat site selection have revealed a strong consensus that animals are capable of making subtle choices among an array of attributes of alternative potential retreat-sites (Huey *et al.*, 1989, Downes & Shine, 1998, Kearney, 2002, Shah *et al.*, 2004). Detailed studies on microhabitat and microclimate are important to understand the biology and evolution of retreat site use, e.g. burrows, at different organisational levels and the adaptive significance of specific morphological, physiological, behavioural and ecological traits (Burda et al., 2007). Furthermore, this type of information is needed to simulate (semi-) natural conditions in diverse laboratory studies. Temperature (Webb & Shine, 1998), humidity (Schlesinger & Shine, 1994) and digestive state (Blouin-Demers & Weatherhead, 2001a) are three predictors that can influence retreat site selection.

The suitability of retreat-sites for ectotherms in particular, is strongly dependent on temperature (Huey, 1982), as temperature has a profound effect on the performance of organisms such as plants, invertebrates, and lower vertebrates (Hochachka & Somero, 1984, Cossins & Bowler, 1987, Angilletta Jr *et al.*, 2002). These organisms therefore need an effective means of coping with, or evaluating spatial and temporal heterogeneity in the thermal environment, and as a consequence, the availability of thermally suitable retreat-sites may determine patterns of habitat use by many ectotherms (Huey, 1991). A burrow can differ from another burrow because of a combination of the following variables: burrow depth, burrow length, position in relation to shade/sun, the nearby presence of potential mates and the presence of either competitors or predators. Knowledge of the criteria used for choice of burrows may elucidate the manner by which animals maintain their associations with particular microhabitats in the field.

One factor that is an important condition in the life of terrestrial vertebrates is relative humidity of the atmosphere, because it plays a major part in determining the rate at which animals lose water. A clean distinction between the effects of relative humidity and temperature is rarely possible, as a rise in temperature leads to an increased rate of evaporation and an increase in the amount of water that can be held in the atmosphere, i.e. an increase in temperature can lead to an increase in humidity. A relative humidity that is tolerable to an organism at a low temperature may therefore be unacceptable at a higher temperature (Begon et al., 1996). Moreover, both relative humidity and temperature may themselves interact with wind speed: the rapid movement of air across an evaporative surface maintains the moisture gradient, increases the rate of evaporation, and the latent heat of evaporation lowers temperature (Begon et al., 1996). For example, the body temperature of a terrestrial reptile may be lowered by the loss of heat due to evaporation of body fluids (Bogert, 1949). Thus, humidity can be limiting in terms of behaviour, as is evident in insects such as the fruit fly, *Drosophilia subobscura*. Their movements are limited to short periods at pre-dawn and post-dusk, during the lowest daylight temperatures but highest relative humidity, as they would rapidly dehydrate if they flew in the middle of the day (Inglesfield & Begon, 1981, Begon *et al.*, 1996). If retreat sites such as burrows, differ in their capacity for providing a thermal and hydric refuge, daily and seasonal movements among burrows may be influenced by variation in burrow microclimate (Bulova, 2002). In bats (*Chalinolobus tuberculatus*), roost cavities with high humidities are preferentially selected (Sedgeley, 2001), as water and energy are factors that contribute to the timing and success of their reproduction (Kurta et al., 1990).

The digestive state of an animal is another factor that can influence retreat site selection. Lizards (*Anolis carolinensis*) selected lower temperatures on a thermal gradient after food deprivation (Brown & Griffin, 2005), and snakes, e.g. *Elaphe obsoleta* selected higher temperatures on a thermal gradient (Blouin-Demers & Weatherhead, 2001b) and in the field, *Crotalus sp.,* (Beck, 1996) after feeding. The primary effect of increasing body temperature during digestion is a marked reduction of the time required for digestion rather than an energetic saving or increased efficiency of digestion (Wang et al., 2002). During environmental conditions where suitable prey items are readily available, a faster rate of digestion with increased body temperatures may enable higher consumption and growth rates. Many ectothermic vertebrates achieve this through behavioural thermoregulation, selecting warmer environmental, and consequently body temperatures, after feeding to increase the rate of processing, a strategy termed post-prandial thermophily (Kitchell, 1969, Gatten Jr, 1974, Lang,

1979, Slip & Shine, 1988). Nevertheless, this strategy may be less prevalent in the field than previously thought, as most studies present only gradient data, and for most lizards, body temperatures are primarily a consequence of mobility, which in turn is a consequence of ingestive state (Wall & Shine, 2008). The presence of food in the gut reduces locomotor speed and/or endurance in some lizards (Huey et al., 1984) and snakes (Garland & Arnold, 1983, Ford & Shuttlesworth, 1986, Shine & Shetty, 2001).

In this study, I examined the factors influencing burrow use by the tuatara, *Sphenodon punctatus*. The tuatara is a medium-sized, long lived reptile (*c*. 100 years; Gaze, 2001) that is endemic to New Zealand, and is the sole, extant representative of the once diverse, ancient reptilian order Rhynchocephalia (*sensu* Gauthier et al., 1988). Although once widespread throughout the main and outlying islands (Holdaway & Worthy, 1997), natural populations are now restricted to small offshore islands, primarily due to predation from introduced mammalian predators. Tuatara are a diurno-nocturnal, burrowing species. They forage mainly at night when air temperatures are typically low (Walls, 1983) and are active at temperatures as low as 5.2 to 11.2°C (Thompson & Daugherty, 1998), but they also bask and feed during the day, attaining body temperatures up to 30°C when the opportunities arise (Walls, 1981, Barwick, 1982). Occupied burrows can be shared occasionally with other individuals and nesting seabirds, and underground burrow systems are dynamic and can be extensive (Newman, 1987). These underground burrows are used as general shelter and are also often the site of basking and social interactions among individuals, including territorial behaviour and aggression. Tuatara can live in very dense populations of up to ~2700 individuals/ha (Moore *et al.*, 2009), therefore some individuals are likely to be living in less than optimal conditions, as larger males may force less dominant individuals into unfavourable microhabitats (Langkilde & Shine, 2004, Moore *et al.*, 2009). Lower quality burrows with microclimates that are suboptimal for preferred body temperatures could potentially be used by non-breeding individuals, which may have differing thermoregulatory requirements. The relatively simple spatial structure of tuatara populations is highly stable over years, possibly decades, and they can maintain particular burrows for long periods of time (Moore *et al.*, 2009), despite the potential availability of many other burrows. For example, on Stephens Island (also known by its Maori name *Takapourewa*), there are many more burrows than there are tuatara, as most burrows are excavated by fairy prions (*Pachyptila turtur*), and there are greater numbers of seabirds than tuatara (approximately 1,000,000: 40,000).

Throughout most of their natural distribution, tuatara coexist often in the same burrows as procellariiform seabirds. This association provides another dimension to the microhabitat of the burrow, as the presence of a bird within a particular burrow would impact upon the suitability of that burrow for habitation by a tuatara. Burrows containing birds are occupied and may therefore be undesirable to a solitary tuatara, but the microclimate within that burrow is also altered as a result of the seabird occupation. The presence of a seabird means that the air in the burrow's enclosed space becomes more humid and warmer than unoccupied burrows (Towns, 1992). This unusual cohabitation provided the impetus to test whether humidity plays a role in burrow selection by reptiles in a temperate environment.

Field observations suggest that not all burrows are suitable for use by a given tuatara at a given time. On the basis of these observations and published literature, a number of microhabitat components were identified (structural and microclimatic), as well as a physiological element which may act as cues for habitat selection by tuatara. The experiments were largely restricted to thermal biology in habitat selection as temperature is a key environmental variable, and one that is physiologically significant as well as easily measured and manipulated (Huey, 1991). Captive tuatara were given a series of choices between burrows varying in these respects, to test hypotheses that tuatara choose burrows based on temperature, humidity and digestive state. It has been established that in a laboratory setting, tuatara are active thermoregulators by using basking opportunities (Besson & Cree, 2010b) but the aim of this study was to investigate whether tuatara also actively thermoregulate by choosing burrows based on temperature. I wanted to answer the following: does digestive state affect retreat choice, for example, when food is more plentiful, is temperature a greater factor in burrow choice? And lastly, when burrows and ambient air are more humid, does temperature selected and burrow use change, i.e. are tuatara more active under humid conditions?

3.3 Methods

3.3.1 Study organisms and maintenance

One-year-old juvenile tuatara (n =24) of unknown sex, with a mass between 17.14g to 39.87g were incubated and raised from eggs originating from Stephens Island (Cook Strait, New Zealand) (e.g.; Nelson et al., 2004). They were housed in a laboratory at Victoria University of Wellington under the following conditions. Six 600 × 700 × 350mm metal containers containing substrate of

a mix of horticultural sand, bark mulch and top soil with leaf litter were used to house groups of four to six individuals. A photoperiod of 12:12 LD (07:00-19:00) was provided by full spectrum lights (D3 reptile tube, Arcadia) placed 750 mm above the enclosures. Fresh food (invertebrates: crickets, mealworms and flies) was released into the enclosures once a week. Food was dusted weekly with calcium and vitamin powder. All 24 individuals were healthy and regularly took food. Water was provided *ad libitum.*

3.3.2 Experimental procedure

Laboratory studies allow the simplification of an ectotherm's environment, enabling the influences of temperature and/or humidity on burrow selection to be teased apart under controlled conditions, something that is not easily achievable in the field. As an animal's thermoregulatory behaviour may be strongly influenced by the particular design of a thermal gradient (Wall & Shine, 2008), every effort was made to conduct this experiment in the same housing conditions within which the tuatara were acclimatised.

Before commencing the experiment, a cloacal thermocouple (a polyethylene coated 30 gauge copper-constantan wire attached to a thermometer (Fluke® 51; precision 0.05% ± 0.3°C)) was inserted ~10mm into the cloaca of three tuatara to determine whether tuatara internal body temperature corresponded to external body temperature taken with an infra-red thermometer (IRT: Raytek, Raynger®model ST80 ProPlus™, Santa Cruz, California; precision 0.1°C, accuracy ± 2°C between -18 and 23°C and ± 1°C above 23°C for surfaces with an emissivity of 0.95). We assumed that the skin of tuatara had a similar emissivity to 0.95, which appears reasonable as most biological materials have an emissivity in the medium to long infrared of between 0.90 and 0.99 (Willmer et al., 2005). The tip of the temperature probe was coated in araldite glue (Araldite® Adhesives) to provide a small, smooth bulb, and the thermocouple was calibrated to 0°C using an ice bath. The IRT was orientated in line with the tuatara's body axis to eliminate the effect of background temperature (Hare et al., 2007) and the target spot size was 19mm at a distance of 300mm. Temperatures taken with the infra-red thermometer were always within 0.05°C of temperatures measured with the internal thermocouple. This result was consistent with research on amphibians (Rowley & Alford, 2007) and both juvenile tuatara and small lizards (Hare et al., 2007). For example, in a previous study with tuatara, 95% of paired temperature values using an IRT differed by no more than 1°C (Hare et al., 2007). Thus skin temperature was assumed to represent core body temperature.

Twelve thermal gradients were constructed using metal containers identical to normal housing conditions for substrate and photoperiod. One end of the thermal gradient was heated from below by Nu-Klear (Nu-Klear©, Auckland, New Zealand) heat pads (435 × 350mm) while the opposite end was cooled using ice packs which were replaced as needed (approximately every 3-4 hrs). This provided a range of temperatures over a length of 700mm, from 8.5 to 30.5° C (± 1.0°C) which is within the range of minimum and maximum recorded body temperatures of tuatara on Stephens Island (4.5 – 34.5 °C I. chapter 2). Four burrows (cardboard tunnels) with a diameter of 50mm were placed at set intervals along the gradient and on top of the substrate, with air temperatures of 10°C, 16°C, 21°C and 27°C (± 1.5°C) respectively. Temperatures along the gradients were spot-checked throughout the experiment with an infra-red thermometer (IRT). A water container was placed at the entrance to all four burrows to ensure access to water was never a factor in choice of burrow. Humidity was measured with dataloggers (Hobo Onset, accuracy: RH: ± 3.5% from 25% to 85% over the range of 15° to 45°C) placed in the centre of the first and last container.

Figure 1. On the left, experimental set-up with 2 rows of 6 metal housing containers and on the right, the inside of a container: substrate, 4 cardboard "burrows" and 4 dishes of water.

Individuals were placed in the centre of each thermal gradient, facing either the hot or cold end (50% each way, random placement), 24 hours before the first observation occurred, to minimize the effects of stress from handling on observations, and to allow exploration of the new environment. All twenty-four animals were tested under "Fed", "Unfed", "Dry" and "Humid" treatments with twelve animals tested at one time. The "Fed" treatment comprised of animals fed immediately prior to the experiment while the "Unfed" treatment was made up of animals fasted for six days prior to the study to ensure they were in a post-absorptive state. The "Dry" treatment was under normal conditions (35.1 – 51.7% RH). Each enclosure including burrows was soaked and misted regularly to maintain a relative humidity of 55.7 – 70.8% RH for the "Humid" treatment. The experiments were completed over the course of four weeks; in week one, 12 animals were tested with six "Fed" and six "Unfed". They were observed in a dry treatment for 24 hours and then in a wet treatment for 24 hours. After 72 hours tuatara were returned to their original housing conditions. In week two, 12 new animals were tested. In weeks three and four, the animals from weeks one and two were tested again but "Fed" and "Unfed" treatments were reversed to ensure that all individuals experienced all treatments.

The thermal gradient was divided into four temperature bands: area 1, the coldest end (8.5-12°C); area 2 (12-19°C); area 3 (19-26°C); and area 4, the warmest end (26-30.5°C). After the initial 24 hours, observations were taken every hour with the help of a small handheld mirror, diameter of 50mm (tuatara were difficult to spot if they were located in the centre of a burrow). Observations consisted of recording the area of gradient in which the tuatara was located, whether it was inside, outside or on top of a burrow, and body temperature (if outside burrow) with the infra-red thermometer.

3.3.3 Statistical Analysis

Data were not normally distributed and there were missing variables (when tuatara were inside burrows, temperatures could not be taken and no substitute values were used). Generalized Estimating Equations (repeated measures generalized linear mixed models) were used to test for differences in body temperature, area selected on gradient, and time spent in burrows as these models do not make any distributional assumptions (Zuur et al., 2009). The predictor variables were digestive state, humidity, and time (day: 0700 - 1900, versus night: 2000 - 0600), and data were repeated across individuals, treatments and time. For each model's estimated slope parameter (β), the precision of β was assessed, based on the extent to which the 95% confidence interval (95% CI) for each β overlapped zero, to better discuss the significance of

each factor effect on the response (Graybill & Iyer, 1994). Data are presented as means ± 1 SE without transformation. All analyses were conducted using the statistical software SPSS, version 18.0 (SPSS Inc.) and P values ≤ 0.05 were considered significant in all tests.

3.4 Results

The order in which each tuatara was tested (trial 1, 2, 3 or 4) had no significant effect on temperature selected (Wald Chi-Square = 6.729, d.f. = 3, P = 0.081), area selected (Wald Chi-Square = 4.202, d.f. = 3, P = 0.240), or burrow use (Wald Chi-Square = 2.213, d.f. = 3, P = 0.529), therefore, for all subsequent analyses, data were pooled from all four trials.

3.4.1 Temperatures selected

Body temperatures of juvenile tuatara on the thermal gradient ranged from 9.6 to 27.1°C (n = 1081 measurements). The mean temperature selected was 19.6 ± 0.1°C (IQR: 17.8 - 21.8°C). The effects of both time (Wald Chi-Square = 16.789, d.f. = 1, P < 0.001) and humidity (Wald Chi-Square = 17.460, d.f. = 1, P < 0.001) had significant influences on the body temperature of tuatara, but digestive state (Wald Chi-Square = 1.041, d.f. = 1, P = 0.308) did not alter temperature selected, and none of the interactions were significant.

Mean body temperatures during the day were 20.3 ± 0.1°C, (IQR: 18.4 - 22.4°C), and were significantly higher than during the night (Wald Chi-Square = 16.789, d.f. = 1, P < 0.001). Night-time body temperatures had a mean of 19.3 ± 0.2°C, (IQR: 17.4 - 21.4°C) (Fig. 1). During the day 59.4% of recorded tuatara were in area 4 (warmest end) and during the night 49.2% were in area 4.

Body temperatures in the dry treatment had a mean of 20.3 ± 0.1°C, (IQR: 18.4 - 22.4°C), and were significantly higher than in the wet treatment (Wald Chi-Square = 17.460, d.f. = 1, P < 0.001), which had a mean of 19.1 ± 0.1°C, (IQR: 17.2 - 21.2°C). During the dry treatment, 59.1% of all recordings were in area 4 (warmest area), with a lower percentage, (49.5%) in this area during the wet treatment (Fig. 2).

Digestive state did not significantly influence body temperature (Wald Chi-Square = 1.041, d.f. = 1, P = 0.308). Tuatara fed prior to the experiment had a mean body temperature of 19.6 ± 0.2°C, while those in post-absorptive state had a mean body temperature of 20.0 ± 0.3°C.
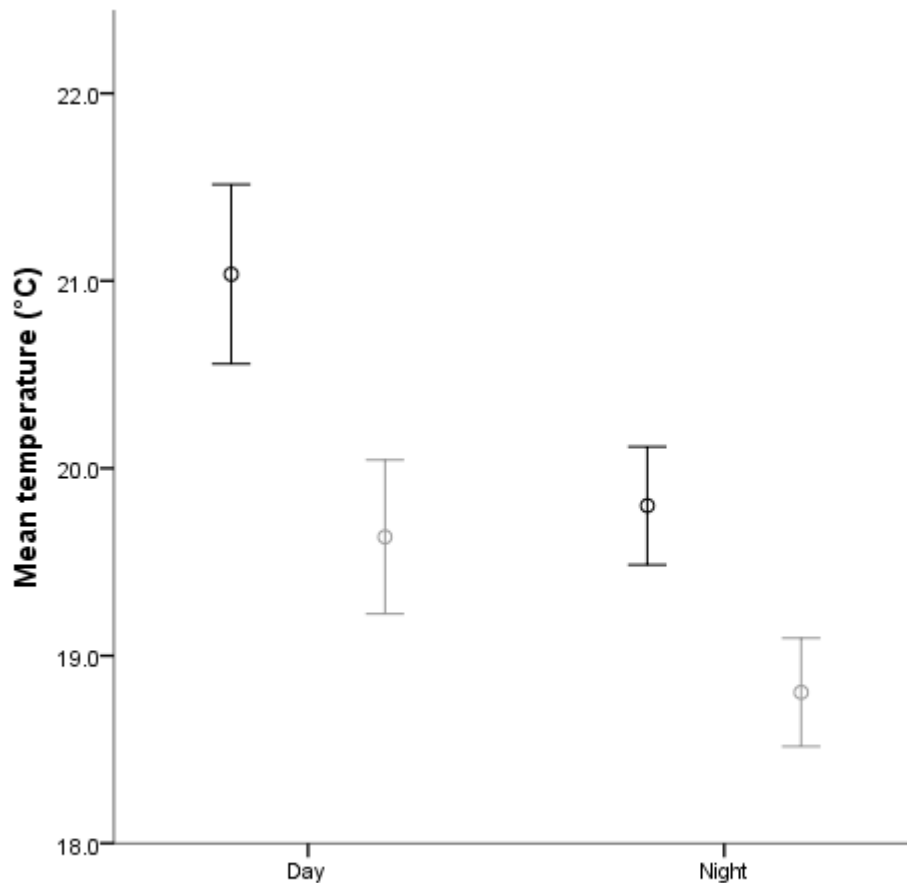
Figure 1. Mean selected body temperatures and 95% confidence intervals of tuatara during night (2000 - 0600) and day (0700 - 1900), and under dry (black) and wet (grey) treatments. Body temperatures were significantly higher during the day and under the dry treatment.
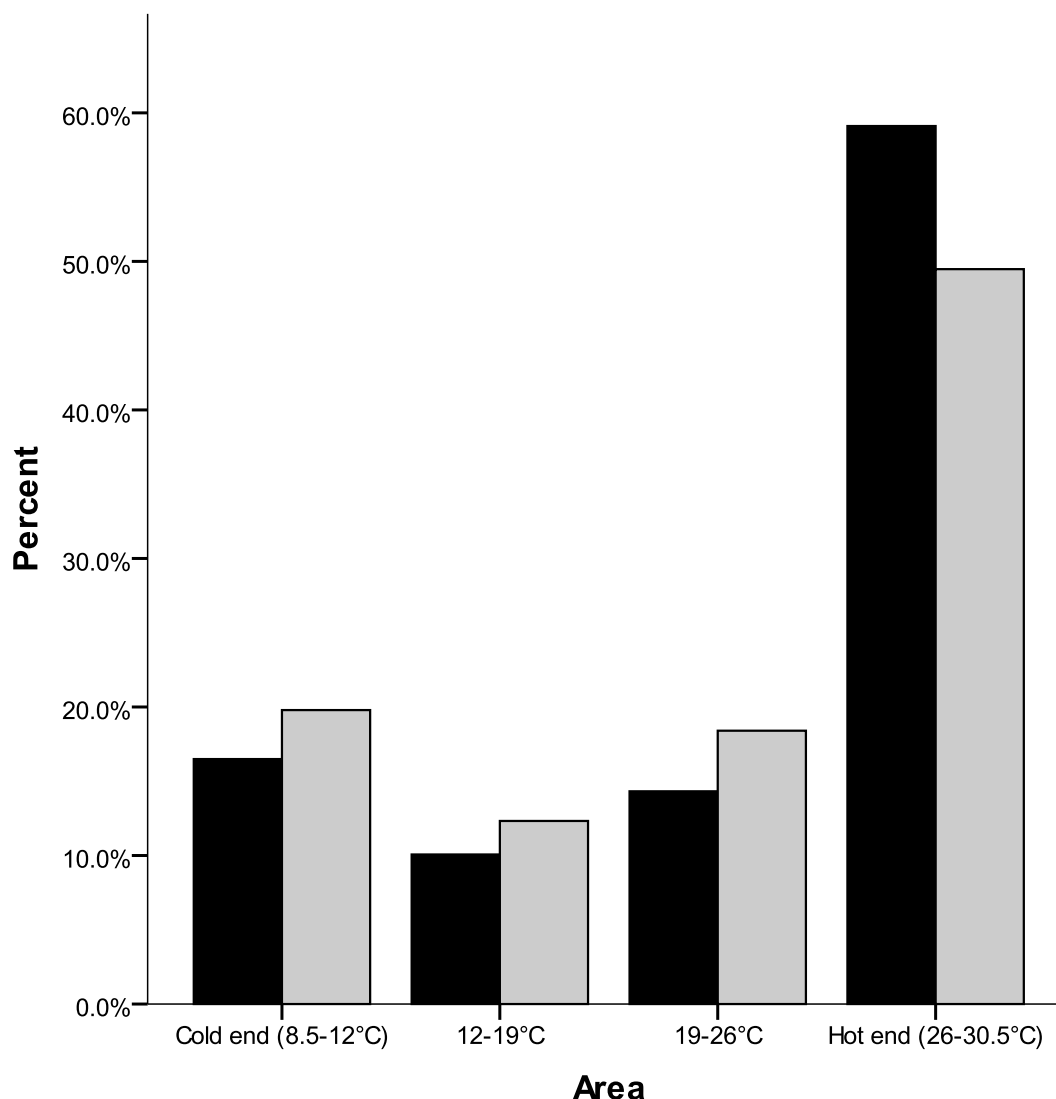
Figure 2. Percentage time spent in each area under dry (black bars) and wet (grey bars) treatments. Tuatara spent most of the time at the hot end of the gradient. Tuatara spent greater amounts of time in areas 1, 2 and 3 under the wet treatment but this pattern was reversed in area 4.

3.4.2 Burrow use

Overall, tuatara were recorded inside their burrows 42.6% of the time (n = 981 observations). Of the tuatara that remained within their burrow for longer than one hour (for at least two consecutive observations), 78% (n = 637) were in the warmest area, 11.5% (n = 93) were in the coldest area, and the remainder were in areas 2 and 3. Humidity and time had significant effects on how a tuatara used a burrow ($\beta_{threshold(out.burrow)}$ = 3.457; 95% *CI* = 0.227 − 3.012, Wald Chi-Square = 231.129, *P* < 0.001). Significantly more tuatara were recorded outside their burrows in humid conditions and more inside their burrow under the dry treatment (Wald Chi-Square =

11.904, d.f. = 1, *P* = 0.001). In the wet treatment, 54.6% of tuatara were outside their burrows (3.8% on top) and in the dry treatment, 44.2% were outside with 4.4% on top (Fig. 3). Significantly fewer (Wald Chi-Square = 25.858, d.f. = 1, *P* < 0.001) tuatara were recorded outside their burrows during the day (31.1% with 3.1% on top of their burrow) compared to during the night, (62.3% with 5.1% on top). Digestive state had no influence on burrow use (Wald Chi-Square = 0.146, d.f. = 1, *P* = 0.702). Those in an unfed state were outside 47.9% (4.3% on top) and inside 52.1% of the time. In a fed state, 54.5 % of tuatara were outside their burrows (4% on top) and 45.5 % were inside. None of the interactions were significant.
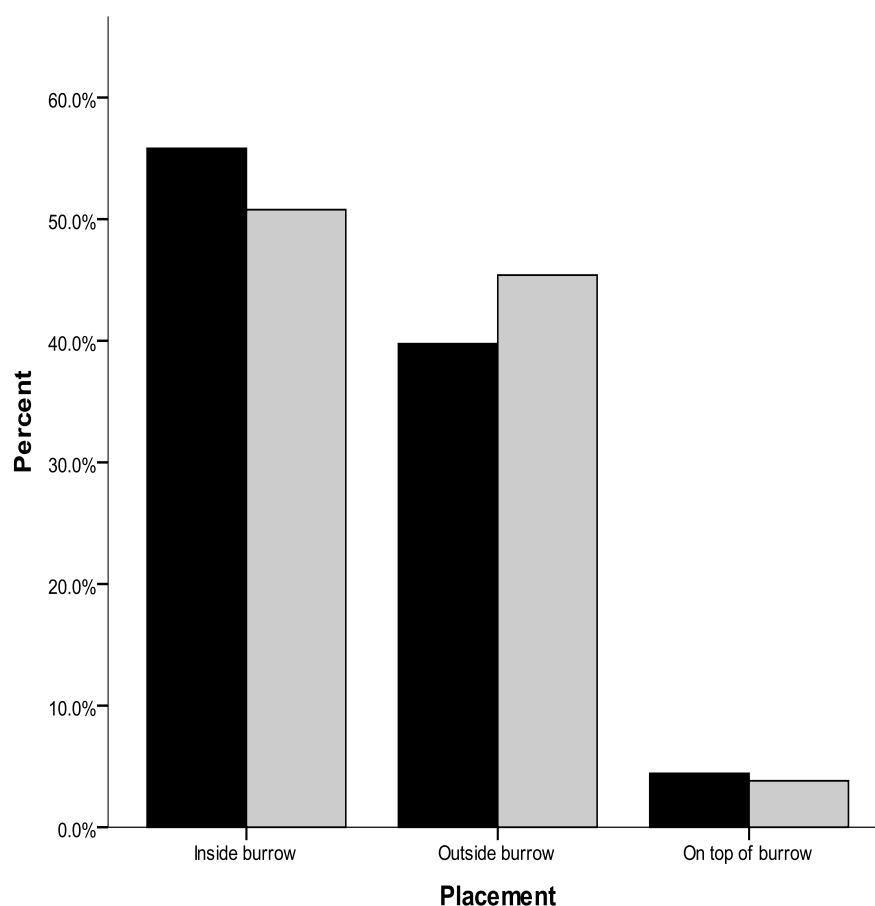
Figure 3. Burrow use of tuatara under dry (black) and wet (grey) treatments. Significantly more tuatara were recorded outside burrows under the wet treatment and more inside during the dry treatment.

3.4.3 Movement on gradient

In 52.1% of the observations, tuatara had not moved out of the area they had been in the hour previously. In 20.3% of cases they had moved to the adjacent area, in 13.9% of cases they had

moved two areas and in 13.6% of cases they had moved from one extreme to the other, i.e., the warmest end to the coldest end, or vice versa. The GEE model investigating movement on the gradient revealed that both time and humidity influenced movement. Juvenile tuatara moved significantly more during the night than during the day (Wald Chi-Square = 6.046, d.f. = 1, P = 0.014). The tuatara were also more active, moving significantly more (Wald Chi-Square = 16.768, d.f. = 1, P < 0.001) in the humid treatment compared to the dry. Digestive state had no influence on movement (Wald Chi-Square = 0.001, d.f. = 1, P = 0.970), and none of the interactions were significant. Of the tuatara which moved from one extreme of the gradient to the other, 52.2% were moving in the hot to cold direction with the remainder moving in the opposite. An analysis on the subset of data in which tuatara which moved the length of the gradient within one hour, revealed that time was the only predictor of movement from one extreme to the other (Wald Chi-Square = 8.335, d.f. = 1, P = 0.004), with more movements of tuatara from hot to cold during the night and more from cold to hot during the day (Fig. 4).
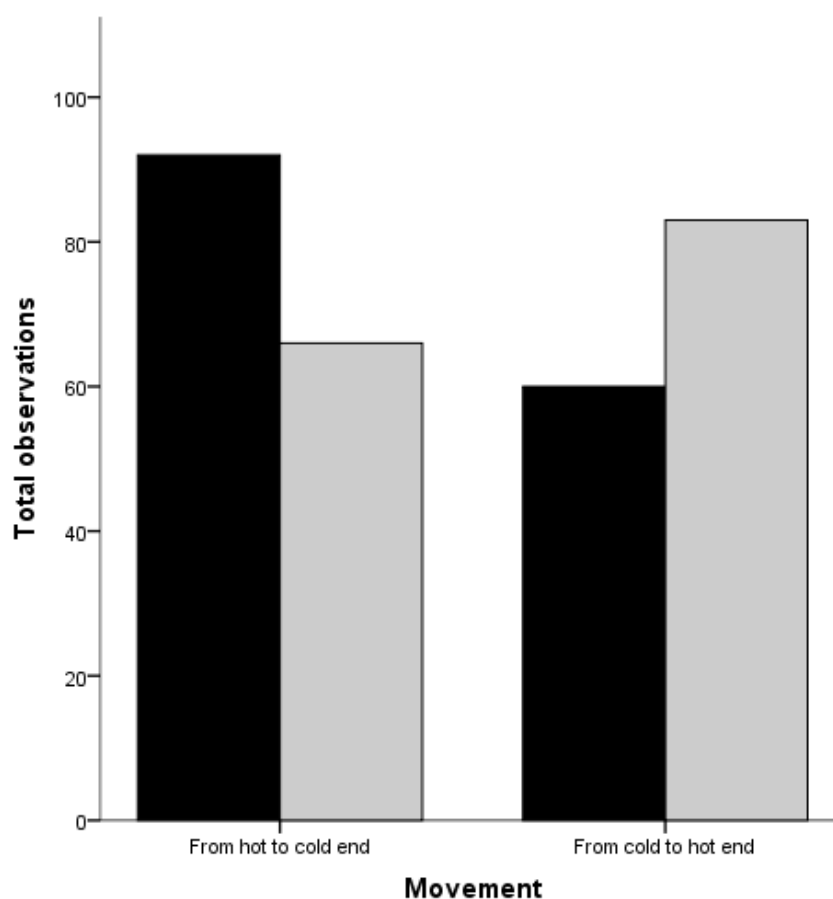
Figure 4. Movements of tuatara from area 4 to area 1 (hot to cold: -3 movements) and from area 1 to area 4 (cold to hot: +3 movements) during the day (grey bars 0800 - 1700) and night (black bars 1800 - 0700). Significantly more tuatara moved from hot to cold during the night and from cold to hot during the day.

3.5 Discussion

A thermal gradient in a laboratory setting enables an individual to move within a wide range of microclimates without risk or constraint (Angilletta Jr et al., 2002). Nevertheless, the temperatures chosen result in physiological costs, and thus laboratory data can represent relevant choices that can then be extrapolated to the field.

3.5.1 Temperatures selected

The temperatures selected by the juvenile tuatara were consistent with previous gradient studies (mean range: 19 -25°C, Besson & Cree, 2010b, mean range: 17 - 21°C, Stebbins, 1958), and reveal that tuatara exhibit a preference for warm temperatures, regardless of digestive state, humidity or time of day. In contrast to previous studies, where a lack of variation in body temperatures selected between scotophase (dark phase) and photophase (light phase) has been reported for juvenile tuatara (Besson & Cree, 2010a), this study revealed a clear diel trend in thermoregulatory behaviour. In the present study, the tuatara had the same choice of temperatures available to them over both day and night, quite a different scenario to that in the field. The mean temperatures selected during the day were higher than those selected at night, and more tuatara chose to position themselves in the warmest quarter of the gradient during the day compared to at night. Both diurnal and nocturnal reptiles often select cooler temperatures at night than during the day (Rismiller & Heldmaier, 1982, Innocenti *et al.*, 1993, Refinetti & Susalka, 1997, Ellis *et al.*, 2006), and in the wild, tuatara would naturally be exposed to colder temperatures at night. Although the selection of higher temperatures during the day may be a necessity in a natural setting (where the heat from the sun is available only during the day), it results in lower body temperatures at night, when nocturnal ectotherms would presumably benefit from higher metabolic rates (Refinetti & Susalka, 1997). As a compensatory mechanism, nocturnal lizards seem to have higher performance capacity at low temperatures than do comparable diurnal lizards (Autumn et al., 1994). Unlike most other reptiles, tuatara are able to survive and function at low environmental temperatures (Cree, 1994, Thompson & Daugherty, 1998), so are well adapted to emerge at night under cold conditions. During the day, tuatara bask in sunspots and can obtain temperatures of up to 34.5°C (chapter 2). Basking behaviour which raises body temperature may be important in maximising foraging ability, as high daytime temperatures are followed by an increase in nocturnal tuatara activity (Walls, 1983). The diel trend in body temperatures in the wild may explain the above results, suggesting that tuatara have an innate requirement for warmer temperatures during the day.

A reduction of preferred temperature under arid conditions could be viewed as an adaptation to facilitate survival on land (Malvin & Wood, 1991), as such a response would lower the driving gradient for evaporative water loss, thereby conserving water. However, in this study, juvenile tuatara tended to select higher body temperatures and were found most often in the warmest quarter of the gradient under the dry treatment. There are very few previous studies investigating the relationship between humidity levels of the atmosphere and/or dehydration and body temperatures in ectotherms, and those that do, report conflicting findings. The lizard, *Anniella pulchra,* selected lower temperatures in a dry thermal gradient than in a moist one (Bury & Balgooyen, 1976), but in the desert iguana, there was no effect of dehydration to 80% initial body weight on behavioural thermoregulation on a thermal gradient (Dupré & Crawford Jr, 1985). One explanation for the current findings is that any additional water loss due to evaporative cooling during the dry treatment, was negated by the fact that tuatara had access at all times to fresh drinking water. It may also be that time is a factor and that a longer experiment might show up a greater importance of humidity. Further studies to investigate the extent to which thermoregulation may be limited by the hydric environment of the tuatara would be useful.

Although statistically significant, the mean temperature differences between both day and night and between humidity treatments were only 1°C. This difference may not be biologically significant in natural conditions where higher variability in temperature would occur in each location, and/or may be influenced by the accuracy of the measuring equipment. It is unknown whether a one degree difference in mean body temperature could affect tuatara, as the thermal sensitivity of physiological processes (apart from metabolic rate: Wilson & Lee, 1970, Cartland & Grimmond, 1994) in tuatara has received little attention. The mass-specific resting metabolic rates of juvenile tuatara increase over an ambient temperature range of 5.0 - 22.5°C (Cartland & Grimmond, 1994) as expected, as the metabolism of ectotherms is strongly temperature dependant (Bennett, 1988). However, the behavioural data from the thermal gradient does support the findings, with a difference of ~10% in the number of animals recorded in the warmest end of the gradient. Thus, despite relatively low differences in body temperature, the tuatara appeared to be selecting areas based on temperature.

3.5.2 Burrow use and movement on the gradient
Juvenile tuatara are difficult to observe in the wild, thus knowledge of their circadian behaviour is relatively scarce, but captive studies indicate that juvenile tuatara may have an innate

preference to emerge during the night regardless of environmental conditions and prior experience (Terezow et al., 2008). I found twice as many tuatara outside their burrows during the night compared to during the day, and significantly more activity (movement on the gradient) during the night. Nocturnal geckos are typically active at body temperatures that are far below their preferred body temperatures (Angilletta Jr & Werner, 1998, Hare *et al.*, 2007), which Autumn *et al.* (1994) demonstrated can reduce the energy expended on maintenance and activity. Thus, tuatara may select night time and the associated lower temperatures as their more active period to reduce energetic costs. This is an additional area which warrants further research.

Under the wet treatment, significantly more tuatara were recorded outside their burrows in comparison to the dry treatment. Humidity has only rarely been monitored during investigations into reptile behaviour, but one such study revealed that the activity patterns of the Malayan pit viper (*Calloselasma rhodostoma*) were found to be more strongly correlated with variation in relative humidity than with temperature, with more snakes active on humid nights (Daltry et al., 1998). Anecdotal evidence also suggests that tuatara are more active and are out in greater numbers on damp, misty nights (Newman, 1977, Barwick, 1982).

3.5.3 Implications of this research

Temperature is important for reptiles but the ecological performance of the animal depends on many factors in its environment, not just its thermal physiology (Huey, 1991). Environmental constraints will limit thermoregulatory precision of any animal, despite thermoregulatory effort. For tuatara, such constraints include low ambient temperatures, possible high densities, conspecific competition for burrows, and the annual presence of seabirds during their breeding season, all of which may lead to competition for the most suitable burrows. The present study suggests that tuatara seek out and remain longer at warmer burrows, and are more active under humid conditions.

Humidity of the environment influences both body temperature selected and burrow use. In temperate environments, with temperature often a limiting factor for thermoregulation, humidity may be a lesser factor governing the activity patterns of reptiles. However, for some species such as the tuatara which are often restricted to islands on which there are no standing bodies of freshwater, humidity may indeed play a greater role in determining habitat selection and timing of activity. Water loss may be the over-riding factor which reduces nocturnal and

daytime activity during warm or dry periods, or indeed the factor which governs the number of days that an animal can repeatedly bask (Barwick, 1982). Thus, any advantage in terms of water conservation could potentially enhance fitness. A burrow occupied by an endotherm such as a seabird would naturally be warmer and more humid (Chapter 5) and may mean that these are also the more desirable burrows for tuatara. Higher humidity could provide tuatara with a means for water conservation, as tuatara demonstrate high rates of cutaneous water loss relative to its body mass (Cree & Daugherty, 1991). Thus higher humidities could facilitate extended activity periods and perhaps enable extended feeding into winter. The lowest humidity recorded on Stephens Island over the period of one year (2008) was 48% RH (Stephens island weather station; NIWA, 2011), which is within the "dry" treatment of this study, but humidities of 100% were regularly recorded on Stephens Island. It is therefore possible that the "wet" treatment needed to be a higher humidity to draw out any behavioural differences. Additionally, removing or limiting access to freshwater may also have revealed behavioural differences between the two treatments.

My experiments revealed that digestive state had no discernable effect on either temperatures selected or burrow use under captive conditions. During environmental conditions where suitable prey items are readily available, a faster rate of digestion with an increased body temperature may enable higher consumption and growth rates (Wang et al., 2002). For juveniles it may also be advantageous to speed up their digestive process so that locomotion is reduced for the minimum period possible in order to make them less vulnerable to predators. However, the idea that animals select body temperatures depending on fed versus fasted state to facilitate a trade-off between energy balance and digestive efficiency, is not always evident in the field (Brown & Griffin, 2005). It is possible that the absence of predators and the continual availability of a wide range of temperatures in the present study resulted in juvenile tuatara which were not subjected to the same pressures regarding digestion as they would face in the field. However, it may also be that digestive state is not the deciding factor in terms of thermoregulation or that temperature is always the limiting factor so they strive for warmer temperatures regardless of digestive state.

Extreme habitat specificity can reduce a species' ability to persist in the face of anthropogenically induced habitat change (Shine et al., 1998, Harwood, 2001). Thus, the features of habitats that make them suitable for a particular species are of considerable significance for understanding phenomena such as the distribution, abundance and conservation

status of that taxon (Shah et al., 2004). This study provides experimental evidence that reptiles are capable of adjusting their habitat selection behaviour in response to different humidity constraints. However, higher temperatures, more frequent extreme weather events such as droughts and floods and a change in rainfall patterns are predicted in New Zealand under climate change (Ministry-for-the-Environment, 2011). Thus, predicted climate warming and also extended periods of drought could be problematic on offshore islands without any permanent freshwater resources. This may mean that despite being able to respond to changes in humidity levels, evolutionary responses by tuatara to current rates of climate change are unlikely given the long lifespan of tuatara (Gaze, 2001) and low reproductive output (Cree, 1994). It is possible that climate change is already threatening the survival of at least one population of tuatara in its current habitat (Mitchell et al., 2008), thus these results have important implications for the conservation of tuatara.

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CHAPTER FOUR

The fairy prions' breeding behavior in relation to the tuatara: How a bird responds to a large reptilian burrow-mate

4.1 Abstract

Associations between species of terrestrial vertebrates are not permanent but may last for periods of a few minutes to several months. Fairy prions spend most of their lives at sea but breeding occurs on land and burrows may be shared with a medium sized predatory reptile, the tuatara. Radio Frequency Identification technology was used to investigate the behaviour and burrow use of fairy prions throughout the breeding season and their concurrent interactions with tuatara. Burrows occupied solely by fairy prions, and by both fairy prions and a tuatara were monitored. The successful incubation of the fairy prion egg to the hatchling stage bore no relation to the presence of a tuatara at the burrow. Arrival time by fairy prions at the burrow each night was dependant on timing of dusk but was also delayed by the presence of a tuatara at the burrow. Tuatara did not affect activity levels of the fairy prions at the burrow in either September or October but in January, use of the burrow by tuatara almost halved the time fairy prions spent at the burrow with their chick. Tuatara are known to predate on eggs and chicks, thus in certain instances, it may be that this interaction is best classed as a parasitism with the tuatara benefitting from burrow use and easy predation opportunities, to the detriment of fairy prion recruitment. In other instances it may simply be a case of competition for a limited resource (a burrow) with the outcome varying depending on the individuals and the circumstances involved.

4.2 Introduction

Overlooked in many field studies, commensal and mutualistic interactions occur frequently among species of terrestrial vertebrates, and have important, but largely unmeasured effects on fitness (Dickman, 1992). Many interactions have the potential to shift from parasitism to

commensalism to mutualism, depending on the ecological circumstances. Parasitism is a biological interaction in which one organism is in continuous, intimate association with another organism (normally a different species), and is also metabolically dependent, directly or indirectly on it to some degree (Smyth & Wakelin, 1994). In commensal interactions, individuals of different species live together with neither being metabolically dependent on the other and one species benefits while the other is unaffected (Smyth & Wakelin, 1994). A mutualism is a biological interaction between individuals of different species where one partner provides a service for the other and receives some kind of reward (Bronstein, 1994a).

Interactions between species rarely fit neatly into just one of these categories. The interaction can depend on the age, size, and physical condition of the individuals, and even on the composition of the community in which the interaction takes place. Rather than being fixed attributes of species interactions, benefits and costs can vary with the distribution and abundance of symbiotic partners, the availability of alternative partners or resources, the need for services provided and/or the abiotic setting in which the interaction occurs. Such context-dependent interactions have been termed conditional (Cushman & Whitham, 1989, Bronstein, 1994b). When external stress is diminished, the benefits derived from the interaction decrease, and the net outcome of a formerly positive interaction may become neutral or even negative (Stachowicz, 2001), either temporarily or over parts of the range of the interacting species (Thompson & Cunningham, 2002). For example, the cleaning relationship between longfin damselfish (*Stegastes diencaeus*) and Caribbean cleaning gobies (*Elactinus evelynae*) is mutualistic in some locations, but sometimes neutral or even parasitic in others (Cheney & Côté, 2005). The spatial variation in the interaction is linked to the variation in ectoparasite load on the damselfish. Sites with more ectoparasties are characterized by greater removal of ectoparisites and lower removal of scales and mucus. Therefore high numbers of ectoparasites on the damselfish results in a mutualism between the damselfish and the gobie, but the interaction becomes neutral or parasitic when the damselfish has a lower ectoparasite abundance.

When investigating the behaviour or ecology of a particular species, it is therefore crucial to attempt to understand the mechanisms and conditions which underlie interactions between that species and any other with which it coexists. When considering interspecies interactions, associations between terrestrial vertebrates and burrow nesting seabirds are not always immediately obvious. However, these seabirds are often ecological drivers of the terrestrial

ecosystems where they breed (Smith, 1976, Mulder & Keall, 2001, Markwell & Daugherty, 2002, Miskelly *et al.*, 2009). As a consequence of their large colonies, petrels can dominate the ecology of breeding sites through their burrowing activity, trampling of vegetation, collection of ground cover vegetation for nest linings and especially the importation of vast quantities of marine-sourced nutrients deposited at the colonies as droppings, regurgitations, failed eggs and corpses (Smith, 1976, Furness, 1991, Warham, 1996). The enrichment of habitat within seabird colonies can even have a positive effect on the lifetime reproductive success of large mammals, such as red deer (Iason et al., 1986).

On Stephens Island, New Zealand, a small petrel, the fairy prion (*Pachyptila turtur*) is closely associated with a reptile, the tuatara (*Sphenodon punctatus*). These animals share burrows, and the fairy prion exerts a major influence on both burrow use and population densities of the tuatara (Newman, 1987). The birds excavate the burrows in which many tuatara live (though the reptiles can dig their own), and by incorporating their mineral-rich guano they create conditions that may encourage ground-dwelling invertebrates which form the bulk of the diet of the tuatara (Dawbin, 1962, Crook, 1974, Walls, 1981, Dawbin, 1982). Thus, higher tuatara densities are found in areas with more prions (Markwell, 1998). Both species are subject to conservation measures to repopulate depauperate island faunas resulting from the effects of invasive rodents. Understanding the inter-specific interactions will inform the likely future success of management actions for both species.

Fairy prions are small Procellariid seabirds (length 25cm, weight 90-175 g) that display high levels of philopatry, exhibiting natal philotropy and site fidelity, choosing to breed close to the site of their own hatching (Greenwood & Harvey, 1982). They have a lifespan of at least 15 years, adults weigh 96-166g, and can possibly fly 322km in a single day while foraging (Harper, 1976). Fairy prions form relatively stable pair bonds (Harper, 1976); lay only one egg, and both adults share in the incubation of the egg and the feeding of the chick. Following breeding, adult prions depart their colonies and spend the winter at sea in the Southern hemisphere.

The close ecological relationship between petrels and tuatara has been noted since the 1800's (Mair, 1871, Reischek, 1881, Ramstad et al., 2007). Despite a long awareness of their coexistence, the exact nature of the symbiotic relationship between tuatara and seabirds such as fairy prions is still unclear. However, there is sufficient evidence to suggest that tuatara benefit greatly from living within the same burrow alongside seabirds such as petrels, prions and shearwaters.

Usually the birds dig the burrows providing the tuatara with a home (Newman, 1987), and the bird's eggs and chicks may provide an easy meal for larger males and important nutrients at an energy demanding time of year as they approach the mating season (Crook, 1975, Walls, 1978, Walls, 1981). Birds also deplete the understory vegetation in forested areas and increase the invertebrate biomass by marine-derived nutrient addition (East et al., 1995), thus potentially improving hunting conditions for tuatara. The increase in prey items potentially allows higher densities of tuatara to occur in an area, as is seen on Stephens Island where greater tuatara numbers are found in areas with more fairy prions (Markwell, 1998). Despite predation on the eggs, chicks and even adults, the prion population as a whole is not significantly decreased by tuatara (Markwell, 1998). To our knowledge there has been no documentation of the behavioural response of fairy prions to tuatara in the burrow, apart from reports of prions expelling tuatara from their burrows (Newman, 1987, Gaston & Scofield, 1995).

Traditional studies based on banding recoveries or ocean sightings have proved valuable for identifying very general movement patterns for many species of seabird, but fail to characterize any behavioural detail at the nesting colonies (Guilford et al., 2009). Since fairy prions breed underground, return faithfully to their nesting burrows, and are relatively easy to capture, they lend themselves to the use of Radio Frequency Identification (RFID) technology. Previous studies with fairy prions were conducted using moderately invasive methods such as burrow excavation or modification to include a viewing hatch, and more recently a less invasive but still potentially disturbing technique, the repeated use of a burrow scope, to gain information on timing of breeding events and diet. Studying breeding events and habitat use of burrow nesting animals is often a challenge as excessive disturbance of these animals may lead to changes in behaviour, which for nesting seabirds can include desertion or hatching failure (Ellison & Cleary, 1978, Warham *et al.*, 1982). For this reason, tagging with Passive Integrated Transponders (PIT) and recording with RFID is highly effective and is now proving invaluable for the monitoring of wild birds such as common terns, *Sterna hirundo* (Becker & Wendeln, 1997) and mammals such as short tailed-bats, *Mystacina tuberculata* (O'Donnell *et al.*, 2011).

In this study, the use of RFID technology was tested to further investigate the breeding behaviour of fairy prions and their interaction with tuatara. Three questions were posed; 1) How does breeding behaviour (specifically arrival time at burrow and activity time at burrow) vary among individuals with respect to the presence of a chick, the presence of a partner and with environmental parameters? 2) Is the breeding behaviour of fairy prions affected by the presence

of tuatara? And 3) Can the relationship between fairy prions and tuatara be classed into either of the three symbiotic interactions explained above?

4.3 Methods

4.3.1 Study area and species

This study was conducted on Stephens Island (also known by its Māori name, Takapourewa), a 150-ha island located in Cook Strait, New Zealand (40°40'S, 174°00'E), where approximately one million fairy prions breed (Harper, 1985). Fairy prions are active at their colonies during their breeding season from spring (October) to late summer (January), and that period is referred to as the field season. This study was conducted over two successive field seasons (October 2009 – January 2011) in an area called Keepers Bush, which consists of regenerating coastal forest. The only other burrowing seabird present in notable numbers at any time of year on Stephens Island are approximately 1,000 individual sooty shearwaters (*Puffinus griseus*) (Markwell, 1997), although little blue penguins (*Eudyptula minor*) are also seen regularly, especially during the breeding season (pers. obs.).

On Stephens Island, fairy prions share their burrows with tuatara. The tuatara, is a medium sized reptile, of up to 450mm total length and 500 g in females, and up to 600mm total length and 1kg in males (Dawbin, 1982). Stephens Island is home to the largest population of tuatara, with estimated densities of up to 2700/ha in Keepers Bush (Moore et al., 2007) and total numbers estimated between 30,000 to 50,000 (Newman, 1982b). Tuatara inhabiting forested areas are active throughout the 24 hour period (Gillingham & Miller, 1991). The burrows range from 0.2m to 0.7m deep (Markwell, 1997), and can be complex with many connected chambers and openings, or simple with only one or two entrances (Newman, 1982b). Most burrows are probably constructed by the fairy prions (Newman, 1982a). It is likely that all burrows within the study area were visited at least once by a tuatara, as tuatara tend to use more than one burrow at any given time (Newman, 1987) and also will opportunistically use any nearby burrow as a retreat when startled (pers. obs). Thus, burrow occupancy was categorized as binomial data in two ways; 1) contains a resident tuatara or not, and 2) a more inclusive category of used regularly or occasionally by one or more tuatara, or not used by any tuatara.

5.3.2 Marking of animals

Within the study area almost all tuatara had been previously identified individually with a passive integrated transponder (PIT, "Allflex" 11.5mm x 2mm tags), toe clip and/or unique sequence of coloured beads in their caudal crest (Moore *et al.*, 2009). Initially, with the aid of a burrow scope, ten burrows occupied by fairy prions were selected; burrows had one entrance and were relatively close to the path to minimize damage to surrounding areas. Birds at each burrow (n=10 pairs) were retrieved by hand, banded on the left leg (D-band, stainless steel) and injected with a PIT tag. The PIT tags were purchased pre-loaded, in sterile hypodermic needles, and were implanted using a reusable applicator. These were inserted subcutaneously on the caudal part of the "scruff of the neck" region (i.e., in the dorsal midline area between the animals shoulder blades (scapulae)) before release. The neck region is minimally accessible by the individual for self mutilation or excessive grooming (Carter, 2009). This tag site allowed detection by an external reading device, and was deemed unlikely to shift position. Insertion sites on birds were thoroughly cleansed pre-implant using ethanol and the site was sealed post implantation with vet bond. A handheld reader was used to confirm that tags were operational prior to implanting and to check captured birds for already implanted tags (Carter, 2009). Twelve more burrows were marked on four subsequent fieldtrips, and the occupying birds were tagged (n=24) to make a total of n=22 study burrows and n=44 monitored birds. Handling time of each fairy prion never exceeded ten minutes, and upon release each bird either resumed incubating the egg if caught in October (day capture) or went back into its burrow and resumed feeding their chick if caught in January (night capture). Burrows occupied by PIT tagged birds were monitored for two to three weeks during pre-breeding (September-only in year 2), egg incubation (October/November) and chick rearing (January) periods spanning two breeding seasons. However, not all birds were present at all burrows for each complete two to three week period.

4.3.3 Recording movements of animals at burrows

An antenna was placed around the entrance to each burrow (Fig. 1). Briefly, the antennae were constructed using 6mm fine copper wire; 20 loops of the wire were wound to form a 0.3m diameter circular loop and were held together and insulated with electrical tape. Both ends of the wire were connected to a data logger (custom built units for the NZ Department of Conservation; fully enclosed, maximum dimensions approximately 12.5cm x 9cm x 5cm; powered by 12 V batteries). The power supplied by the battery enabled a passing tag to be activated, received by the antenna and stored in the data logger as a tag number, time, date,

and logger number. The loggers were set to a default one minute re-read settings to prevent excessive readings of the same individual if it was sitting at the entrance to the burrow. Scanners were checked daily with a tester PIT tag placed inside a plastic rod and passed through the scanner (a light on the logger lit up as it read a PIT number). Data were downloaded in the field directly into a laptop computer most afternoons, weather permitting. Upon finding a flat battery, any absence of readings from the previous night was not taken as absence by individuals from the burrow; the night's data were omitted from the analysis.

Figure 1. Field recording devices; an antenna (marked by arrow) was fixed into position around the entrance to a burrow and attached to a logger and battery.

Observations were made at 1400, 1600, 2200, 2400 and 0200 every day to monitor tuatara and fairy prion use of the burrows by walking a 20 minute circuit through the forest, past all marked burrows. These observations were then cross-checked with the readings from the scanners. At 2400 each night, a section of the forest (a path roughly 50m in length) was walked, and fairy prions and tuatara within 1m either side of the path were counted. This served as a crude estimate of abundance/emergence of both tuatara and fairy prions on any given night. Ambient temperature was recorded hourly with the use of a temperature datalogger (Hobo Tidbits®). This was placed in the shade in the forest at ground level at 1m above ground level (tied to tree).

4.3.4 Data analysis

Data were analysed using the statistical software SPSS, version 18.0 (SPSS Inc.) and R, version 2.11.1 (R Development Core Team, 2007). Data were tested for normality and are expressed as the mean ± 1 SE. Data transformations were performed as required to meet assumptions of normality.

Generalized linear mixed models (Lindstrom & Bates, 1990) in the package "lme4" with procedure "glmer" in program R were used to account for individual random effects within a linear regression framework. These models were used to investigate the predictors of first arrival of fairy prions at the burrow each night (measured as time to the nearest minute) and activity at the burrow entrance (measured as time to the nearest minute between first and last pass through the scanner in a night). In addition to an individual random effect of ID (bird), the effects of year, month, night (ind.night), temperature measured at 12am in degrees Celsius (temp.12am), burrows with a resident tuatara (tuat.res) and burrows subject to infrequent visits by tuatara (tuatara) were initially tested. A burrow was identified as having a resident tuatara if the same tuatara passed through the scanner every day of the sampling period and categorised as "subject to infrequent visits" where tuatara (often a number of different individuals) passed through the scanner at least 25% of the dates during the sampling period. Potentially important interaction terms in these mixed-effects models were also examined: including interactions of month*year, tuat.res*year and tuatara*year, as annual variation was possible, particularly with respect to weather and individual behaviour.

Akaike's information criterion corrected for small sample size (AIC_c; Akaike, 1978, Anderson et al., 1998) defined as AIC_c = -2 x log-likelihood + {$2K(K + 1)/ (n - K - 1)$}, where K is the number of parameters in the model and n the number of observations, was used to evaluate the model(s). Akaike model weights (*wi s*) were calculated to compare models and determine which model(s) served as the best approximation(s) to the data: *wi* = exp (-0.5 x ΔAIC_c /$\sum$ exp (-0.5 x ΔAIC_c), where ∆AICc is the difference in AIC_c values between the best performing model and the model of interest. If several models share some weight in explaining the variability within the data set (i.e., *wi* > 0), or if ΔAIC_c was < 3 points, each model and the effect of all the covariates involved in those models was briefly discussed.

The first record of an individual bird passing through a scanner on any given night was assumed to represent arrival at a burrow. Time spent feeding a chick was the time interval (minutes)

between first entry through the scanner (assumed arrival) and last pass through the scanner (assumed departure) in one night. Visits of less than five minutes were discounted (three records), as this time was deemed too short for a feeding event to have occurred. While it was possible to detect how much time each bird spent at the entrance to the burrow each night, the time spent incubating an egg was not investigated. Due to the volume of passes through each scanner and the default one minute re-read settings, the individual bird left behind each night to sit on the egg during the day was unable to be identified with certainty (burrows could have been checked manually during the day but it was decided that this would create too much disturbance and compromise the non-invasive monitoring with the scanners). Therefore, because we could not identify with certainty an individual bird, we could not detect the amount of time each bird spent incubating.

Activity at the burrow was defined as the total length of time that an individual bird spent at the burrow in a night. It was measured as the difference in time between the last pass and the first pass through the scanner at the entrance of the burrow on each night. Activity for September and the October/November periods was the amount of time spent socialising at the entrance (revealed by the number of passes through the scanner in a night), while in January, activity at the burrow consisted of time spent inside with the chick.

A linear regression was used to test for the strength of the relationship between temperature and time spent at the burrow in September. The presence of correlations within an individual were tested for first arrival time among seasons and between years using Pearson's correlation coefficients. Repeated measures general linear models were used to investigate the effect of the presence of a partner on activity levels at the burrow.

4.4 Results

Between October 2009 and January 2011, 45 individual fairy prions at 22 burrows were tagged and monitored. Data available across two years for individual fairy prions varied from one period of three weeks to five periods covering 15 weeks (Table 1). During each period, ten burrows were monitored simultaneously (only nine were monitored in January 2011, due to a faulty logger). A total of 6,864 fairy prion tag readings were obtained. All records of birds at burrows from our daily observations of the burrow had a corresponding tag recorded by the data logger

except for one, when an untagged bird entered the burrow of another pair and immediately re-exited and entered an adjacent, unmarked burrow. Two tuatara without PIT tags occasionally used two marked burrows, thus these observations were added to the data set of tag readings from the scanners. Most burrows were visited at least once by a tuatara. However, considerable variation was observed among burrows, one burrow during one time period was regularly used by three tuatara, while another went through a full two weeks without any visits from a tuatara.

Nightly counts of fairy prions in each breeding period, based on numbers along a transect, gave an indication of fairy prion activity levels (Table 2). In September fairy prions were prospecting burrows, with records from the scanners reflecting a high number of entries and re-entries at each burrow and 30.7 ± 9.5 fairy prions were counted per night. In October to early November, eggs were laid and the activity records of pairs with an egg reflected typical incubation behaviour, with individuals in a pair taking it in turns to incubate the egg (Richdale, 1945b). During this period there was still high levels of activity on the forest floor, with counts of 27.9 ± 5.5 birds per night (Table 2), and with pairs of birds constantly emerging from burrows and often sitting together outside the entrance. In January, the chicks were left alone in the burrow during the day, and the adult birds arrived singly at night at the colony and stayed only a short time to feed the chick. There was less socialising (lower numbers of passes through the scanner relative to September and October periods) between the adult birds and they tended to arrive at the burrow, feed their chick and often leave within the hour. Nightly counts of fairy prions within this period were 1.8 ± 0.6. Tuatara numbers were less variable throughout the months; 5 ± 1.7 tuatara a night in September, 3.2 ± 0.6 in October, and 3.7 ± 0.5 in January.

Table 1: List of burrows monitored over 5 fieldtrips (only 9 burrows in January 11 due to faulty logger). ** indicates burrows with a resident tuatara, * indicates burrows with occasional tuatara visits. Status indicates whether an egg (October) or chick (January) was present at the end and start of a field trip respectively. A double tick indicates a fledged chick. Grey boxes indicate burrows checked at the start of a fieldtrip but not monitored.

Year 1					Year 2						
Oct-09		Jan-10			Sep-10	Oct-10			Jan-11		
burrow	end status	start status	burrow	end status	burrow	start status	burrow	end status	start status	burrow	end status
1	√	√	1	√	1	√	1	√	x	1	
2	√	x	2		2	x	2				
3	√	x	3		3*	√	3	√	x	3	
4	√	√	4	√	4	√	4*	√	√	4	√
5*	√	x	5								
6	√	√	6	√	6	√	6*	√	√	6	√√
7**	√	x	7								
8**	√	x	8		8**	x	8				
9**	√	√	9	√	9**	√	9**	√	√	9**	√
10**	√	√	10*	√	10	x	10		√	10**	√
			11	√	11	√	11	√	√	11	√
			12	√							
			13	√							
			14	√	14	√	14	√	x	14	
			15	√							
						√	16	√	x	16	
						√	17	√	x	17	
						√	18	√	x	18	
									√	19	√√
									√	20	√
									√	21	√
									√	22	√

Table 2: Total numbers of fairy prions and tuatara counted along a 50m track at midnight in September, October/November and January. '/' indicates nights for which a count did not take place (due to concurrent fieldwork).

September			2010	
date	Fairy prion	tuatara	Fairy prion	tuatara
11			26	5
12			49	2
13			17	8
Oct/Nov	2009		2010	
27			27	6
28	74	6	33	5
29	20	0	1	1
30	8	1	0	0
31	29	2	9	3
1	52	5	27	2
2	28	7	49	2
3	34	5		
January	2010		2011	
9	4	3		
10	8	8		
11	5	4	2	5
12	/	/	0	1
13	1	4	0	3
14	/	/	0	3
15	1	1	0	1
16	/	/	1	2
17	2	3	1	6
18	2	6		
19	/	/		
20	1	5		

4.4.1 Success of individual burrows

Five out of ten burrows in the first field season successfully incubated eggs to the hatchling stage (Table 1). Of these, two were used by tuatara, and three of the five failed burrows were used by tuatara. Only four of the ten eggs in the second field season resulted in live chicks in January 2011 (one with a resident tuatara) and of the six failed nests, three were occupied by a resident tuatara. All chicks, in all burrows, in both years survived until at least the end of January, and at the end of the sampling period, none had yet fledged in 2010 but two had in 2011.

Of the original ten burrows with marked prions, 100% of the tagged birds from year one returned in September of year two prospecting the same burrows. However, only seven out of the ten pairs actually laid an egg in the same burrow a month later. There was a possibility that others laid an egg at the very beginning of the breeding season before monitoring started in October, but all burrows were searched for any signs of broken eggs and none were detected in these four burrows. Four birds from three burrows in September, only visited their nest on one night, and two of these three burrows did not contain an egg the following October. In January 2010, one bird in a pair was replaced by a new bird which had played no role in the incubation of the egg but fed the chick at burrow one for the duration of the sampling period. This pair did not lay an egg in the same burrow the following year. The original bird which had incubated the egg in October did not reappear during the chick rearing period. There were also two burrows where only one adult fairy prion ever visited each chick respectively.

4.4.2 Arrival time at the burrow

First arrival at the burrow by individual birds on any given night varied from 1847 to 0519. The model selection analyses revealed that two models shared some weight in predicting first arrival time at the burrow (Table 3). The top model which explained 62% of the overall AIC_c weight, retained a fixed effect of month and individual heterogeneity (an individual random effect (bird)).

The timing of first arrival at the burrow grew significantly later as the season progressed ($F_{2/617}$ = 131.835, P = 0.001), but there was no significant difference between field season one and two ($F_{1/618}$ = 6.474, P = 0.110). In September, dusk fell between 1805 and 1814, and the prions arrived at their burrows 2.7 ± 0.4 hours later, with a mean arrival time of 2244 hours ± 12 minutes. In October/November when the fairy prions were incubating their eggs, dusk fell between 1951 and 2014, and the prions arrived 3.3 ± 0.1 hours after dusk with the mean first arrival at the burrow 2331 hours ± 9 minutes. January had the latest arrival times, with dusk

falling between 2057 and 2049, and the prions arrived 4.2 ± 0.1 hours later, at 0106 hours ± 7

minutes (Fig. 2). Thus, birds arrived later each month even when dusk was accounted for.

Individual arrival time was found to be highly correlated among all months (r = 0.167, *P* < 0.01

for all correlations). Thus, birds with early arrival times in September, had early arrival times in

October and January, and birds with early arrival times in field season 1 had early arrival times in

field season 2.

Table 3: Selection results for models testing for the effects of year, month, night (ind.night), temperature measured at 12am in °C (temp.12am), resident tuatara at burrow (tuat.res) and infrequent visits by tuatara (tuatara) on first arrival at burrow (measured as time to the nearest minute). All models except the model testing for an effect of ID alone (generalized linear model without fixed effect) are generalized linear mixed models (see methods for details) controlling for individual heterogeneity via an individual random effect (re(bird)). Only the top ten models are displayed and the blue box highlights the two models which explain 79% of the overall AIC_c weight and which were less than 3 points in **Δ**AIC_c.

Model	K	AIC_c	ΔAIC_c	Weight
month+(1|bird)	2	7827.816	0.00	0.62
month+tuatara+(1|bird)	3	7830.438	2.62	0.17
month+temp.12am+(1|bird)	3	7831.444	3.63	0.10
tuatara+temp.12am+month+(1|bird)	4	7833.068	5.25	0.04
month+tuat.res+(1|bird)	3	7833.457	5.64	0.04
month+season+(1|bird)	3	7835.470	7.65	0.01
tuat.res+temp.12am+month+(1|bird)	4	7836.093	8.28	0.01
tuatara+month+season+(1|bird)	4	7837.101	9.29	0.01
month+season+temp.12am+(1|bird)	4	7839.117	11.30	0.00
month+night.of+(1|bird)	3	7839.496	11.68	0.00
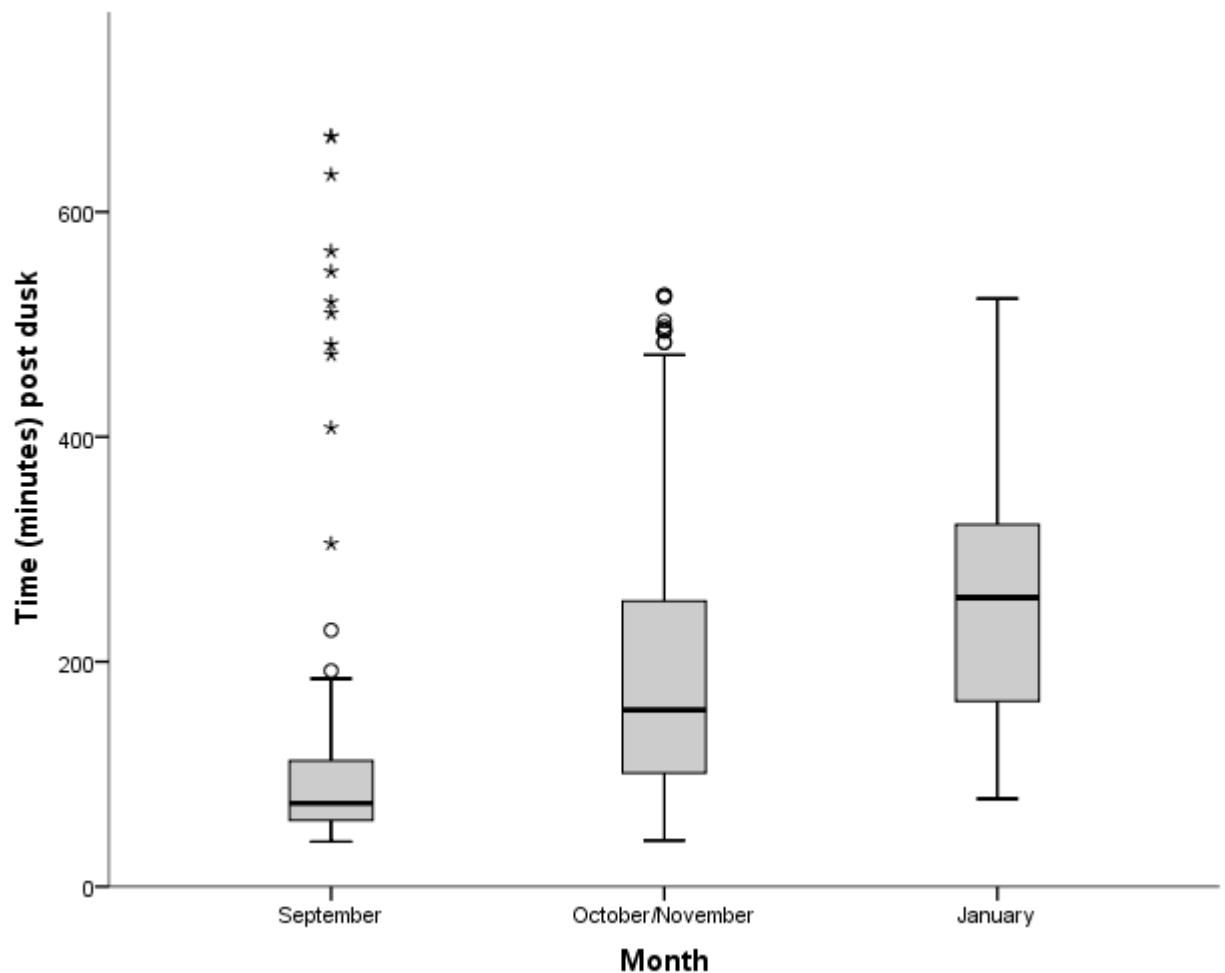
Figure 2. Timing of first arrival (minutes post dusk) of birds at the burrow. There were significant differences in arrival time among months.

The 2nd model which received a further 17% of the overall AIC_c weight included the effect of month and infrequent visits from tuatara (tuatara). These results suggest that the presence of a tuatara has a significant positive effect on first arrival time at the burrow. This indicates that birds at burrows frequented by tuatara arrive later (mean first arrival = 0010 hours ± 7 minutes) than when they are the sole occupants of a burrow (mean first arrival = 2344 hours ± 9 minutes).

4.4.3 Activity at the burrow

Table 4: Selection results for models testing for the effects of year, month, night (ind.night), temperature measured at 12am in °C (temp.12am), resident tuatara at burrow (tuat.res) and infrequent visits by tuatara (tuatara) on activity at the burrow (measured as time to the nearest minute) in September, October/November and January. All models except the model testing for an effect of ID alone (generalized linear model without fixed effect) are generalized linear mixed models (see methods for details) controlling for individual heterogeneity via an individual random effect (re(bird)). Only the top model(s) plus next best model for comparison are displayed, and the blue box highlights the top models which contributed the majority of the overall AIC$_c$ weight and which were less than 3 points in **Δ**AIC$_c$.

Month	Model	K	AICc	ΔAICc	Weight
September	(1|bird)	1	705.848	0.00	0.44
	partner+temp.12am+(1|bird)	3	706.563	0.72	0.31
	1st.arrival+(1|bird)	2	707.943	2.09	0.15
	tuat.res+(1|bird)	2	711.551	5.70	0.03
October/November					
	1st.arrival + (1|bird)	2	2684.608	0.00	0.87
	tuat.res + X1st.arrival + (1|bird)	3	2690.926	6.31	0.04
January					
	tuatara*year + (1|bird)	2	2202.638	0.00	0.50
	tuat.res*year + (1|bird)	2	2202.638	0.00	0.50
	tuatara + (1|bird)	2	2226.190	23.55	0.00

4.4.3.1 September

During the pre-laying period (September), the mean number of nights a bird visited their prospective burrow (sampling period: n= 9 nights) was 3.3 ± 0.3 and ranged from 1 to 6. When the prions visited the colony, they stayed at the burrow for an average length of 8.4 ± 0.4 hours, and went in and out of the burrow on average 21.7 ± 3.9 times per night (not allowing for the one minute re-read limitation of the recording device). The best model was the null model, that which contained no factor other than an individual heterogeneity via an individual random effect (bird) and this explained 44% of the variation. Two other models shared some weight in explaining the variability within the data set. The second included the presence of a mate (partner) at the burrow and temperature at 12am. When both birds of a pair were present at the

burrow on any night, they were more active, with 24.91 ± 5.2 passes through the burrow entrance versus 17.9 ± 6.2 when only one of a pair was present (F_1= 8.937, P = 0.003), although there was a lot of variation, with three birds recorded over one hundred times at the entrance in one night (one lone bird and two in a pair). On warmer nights, there was a trend for birds to stay longer at the burrow (Fig. 3), however this was not significant (r^2 = 0.006, P = 0.583), and the later the first arrival time, the less time they spent at the burrow (Fig. 4). The third model included first arrival time at the burrow. Neither a resident tuatara nor occasional visits by tuatara had any effect on activity time spent at the entrance in September.
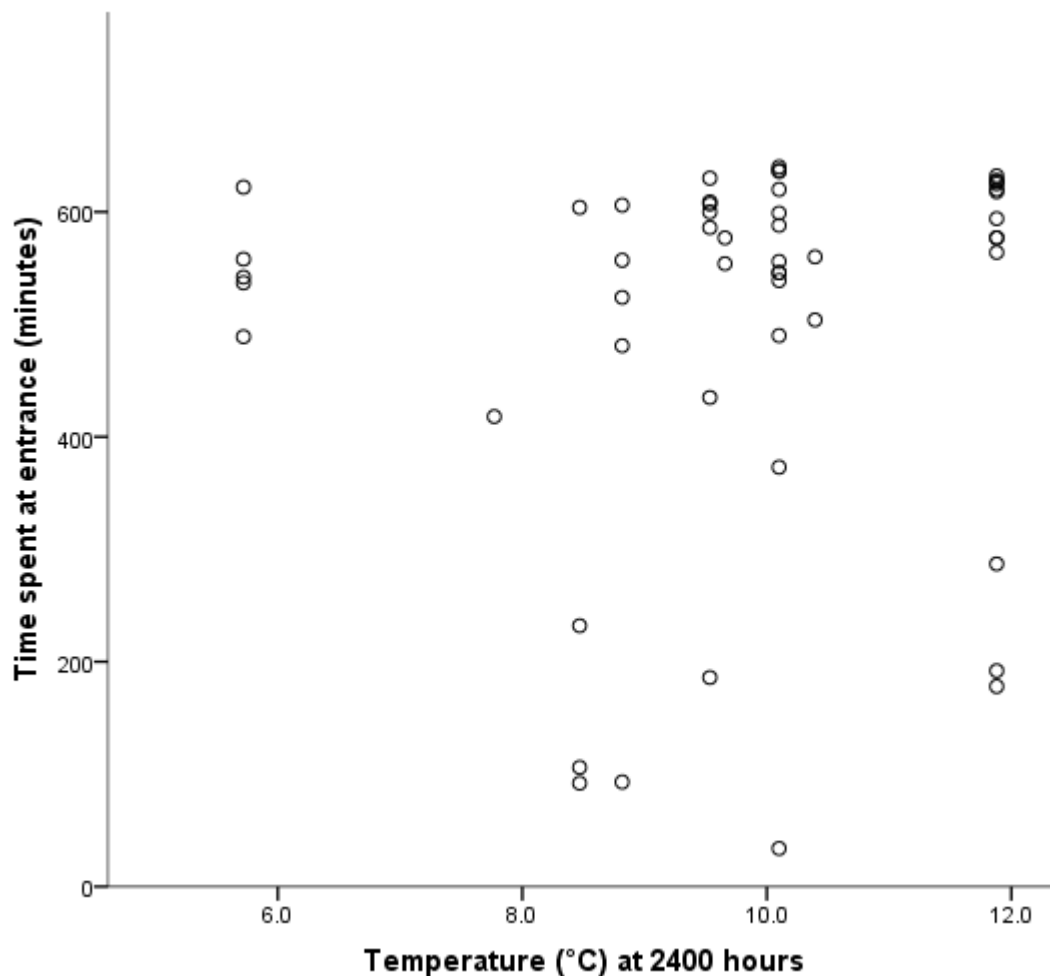
Figure 3. Time spent at the burrow (minutes) during September, in relation to temperature (°C).
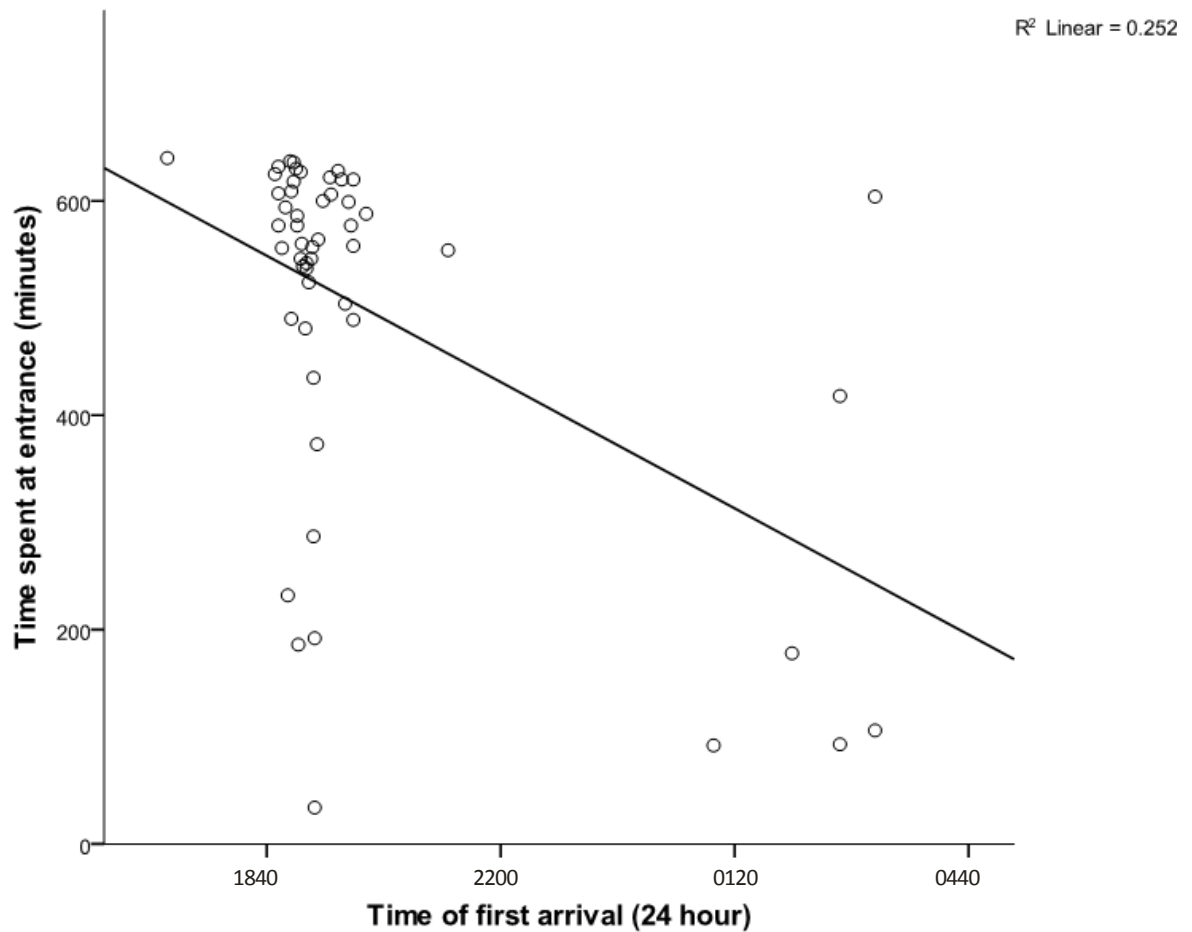
Figure 4. Time spent at the burrow (minutes) in relation to time of first arrival at the burrow (24 hour) in September.

4.4.3.2 October/November

During the period of egg incubation (October/November), the prions spent between one and four days on the egg before being relieved by their partner. They spent an average of 4.5 ± 0.3 hours (last record through scanner minus first record in a night) at the entrance of their burrows on the nights they were present at the colony. The model selection analyses revealed the top model which explained 87% of the overall AIC_c weight retained a fixed effect of first arrival time at the burrow as well as individual heterogeneity via an individual random effect (bird), and time spent at the burrow decreased as arrival time increased (Fig. 5).
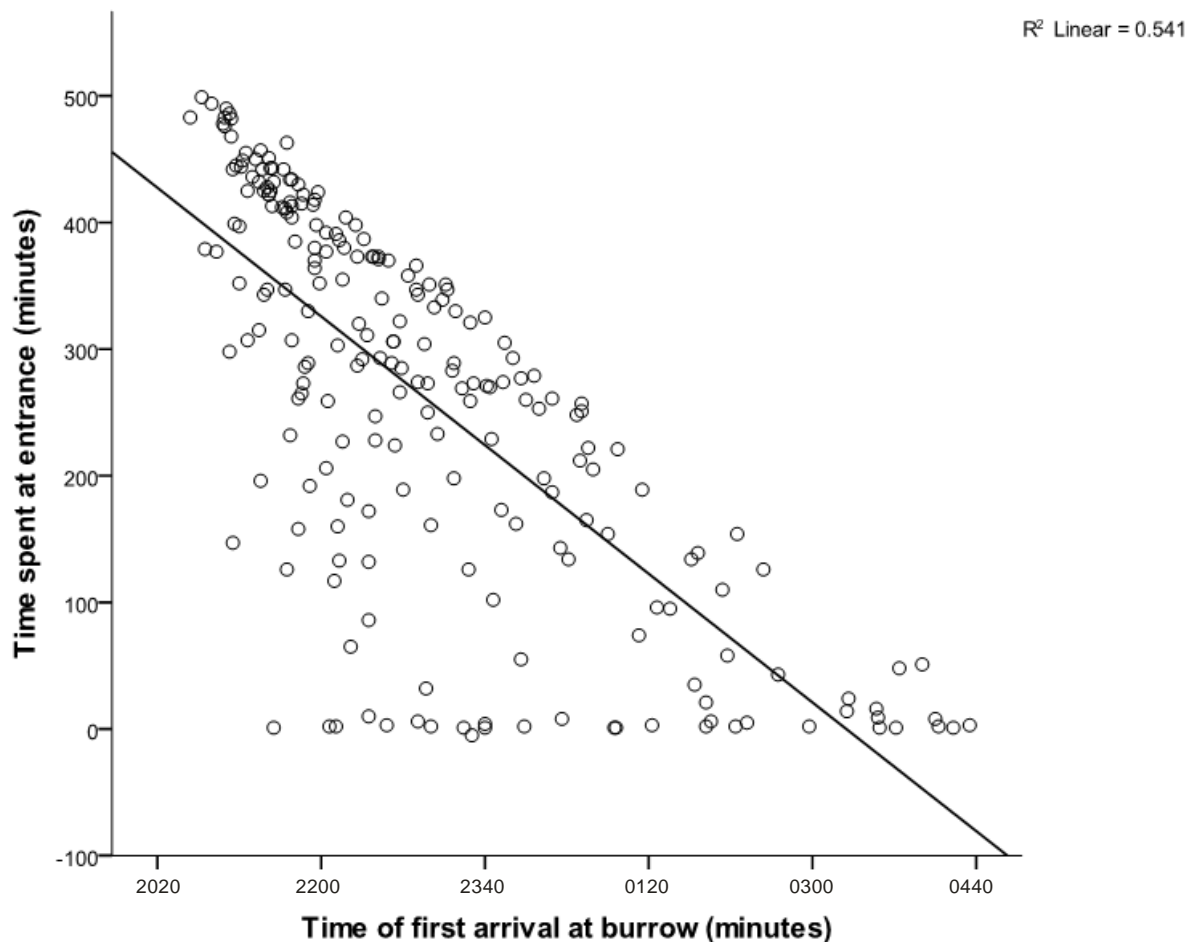
Figure 5. Time spent at the burrow (minutes) in relation to time of first arrival at the burrow (24 hour) in October/November.

4.4.3.3 January

Fairy prions spent an average time in the burrow with a chick of 24.6 ± 1.7 minutes but varied from 5 to 182 minutes in duration. In the majority of cases (88.3%, n= 300), birds only made one entry and one exit through the burrow entrance in a night, however one bird passed through the scanner 32 times over the course of 183 minutes. The average time between burrow visits when prions were feeding their chick was 29.8 ± 1.1 hours. Two models explained a total of 100% of the overall AIC_c weight to explain length of activity at the burrow. A model retaining a fixed effect of a resident tuatara interacting with year and individual heterogeneity via an individual random effect (bird), and a model which retained a fixed effect of random visits by tuatara*year and individual heterogeneity via an individual random effect (bird) each explained 50% of the AIC_c weight. The effect that a resident tuatara had on time spent with chick varied over both seasons. In 2010, prions occupying a burrow with a resident tuatara spent 20.0 ± 2.3 minutes a night with their chick while those without a resident tuatara spent a mean time of 23.1 ± 2.9

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minutes with their chick. In 2011 this difference was more pronounced, prions occupying a burrow with a resident tuatara spent 15.4 ± 1.4 minutes a night with their chick while those without a resident tuatara spent a mean time of 33.7 ± 8.4 minutes with their chick. There was a similar effect with those burrows subject to visits from non-resident tuatara, in 2010 those in burrows never used by tuatara spent a mean total of 30.0 ± 1.9 minutes with their chick, and those occasionally used by tuatara spent 22.8 ± 4.5 minutes with the chick. In 2011 these differences were again magnified, those in burrows never used by tuatara spent a mean total of 15.4 ± 1.4 minutes with their chick, and those occasionally used by tuatara spent 35.7 ± 9.2 minutes with the chick.

4.5 Discussion

Recent studies on seabird behaviour have been largely aided by advances in technology, for example with individual tags (Guilford *et al.*, 2009, Freeman *et al.*, 2010), and focused on behaviour out at sea. These have revealed fascinating insights into foraging behaviour, flight patterns and distances. However, behaviour at the colony is of equal importance in terms of conservation, as recruitment depends on activity at the natal colony. The advantage of using Passive Integrated Transponders and dataloggers as a means of documenting activity at a seabird colony compared to previous methods such as magnetic detection systems (Granadeiro et al., 1998), is the ability to identify individuals, and PIT tags have shown to be suitable for a wide range of species. This was a crucial consideration in the present study, as it enabled the investigation of the concomitant occupation of a burrow by two different taxa, with limited disturbance to behaviour.

Presence and activity patterns of petrels and shearwaters have been described for several species (Harris, 1974, Schramm, 1983, Hatch, 1990, Ross & Brunton, 2002), and predominantly focused on the analyses of abiotic factors, such as, moonlight and wind (Bourgeois et al., 2008). However, the coexistence with tuatara is perhaps the most striking feature of the natural history of the fairy prion, and has always been cause for comment by Maori (Ramstad et al., 2007) and ever since the first European naturalists began to visit the islands on which it occurs (Crook & Moran, 1975). Since the influences of weather and climatic variables on seabird behaviour have been well documented, the focus of this work was on the interaction between fairy prions and tuatara. Much of the documented interactions between reptiles and birds have been examples

of predation (Martín & López, 1996, Caudell *et al.*, 2002, Anderson & Burgin, 2008) or competition (Wright, 1981). Some notable exceptions include the possible symbiotic interaction between the lizard (*Podarcis lilfordi*) and Eleonara's falcon (*Falco eleonorae*). The lizard enters the nests of the falcon when females are brooding chicks, crawling between chicks and eating the remains of prey and flies without being molested by the falcons (Salvador, 1980). A similar example occurs with the fossorial snakes, (*Leptotyphloips dulcis)*, which live in nest debris of screech owls, (*Otus asio*) and eat insect larvae (Gehlbach & Baldridge, 1987). Nestlings associated with snakes had greater survival rates, grew faster and fledged earlier than those in nests without snakes, possibly because the consumption of larvae may reduce larval parasitism of nestlings.

Fairy prion breeding activity at the population level, has been studied in detail previously on: Whero Island (Foveaux Strait) (Richdale, 1945a, Richdale, 1945b), Poor Knights Islands, (Harper, 1976) and Stephens Island (Walls, 1978). Although similar in pattern, the dates of breeding events differ between these three studies, and conform to a latitudinal trend in which the breeding cycle occurs earlier in the north and later in the south (Walls, 1978). Laying and hatching dates were not assessed for all nests during this study, but the broad timing of incubation and dates when all monitored burrows contained a chick matched well with information from these previous studies.

4.5.1 Success of individual burrows
The successful incubation of the egg to the hatchling stage bore no relation to the presence of a tuatara and none of the chicks in our study burrows suffered predation by tuatara. Unfortunately there was no way of ascertaining whether any of the failed eggs were a result of tuatara predation/interference or some other factor such as inexperienced breeding adults. This study confirmed that fairy prions return not only to the same area each year but also initially to the same burrow, regardless of tuatara occupation or previous nest success. However, despite prospecting the same burrows, some pairs did not commence laying. It is possible that these birds chose a different burrow to breed in, which would indicate that not all pairs remain faithful to the same burrow year after year. Apart from their unique association with a reptile, two unusual occurrences for petrels were documented and confirmed. This was the occurrence of single parent clutches and a helper bird at one nest. Seabirds are generally unable to raise offspring alone (Lack, 1968), and documented instances of successful rearing by single parent seabirds are rare (Nisbet et al., 1978). There were two instances where only one bird visited a

nest to feed its young. It is unknown whether either of these two nests resulted in successful fledglings, however at the end of the study both chicks were of a comparable size to chicks with two parents. A "helper" is a bird which assists in the nesting of an individual other than its mate, or feeds or otherwise attends a bird which is neither its mate nor its dependant offspring (Skutch, 1961). Helpers have been observed in a wide range of species, such as, Florida Scrub Jays (*Aphelocoma coerulescens*) (Quinn et al., 1999) and Pied-Kingfishers (*Ceryle rudis*) (Reyer, 1980), but are thought to be relatively rare in seabirds. In petrels, additional adults visiting burrows during the chick rearing period are most probably pre-breeding birds or failed breeders inspecting burrows for future use (Quillfeldt et al., 2001). However, in this instance, there were records of a third bird which assisted in the parental care of the chick over a two and half week period.

4.5.2 Arrival time at the burrow

Arrival times at the colony were found to be highly variable but the intervals between dusk and arrival time at the colonies increased throughout the breeding period. This was not an unexpected result, as previous studies had recorded fairy prions as arriving just after dusk (Richdale, 1945a) and the timing of dusk varies with respect to time of year. However, most birds arrived substantially later than dusk. This may be linked to variation in duties during the breeding cycle (Bourgeois et al., 2008). For example, in September, the birds return to colonies to prepare and defend their burrows and to re-establish pair bonds with the previous year's mate or seek a new mate (Warham, 1990). It is therefore advantageous to arrive earlier in order to secure both the desired burrow and mate. Once the egg is laid, both birds of a pair take turns in the incubation and chick feeding duties with the burrow nearly always occupied day and night by at least one bird or the chick which means that early return becomes less important. In addition, later arrival during chick-rearing may be linked to a longer time spent out foraging at sea in order to provide the chick with a sufficient meal size (Klomp & Furness, 1992).

Birds tended to arrive later at those burrows that were frequented by tuatara. Tuatara may sit at the entrance to their burrow for several hours (pers.obs.) and may temporarily block a fairy prion's access. This may be a function of the timing of the prions arrival at the colony and the subsequent frenetic use of the burrow coinciding with nightfall, when tuatara tend to emerge from their burrows (Saint Girons et al., 1980), which could mean that fairy prions are delayed from entering their burrow if tuatara are at or near the entrance.

4.5.3 Activity at the burrow

The influences on the activity levels at the burrow each night varied among months. This is intuitive as the purpose of activity also varied with respect to month. In September, birds are renewing old bonds and investigating suitable burrows. In October, birds spend relatively long periods of time at the burrow whilst incubating their egg (24 hours +), but still linger at the entrance in an apparent need to socialise. In January, birds arrive with a definite purpose, to feed their chick and stay a relatively short time.

In September, neither a resident tuatara nor visits by random tuatara seemed to have any effect on the level of activity at a burrow. It is possible that when the birds are socialising there is too much disturbance for the tuatara so it vacates the burrow. The nesting activity of the prions involves a great deal of activity on the forest floor and potentially may interfere with tuatara social behaviours (Gillingham et al., 1995). When both individuals of a pair are present on any one night, they enter and exit the burrow more often than when alone at the burrow. This may also be an opportunity for birds to strengthen pair bonds. Breeding success amongst seabirds is strongly associated with continued partnership with the same mate (Bradley et al., 1990). September is also the only period in which the only environmental factor, temperature, affects activity levels at the burrow. It is possible that weather conditions play a greater role during this period in the absence of any parental duties.

During the egg incubation period in October and November, tuatara again have no significant effect on activity levels at the burrow. Arrival time was the only predictor of time spent at the entrance; those birds that arrived at the burrow earlier spent noticeably longer socialising at the burrow entrance than those birds which arrived later. The fairy prions leave their colonies in the darkness preceding daybreak (Harper, 1976) to avoid daytime predators such as skua and falcons. Therefore, those that arrive later, have fewer hours of darkness in which to linger at the colony, and despite arrive late, no fairy prions were recorded leaving during daylight hours.

In January when fairy prions visit their chick, they spend much longer at the burrow than necessary to complete feeding. Our analyses showed that tuatara affect the amount of time that an adult fairy prion will spend in a burrow with their chick. Both a resident tuatara and visits from random tuatara almost halved the time that an adult prion spent in the burrow. If tuatara are disturbing the prions' use of the burrow to an extent that it causes stress to the bird this could impact upon chick survival. Studies have shown that reproductive effort in seabirds

reduces adult body condition and survival (Golet *et al.*, 1998, Golet & Irons, 1999), and the tenet of life-history theory dictates that long-lived animals such as seabirds should maximise expected lifetime reproductive success by limiting investment in any single reproductive event (Stearns, 1992). Therefore, if a burrow in a single year presents above average challenges for a successful reproductive event, due perhaps to the presence of a predator such as the tuatara, the birds may reduce the amount of effort put into the rearing of their offspring in that particular year.

4.5.4 Conclusions

In contrast to previous studies which have targeted the association between fairy prions and tuatara from the tuatara perspective (Newman, 1987), in terms of predation levels (Walls, 1978) or looked at the burrow occupation of both (Newman, 1978, Gaston & Scofield, 1995, Markwell, 1998), this study investigated the interaction in terms of potential effects on the fairy prions' use of the burrow. As a result, new aspects of this association and new insights into fairy prion breeding ecology have been achieved. Since there is some evidence that tuatara are having a negative effect on fairy prions' use of their burrow, we cannot call this interaction a commensalism. Neither can we call it a mutualism as there is no evidence to support the fact that fairy prions are gaining any fitness benefits from the association. In certain instances, it may be that this interaction is best classed as a parasitism with the tuatara benefitting from burrow use and easy predation opportunities (Walls, 1978, Markwell, 1998), to the detriment of the fairy prions' lifetime reproductive success. In other instances it may simply be a case of competition for a limited resource (a burrow) with the outcome varying depending on the individuals and the circumstances involved.

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CHAPTER FIVE

Sharing a burrow with a seabird increases the body temperature of a reptile

5.1 Abstract

The tuatara is a medium-sized burrowing reptile, active primarily at night in a temperate climate. Throughout most of their natural distribution, tuatara coexist often in the same burrows as procellariiform seabirds. The presence of a seabird within a particular burrow would have an impact on the suitability of that burrow for habitation by tuatara. Burrows containing birds are occupied and may therefore be undesirable to a solitary tuatara, but the microclimate within that burrow may also be modified. The body temperatures of tuatara in both occupied and unoccupied fairy prion burrows were recorded with the use of dataloggers. Tuatara that occupy burrows containing a fairy prion were able to maintain up to 1.8°C higher body temperatures through the night for several months of the year. For two out of the three years studied, tuatara cohabiting with fairy prions were significantly warmer for mean hourly body temperature between 1900 and 0800 hours in October. The presence of a bird had no significant effect on the amount of time tuatara spent in their preferred temperature range but it did influence the effectiveness of thermoregulation. In January there was an overall trend for tuatara cohabiting with a seabird to have warmer body temperatures but this was not statistically significant for most of the time. These results show for the first time that the presence of a seabird within a burrow has direct transferable thermal benefits to a reptile. The next step is to investigate whether these thermal benefits increases fitness through increased growth rates or reproductive output.

5.2 Introduction

Terrestrial vertebrates can confer benefits on other species by two major mechanisms: a) behaviours that increase feeding efficiency and/or decrease predation risk (Dickman, 1992,

Chapman & Chapman, 2000), and b) physical modification of the environment, i.e. ecosystem engineering (Jones et al., 1994, Lawton, 1994). Most positive interactions among terrestrial vertebrates appear to be commensalism (+/0 interaction), where one species provides a benefit to a partner without being negatively affected (Dickman, 1992). The interaction between the species may be dynamic with direct behavioural interactions and coordinated activities, or just passive associations with no sign of direct interaction (Stensland et al., 2003). A passive association can be the result of two or more species selecting similar habitats or sites because of a common resource (Stensland et al., 2003) , for example, different bat species in Mexico occupy the same caves where they day roost (Arita & Vargas, 1995). Mixed species associations have been described for a lot of species within fish (Barlow, 1974, Wolf, 1985), birds (Berner & Grubb Jr, 1985, Graves & Gotelli, 1993, Develey & Stouffer, 2001) and mammals (reviewed in Stensland et al., 2003), but detailed behavioural studies are rare except in primates (Stensland et al., 2003). In general, linkages among population dynamics of ecosystem engineers, dynamics of species that depend on those engineers, and processes that condition their interactions are poorly known (Gurney & Lawton, 1996). In order to preserve ecosystem integrity such information is of fundamental importance, because humans influence both the abundance and distribution of ecosystem engineers, and the range of natural processes in many ecosystems (Gutiérrez et al., 2003, Machicote et al., 2004).

Many studies have described intraspecific interactions for thermal benefits, for example, communal nesting in mammals such as muskrats *Ondatra zibethicus* (Bazin & MacArthur, 1992, MacArthur *et al.*, 1997), and huddling in birds, e.g., common bushtits, *Psaltriparus minimus* (Chaplin, 1982). Emperor penguins (*Aptenodytes forsteri*) form huddles raising ambient air temperatures from -17°C up to 37.5°C (Gilbert et al., 2006). Communal hibernacula where snakes overwinter are also seen in many species of snakes (e.g. garter snakes *Thamnophis sirtalis* and rattlesnakes *Crotalus viridis*; Gregory, 1974). However, studies on interspecies interactions based on thermal benefits are poorly represented in the literature.

When considering interspecies interactions, associations between terrestrial vertebrates and burrow nesting seabirds are not always immediately obvious because outside of the breeding season, seabirds spend most of their time out at sea (Falla, 1993). However, these seabirds are often ecological drivers of the terrestrial ecosystems where they breed (Smith, 1976, Mulder & Keall, 2001, Markwell & Daugherty, 2002, Miskelly *et al.*, 2009). As a consequence of their large colonies, petrels can dominate the ecology of breeding sites through their burrowing activity,

trampling of vegetation, collection of ground cover vegetation for nest linings, and especially the importation of vast quantities of marine-sourced nutrients deposited at the colonies as droppings, regurgitations, failed eggs and corpses (Smith, 1976, Furness, 1991, Okazaki *et al.*, 1993, Warham, 1996). The enrichment of habitat within seabird colonies can even have a positive effect on the lifetime reproductive success of large mammals, such as red deer (Iason et al., 1986). On Stephens Island, New Zealand, a small petrel, the fairy prion (*Pachyptila turtur*) forms a close association with a reptile, the tuatara (*Sphenodon puctatus*). These animals share burrows and the fairy prion exerts a major influence on both burrow use and population densities of the tuatara (Newman, 1987).

The close ecological relationship between petrels and tuatara has been noted since the 1800's (Mair, 1871, Reischek, 1881, Ramstad et al., 2007). In the past, the whole New Zealand coastline, and many inland areas, were honeycombed with burrows of hundreds of millions of petrels, prions, penguins, and shearwaters (Worthy et al., 2002). Despite a long awareness of their coexistence, the exact nature of the symbiotic relationship between tuatara and seabirds such as fairy prions is still uncertain. However, it appears that this association has positive effects on the tuatara population. Seabirds deplete the understory vegetation in forested areas and increase the invertebrate biomass by nutrient addition (East et al., 1995). The increase in prey items potentially allows higher densities of tuatara to occur in an area, as is seen on Stephens Island where greater tuatara numbers are found in areas with more fairy prions (Markwell, 1998), up until high densities of prions (>2 burrows/m^2) when tuatara numbers are reduced (Newman, 1987). It is well established that tuatara frequently occupy seabird burrows despite being able to construct their own (Mair, 1871, Reischek, 1886). Predation by the tuatara on the birds' eggs and chicks may provide important nutrients at an energy demanding time of year as they approach the mating season (Crook, 1975, Walls, 1978, Walls, 1981). However, despite occasional predation on the eggs, chicks and even adults, the prion population as a whole is not significantly decreased by tuatara (Markwell, 1998).

Additionally, little is known about the thermal aspects of the tuatara-seabird coexistence. Previous studies (Godfrey et al., 2008, Besson, 2009) have hypothesised that burrows containing a seabird would naturally be warmer and therefore any tuatara living in such a burrow would also be warmer. Traditional ecological knowledge by Maori have also noted this association (Ramstad et al., 2007). However, to my knowledge, no prior published study has actually tried to substantiate this idea or quantify the degree to which tuatara living with a bird might be warmer.

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To better understand the association between tuatara and fairy prions I measured the body temperatures of tuatara sharing burrows with fairy prions and those occupying empty burrows, and the effect that an increase in body temperature could have for a tuatara's fitness is discussed. Do seabirds provide thermal benefits for tuatara? If they do increase the body temperature of tuatara, could this influence fitness?

5.3 Methods

5.3.1 Study site

Stephens Island (also known by its Māori name, Takapourewa), is a 150-ha island located in Cook Strait, New Zealand (40°40'S, 174°00'E). This research was conducted over three years (2008-2011) in a forest patch called Keepers Bush which consists of a mix of degraded original forest and regenerating scrub following fencing in 1951. Canopy height is approximately 3-5m (Newman, 1987). Soils are either clay and shallow, or where burrowing seabird activity is greatest, very deep, acidic and friable (Ward, 1961).

5.3.2 Burrow inhabitants and use

The tuatara, *Sphenodon puctatus,* is a medium-sized reptile, up to 450mm total length and 500g in females, and up to 600mm total length and 1kg in males (Mulder & Keall, 2001). Tuatara inhabiting forested areas show diurnal, crepuscular and nocturnal activity (Gillingham & Miller, 1991), coming out of their burrows to bask during the day, and hunting at night. Stephens Island is home to the largest population of tuatara with estimated densities in the forest of up to ~2700 individuals /ha (Moore et al., 2009b). There are no other reptiles of a comparable size on the island, the closest being three species of geckos which occupy shrubs, and four species of skink which may also be found within burrows.

Tuatara differ from most lizards in that they are long-lived (80-100 years), and breeding intervals are prolonged for females (i.e. asynchorous reproduction occurs every 2-5 years, with 8-10 months from insemination to oviposition (Cree et al., 1992)). Tuatara courtship begins in late January and continues throughout February (Gillingham et al., 1995). Mating peaks in March (Austral autumn) (Moore et al., 2009a). During late summer tuatara are physically most active, and especially in times of drought, predation on prion chicks could alleviate a desperate need for nutrients and water (Walls, 1978).

There are approximately one million fairy prions that use Stephens Island as a breeding ground (Harper, 1985). Fairy prions are small seabirds (length 25cm, weight 90-175g) and feed entirely out at sea (Marchant & Higgins, 1990). They arrive on Stephens Island throughout June, and by late July old burrows are cleared out and pairing begins (Walls, 1978). Prions lay eggs in October, incubate them for approximately 55 days (Falla, 1993), resulting in fledging in late January and departure from the island by late February (Walls, 1978). Nests are visited only at night (Marchant & Higgins, 1990). The only other seabird present in notable numbers at any time of year is approximately 1,000 sooty shearwaters (*Puffinus griseus*) (Markwell, 1997), although little blue penguins (*Eudyptula minor*) are also seen regularly during the breeding season but not in large numbers (pers. obs.).

Tuatara and fairy prions share burrows in the ground and most are probably constructed by the birds (Newman, 1982a). On Stephens Island the burrows range from 0.2 to 0.7m below the soil surface (Markwell, 1997), and the burrows can be complex with many connected chambers and openings, or simple with only one or two entrances (Newman, 1982b). A burrowscope was used to determine the occupancy of 150 randomly selected burrows in October 2009. Burrows were checked between 0900 and 1100 hours when tuatara were likely to be in their burrows or at the burrow entrance.

5.3.3 Temperature monitoring

Fieldtrips were carried out in October and January from 2008 to 2011. On each trip 20-30 adult tuatara were caught by hand. Tuatara were weighed and measured (snout-to-vent length (SVL), vent-to-tail length and regrowth of tail) and sex was recorded based on secondary sexual characteristics (tuatara are sexually dimorphic). Dataloggers (Thermochron iButton DS1921G, reported accuracy ± 1°C; Dallas Semiconductor, TX, USA), set to record temperature every 15 minutes, were attached to the base of the tail of each tuatara with surgical tape. This method of recording body temperature is described in chapter 2. The iButtons remained attached for a period of 7-10 days. Compared to other individuals within the population, the tuatara in this study showed no obvious modification of behaviour as the result of thermochron attachment.

The majority of individuals were identified by a unique bead tag on their nuchal crests and tuatara that were not tagged with beads were marked with a number on their left side by a non-toxic marker. Daily observations were then made at 1400, 1600, 2200, 2400, 0200 and sometimes 0400 hours to note the location of the tuatara, to confirm datalogger attachment

and note any bird activity at the burrow. A burrowscope was used to determine occupation of each burrow, during the afternoon at the beginning and end of each fieldtrip to establish occupancy by a bird or chick.

Ambient temperature was recorded with the use of a temperature dataloggers (Tidbits®; reported accuracy ± 0.2°C Onset Computer Corporation, Massachusetts, USA). These were positioned in the field in areas of both full shade and full sun (just outside forest). A datalogger was placed on the ground surface and covered with leaf litter in both areas and one was tied to the north face of a tree trunk at the height of 1m in the forest. These were left in the habitat for 2.5 years (October 2008 - March 2011) and the dataloggers recorded temperature every hour. This method did not capture every nuance of habitat variability but it represented the general thermal properties of the two extremes available in the operative thermal environment: full shade versus full sun.

5.3.4 Analyses

Data from the first 24 hrs were omitted from the analyses while tuatara were conditioned to wearing the dataloggers. The temperatures were averaged to give the mean temperature for each hour. All data were analysed using the statistical programme SPSS version 18.0 and significance was assumed at $P < 0.05$.

Tuatara body temperature data (T_b) were not normally distributed and could not be transformed using any of the conventional methods. The data were not independent and contained repeated measurements from the same individuals both within days (at each hour) and across days, therefore Generalised Estimating Equations (GEE) were used as these do not make any distributional assumptions (Zuur et al., 2009). A Gamma distribution with log link was inputted for the probability distribution, as the dependent variable T_b was a scaled, non-normal response. Ar(1) was used for the working correlation matrix structure as this matrix assumes regular distances (or time intervals) between observations and can be used for any data set in which there is a time order (Zuur et al., 2009). Data were initially analysed separately for each month (adult bird in burrow in October, chick in burrow in January) and year (ambient temperatures can vary between years) with the presence of a bird in the burrow a categorical predictor. Sex is not a predictor of temperature alone (chapter 2), but since males and females behave differently, sex was incorporated as a covariate, and this also helped explain size differences as sex is correlated with both SVL and mass in tuatara (Dawbin, 1982).

The same data were further explored by analysing separately each hour to minimise the amount of longitudinal observations per individual and also to tease out temperature differences at a finer scale. Relatively large numbers of longitudinal observations from only a few individuals in a GEE means that the standard errors produced are less reliable (Zuur et al., 2009). All T_b data at each hour in October 2008, 2009, 2010 and January 2009, 2010 and 2011 were analysed using GEE to test whether the presence of a bird in a burrow influenced T_b data.

The mean hourly T_b for individuals cohabiting with fairy prions minus the mean hourly T_b for individuals which were the sole occupant of their burrow was graphed to illustrate any differences in body temperature between the two groups. This was calculated and graphed for all years in both October and January.

The effectiveness of thermoregulation (d_e-d_b) and the index of thermoregulation (E_x) were also compared between tuatara which occupied burrows containing a bird and those that were the sole occupants of their burrows. Terminology and symbols used in all analyses of tuatara thermoregulation were the same as those used in chapter 2: T_e = environmental temperature, T_b = tuatara body temperature, T_{set} = range of preferred body temperature, d_b = deviation of T_b from T_{set}, d_e = deviation of T_e from T_{set}. If animals thermoregulate precisely then d_e-d_b will be a positive number, if animals select habitats randomly with respect to T_e then this index will be close to zero and if animals actively avoid habitats in their T_{set} range d_e-d_b will be a negative number. E_x is the proportion of T_b values that fall within T_{set} when T_e permits those temperatures to be achieved.

The effectiveness of thermoregulation index (d_e-d_b) was normally distributed but again the data were not independent and contained repeated measurements from the same individuals both within days (at each hour) and across days, therefore Generalised Estimating Equations (GEE) were used. The linear probability distribution was used, as the dependent variable d_e-d_b was a scaled, normal response with values both below and above zero. Ar(1) was again used for the working correlation matrix structure.

5.4 Results

A total of 72 complete temperature records were obtained for tuatara (57 individuals) in October over the three years (n = 45; with bird, n = 27; without bird), and 82 temperature records for tuatara (63 individuals) in January over the three years (n = 61; with bird, n = 21; without bird). A total of 91 individual tuatara were sampled in October and January over the three year period, with some individuals sampled only once and some sampled up to four times. Temperature records every 15 minutes were summarised as 25,857 hourly records. Of the 150 burrows checked for occupancy, 104 were occupied, 43 were unoccupied and I was unable to determine the occupancy of three burrows with certainty. Of those occupied, 22 contained a resident tuatara, 57 burrows contained an adult fairy prion and 25 burrows contained both a tuatara and a fairy prion.

5.4.1 October

Daily mean ambient temperatures in the shade for the periods corresponding to T_b measurements were: October 2008, 11.9 ± 0.1°C (range: 10.7 – 13.7°C), in 2009, 11.0 ± 0.1°C (range: 9.4 – 12.9°C), and in 2010, 11.2 ± 0.1°C (range: 9.4 – 13.2°C).

In October 2008, both the presence of a bird (Wald Chi-Square = 11.919, df = 1, P = 0.001), sex (Wald Chi-Square = 13.381, df = 1, P < 0.001), and the interaction between the two (Wald Chi-Square = 17.426, df = 1, P < 0.000), were significant influences on body temperature. Tuatara sharing burrows with birds had an overall mean temperature of 13.0 ± 0.1°C, and were warmer than those without a bird in their burrow, mean 12.4 ± 0.1°C. Overall, males were on average warmer than females with a mean of 12.7 ± 0.1°C and 12.3 ± 0.1°C respectively.

In October 2009, the presence of a bird was a significant influence on body temperature (Wald Chi-Square = 9.760, df = 1, P =0.002), and the interaction with sex (Wald Chi-Square = 10.682, df = 1, P = 0.001), but sex alone was not significant (Wald Chi-Square = 0.501, df = 1, P = 0.479). Tuatara sharing burrows with birds had an overall mean temperature of 11.5 ± 0.1°C, and were warmer than those without a bird in their burrow (mean 11.3 ± 0.1°C).

In October 2010, none of the predictors were significant within the model including bird (Wald Chi-Square = 0.033 df = 1, p = 0.855), sex (Wald Chi-Square = 0.831, df = 1, P = 0.362), and bird*sex (Wald Chi-Square = 0.888, df = 1, P = 0.346). Although not statistically significant,

tuatara sharing burrows with birds had an overall mean temperature of 13.8 ± 1.6°C, which was warmer than those without a bird in their burrow (mean 11.7 ± 0.1°C).

During the night in October, tuatara cohabiting with birds were significantly warmer for mean hourly temperatures between 1900 to 0800 hours for both 2008 and 2010 (Table 1.). The greatest difference between body temperatures of tuatara cohabiting with birds and those without a bird in their burrow was 1.1°C at 1200 hours in 2008, 0.7°C at both 0400 and 1200 hours in 2009, and 1.4°C at 1200 hours in 2010 (Fig. 1). In 2010, the mean T_b of the group of tuatara with birds in their burrows was higher than the group of tuatara without a bird in their burrow at every hour. In 2009, there was no difference between the two groups from 1200 – 2400 hours and in 2008 the difference between the two groups fluctuated above and below zero throughout the day. In 2009, there were only significant differences at 0100 and 0300 hours, but there was an overall trend for warmer temperatures for the group of tuatara cohabiting with a bird (Fig. 2). During the day, tuatara cohabiting with a bird were significantly warmer early in the morning: 0800 hours (in years 2008, 2009 and 2010), 0900 (2009 and 2010), 1000 (2010) and 1100 (2010) and also in the early evening: 1800 (2008 and 2010) and 1900 hours (2010).

Tuatara inhabiting burrows with a bird incubating an egg had significantly higher d_e - d_b values than those tuatara without a bird in their burrow (Wald Chi-Square = 11.106, df = 1, P = 0.001). Those with a bird in their burrow had a mean d_e - d_b value of - 0.3 ± 0.1°C, and those without had a d_e - d_b value of - 0.7 ± 0.1°C. This index is a negative number when animals avoid habitats within their preferred body temperature range, is close to zero if animals select habitats randomly with respect to their preferred body temperature range, and is a positive number if animals actively thermoregulate.

The E_x indices for tuatara with a bird compared to those without a bird in their burrow revealed no difference between the two groups (Wald Chi-Square = 1.511, df = 1, P = 0.219). The index of thermoregulation (E_x) was 12% for those without a bird, 13.5% with a bird. Tuatara without a bird were below T_{set} 85% of the time when conditions permitted, whereas those with a bird, were below T_{set} 77.8% of the time. Tuatara were above T_{set} 3.5% of the time without a bird and 8.7% of the time with a bird.
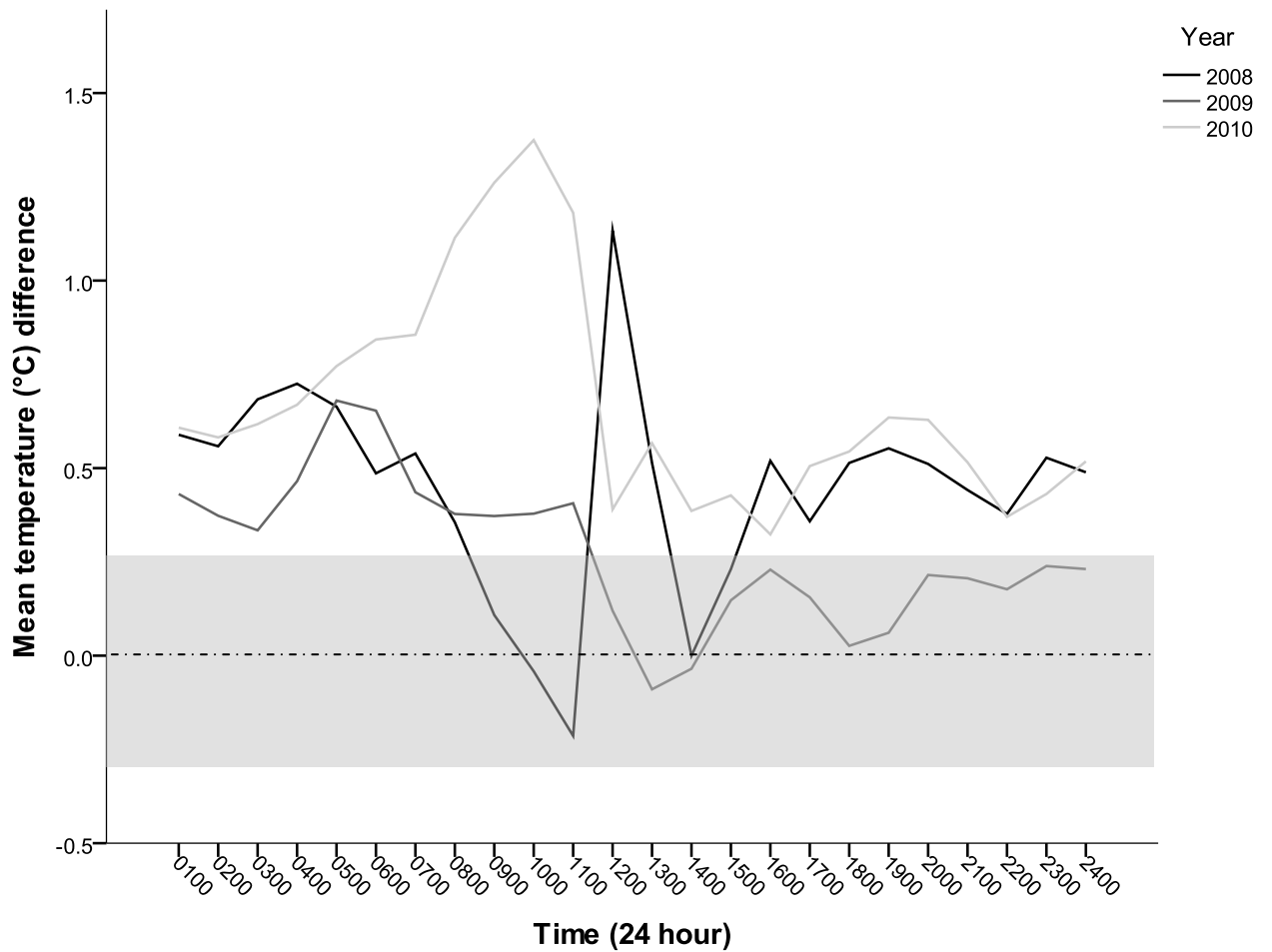
Figure 1. Mean hourly temperature of tuatara with a bird in their burrow minus mean hourly temperature of tuatara without a bird in their burrow in October in 2008, 2009 and 2010. The grey box highlights mean temperature differences which are close to zero (within 0.25°C).

Table 1. Results of GEE models to test whether the presence of a bird in a burrow influenced T_b data at each hour in October. Highlighted times indicate significant differences between T_bs of tuatara with a bird in their burrow compared to T_bs of tuatara that are the sole occupants of their burrow.

| Oct-08				Oct-09				Oct-10			
Time (hrs)	Wald Chi-Square	df	P	Time (hrs)	Wald Chi-Square	df	P	Time (hrs)	Wald Chi-Square	df	P
0100	21.103	1	0.000	0100	6.760	1	0.009	0100	9.225	1	0.002
0200	22.617	1	0.000	0200	4.395	1	0.036	0200	7.157	1	0.007
0300	32.299	1	0.000	0300	2.208	1	0.137	0300	10.037	1	0.002
0400	25.375	1	0.000	0400	2.790	1	0.095	0400	14.018	1	0.000
0500	18.709	1	0.000	0500	6.047	1	0.014	0500	19.824	1	0.000
0600	14.486	1	0.000	0600	2.941	1	0.086	0600	19.288	1	0.000
0700	20.416	1	0.000	0700	3.285	1	0.070	0700	13.825	1	0.000
0800	8.886	1	0.003	0800	3.847	1	0.050	0800	8.535	1	0.003
0900	0.537	1	0.464	0900	5.192	1	0.023	0900	5.785	1	0.016
1000	0.290	1	0.858	1000	2.491	1	0.115	1000	4.165	1	0.041
1100	0.396	1	0.529	1100	4.813	1	0.028	1100	3.080	1	0.079
1200	1.105	1	0.293	1200	0.290	1	0.590	1200	0.000	1	0.991
1300	0.104	1	0.747	1300	0.027	1	0.869	1300	0.145	1	0.704
1400	0.933	1	0.933	1400	0.003	1	0.958	1400	0.001	1	0.970
1500	0.269	1	0.604	1500	0.022	1	0.883	1500	0.007	1	0.935
1600	2.090	1	0.148	1600	0.072	1	0.788	1600	0.001	1	0.973
1700	2.404	1	0.121	1700	0.106	1	0.745	1700	0.497	1	0.481
1800	7.346	1	0.007	1800	0.016	1	0.900	1800	1.571	1	0.210
1900	16.422	1	0.000	1900	0.036	1	0.849	1900	4.170	1	0.041
2000	15.430	1	0.000	2000	1.084	1	0.298	2000	5.275	1	0.022
2100	11.981	1	0.001	2100	1.094	1	0.296	2100	6.699	1	0.010
2200	9.216	1	0.002	2200	0.088	1	0.148	2200	6.193	1	0.013
2300	22.802	1	0.000	2300	3.087	1	0.079	2300	8.202	1	0.004
2400	15.520	1	0.000	2400	1.802	1	0.180	2400	7.018	1	0.008
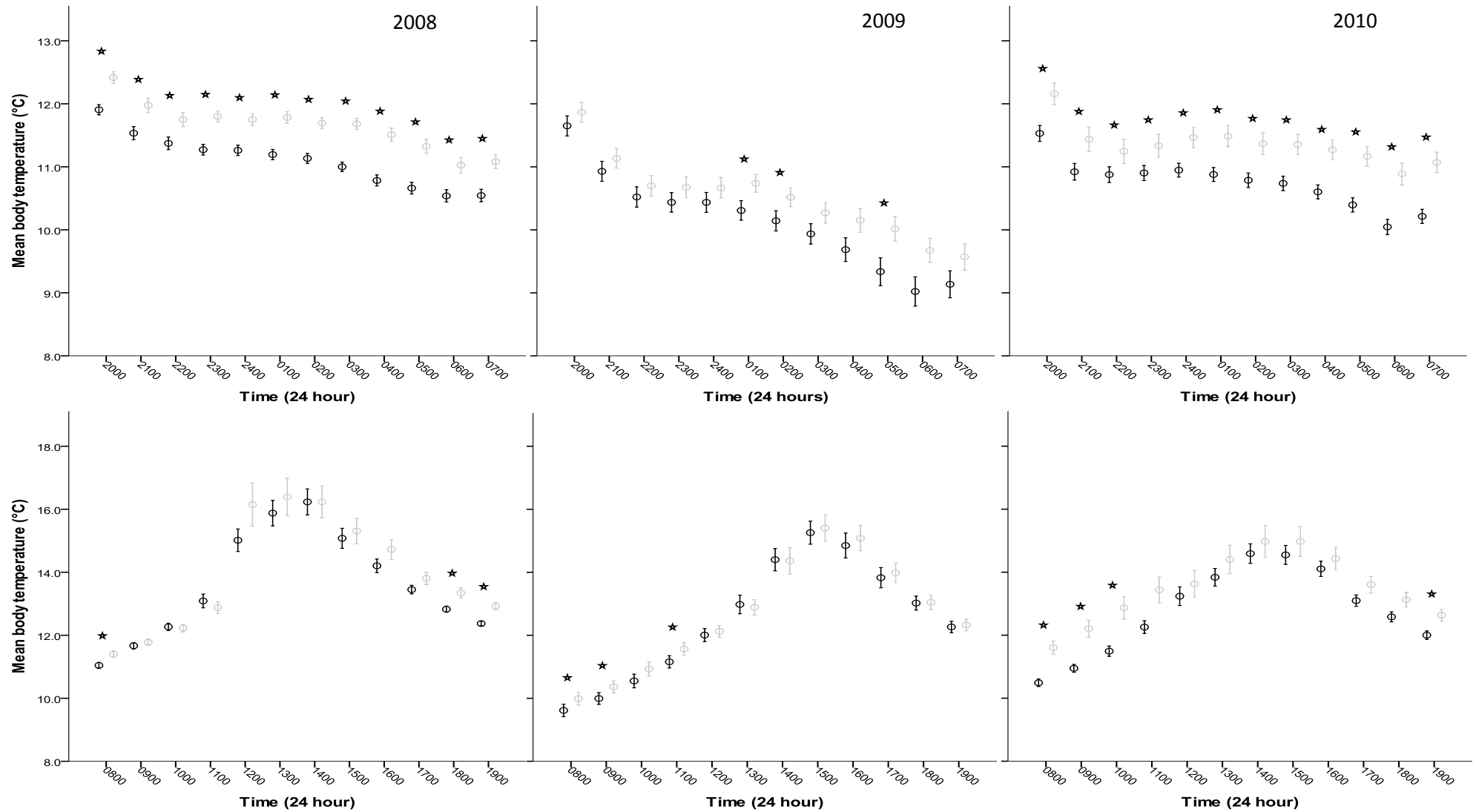
Figure 2. Mean hourly temperature ± 1SE during October 2008, 2009 and 2010. Grey circles represent tuatara cohabiting with birds and black represent tuatara that are the sole occupants of their burrow. Stars indicate significant differences (P ≤ 0.001). Top row = 2000 – 0700 hours, bottom row = 0800 – 1900 hours.

5.4.2 January

Mean ambient temperatures in the shade for the periods corresponding to T_b measurements were: January 2009, 14.6 ± 0.1°C (range: 12.3 – 17.2°C), in 2010, 13.8 ± 0.1°C (range: 11.8 – 17.2°C), and in 2011, 15.2 ± 0.1°C (range: 13.5 – 17.3°C).

In January 2009, the effect of a bird (chick) in the burrow had a significant positive effect on tuatara body temperature (Wald Chi-Square = 5.059, df = 1, *P* = 0.025), while sex (Wald Chi-Square = 0.211, df = 1, *P* = 0.646), and the interaction bird*sex did not (Wald Chi-Square = 0.354, df = 1, *P* = 0.552). Mean T_b for tuatara without a chick in their burrow was 15.9 ± 0.1°C and with a chick was 16.4 ± 0.1°C.

 In 2010, none of the predictors had significant effects on T_b, bird (Wald Chi-Square = 0.230, df = 1, *P* = 0.631), sex (Wald Chi-Square = 0.723, df = 1, *P* = 0.395), or bird*sex (Wald Chi-Square = 0.016, df = 1, *P* = 0.901), but the slopes revealed that the presence of a bird did have a positive effect on T_b, $\beta_{bird=1}$ = 2.705 (95% CI = 2.560 – 2.844; *P* < 0.000). Mean T_b for tuatara without a chick in their burrow was 14.9 ± 0.2°C and with a chick 15.4 ± 0.4 °C.

In 2011, again none of the predictors had significant effects on T_b, bird (Wald Chi-Square = 0.733, df = 1, *P* = 0.392), sex (Wald Chi-Square = 0.523, df = 1, *P* = 0.470), or bird*sex (Wald Chi-Square = 0.375, df = 1, *P* = 0.540) but the slopes revealed that the presence of a bird does have a positive effect $\beta_{bird=1}$ = 2.814 (95% CI = 2.741 – 2.887; *P* < 0.000). Mean T_b for tuatara without a chick in their burrow was 16.5 ± 0.1°C and with a chick was 16.7 ± 0.1°C.

For differences in hourly temperatures between tuatara cohabiting with a bird and those not, January was similar to October but with fewer significant differences among the periods (Table 2). The greatest difference in T_b between tuatara cohabiting with birds and those without a bird in their burrow was 0.4°C at 1600 hours in 2009, 1.8°C at 1200 hours in 2010 and 1.4°C at 1300 hours in 2011 (Fig. 3). In 2011, there was very little difference in mean temperature between tuatara cohabiting with a bird and those not. The overall trend was for the tuatara cohabiting with birds to have a higher mean hourly temperature during the night (2000 – 0700) (Fig. 4). However, in 2009 there were only significant differences between the two groups at 0600, 0700, 0900 and 1000 hours and never during the night (Table 2). In 2010, the two groups were not significantly different at any hour and in 2011, it was only at 0100 and 0200 hours that the two groups differed with those cohabiting with a bird always maintaining a warmer mean body temperature at any of the significant differences.

Tuatara with a chick in their burrow had significantly higher d_e-d_b values than those tuatara without a bird in their burrow (Wald Chi-Square = 5.841, df = 1, P = 0.016). Those with a bird in their burrow had a mean d_e-d_b value of 0.4 ± 0.2°C, and those without had a d_e-d_b value of -0.1 ± 0.1°C. There was no significant difference between the E_x indices for tuatara with a bird compared to those without a bird in their burrow (Wald Chi-Square = 0.105, df = 1, P = 0.746). The index of thermoregulation (E_x) was 31.4% for those without a bird, and 41% with a bird. Tuatara without a bird were below T_{set} 60.5% of the time when conditions permitted, and below T_{set} 47% of the time with a bird. They were above T_{set} 8.1% of the time without a bird and 12% of the time with a bird.
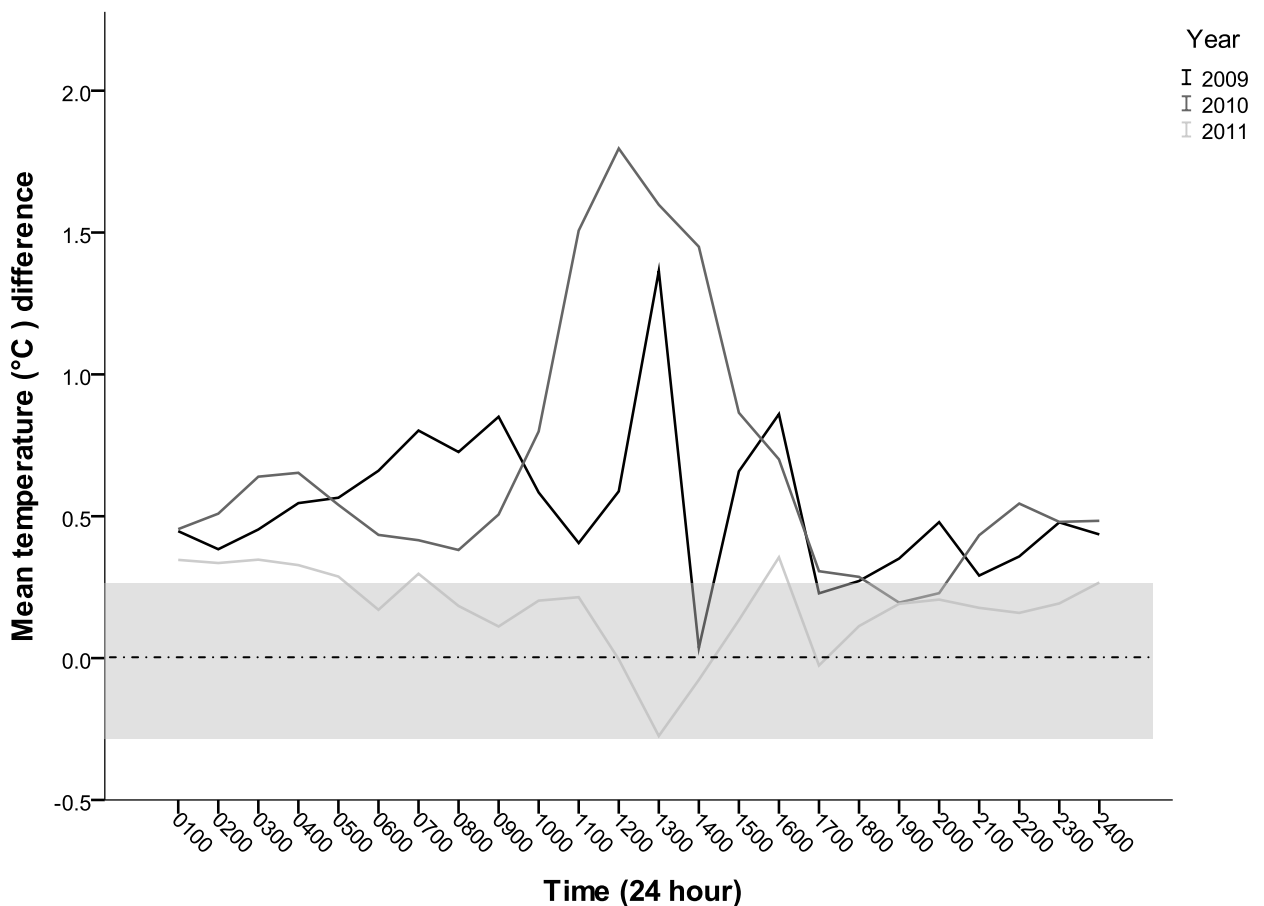

Figure 3. Mean hourly temperature of tuatara with bird in their burrow minus mean hourly temperature of tuatara without a bird in their burrow in January in 2009, 2010 and 2011. The grey box high lights mean temperature differences which are close to zero (within 0.25°C).

Table 2. Results of GEE models to test whether the presence of a bird in a burrow influenced T_b data at each hour in January. Highlighted times indicate significant differences between T_bs of tuatara with a bird in their burrow compared to T_bs of tuatara that are the sole occupants of their burrow.

Jan-09				Jan-10				Jan-11			
Time (hrs)	Wald Chi-Square	df	P	Time (hrs)	Wald Chi-Square	df	P	Time (hrs)	Wald Chi-Square	df	P
0100	2.216	1	0.137	0100	1.26	1	0.262	0100	4.207	1	0.04
0200	1.305	1	0.253	0200	1.567	1	0.211	0200	4.576	1	0.032
0300	1.947	1	0.163	0300	1.936	1	0.164	0300	3.179	1	0.075
0400	3.49	1	0.062	0400	1.511	1	0.219	0400	1.847	1	0.174
0500	3.382	1	0.066	0500	1.302	1	0.254	0500	1.59	1	0.207
0600	4.867	1	0.027	0600	0.904	1	0.342	0600	1.008	1	0.315
0700	4.187	1	0.041	0700	0.734	1	0.392	0700	2.829	1	0.093
0800	2.944	1	0.086	0800	0.666	1	0.415	0800	1.008	1	0.297
0900	4.927	1	0.026	0900	1.548	1	0.213	0900	0.445	1	0.505
1000	4.039	1	0.044	1000	2.592	1	0.107	1000	0.157	1	0.692
1100	2.644	1	0.104	1100	3.389	1	0.066	1100	0.08	1	0.777
1200	0.744	1	0.388	1200	2.915	1	0.088	1200	0.001	1	0.981
1300	0.93	1	0.335	1300	1.744	1	0.187	1300	0.331	1	0.565
1400	0.037	1	0.846	1400	1.728	1	0.189	1400	0.008	1	0.93
1500	3.463	1	0.063	1500	0.95	1	0.33	1500	0.072	1	0.789
1600	2.636	1	0.104	1600	0.731	1	0.392	1600	0.365	1	0.546
1700	1.222	1	0.269	1700	0.211	1	0.646	1700	0.01	1	0.922
1800	0.805	1	0.37	1800	0.277	1	0.599	1800	0.108	1	0.743
1900	1.434	1	0.231	1900	0.137	1	0.711	1900	0.408	1	0.523
2000	2.774	1	0.096	2000	0.224	1	0.636	2000	0.66	1	0.417
2100	2.51	1	0.113	2100	0.97	1	0.325	2100	1.35	1	0.245
2200	3.205	1	0.073	2200	1.768	1	0.184	2200	0.826	1	0.363
2300	3.715	1	0.054	2300	1.459	1	0.227	2300	1.122	1	0.29

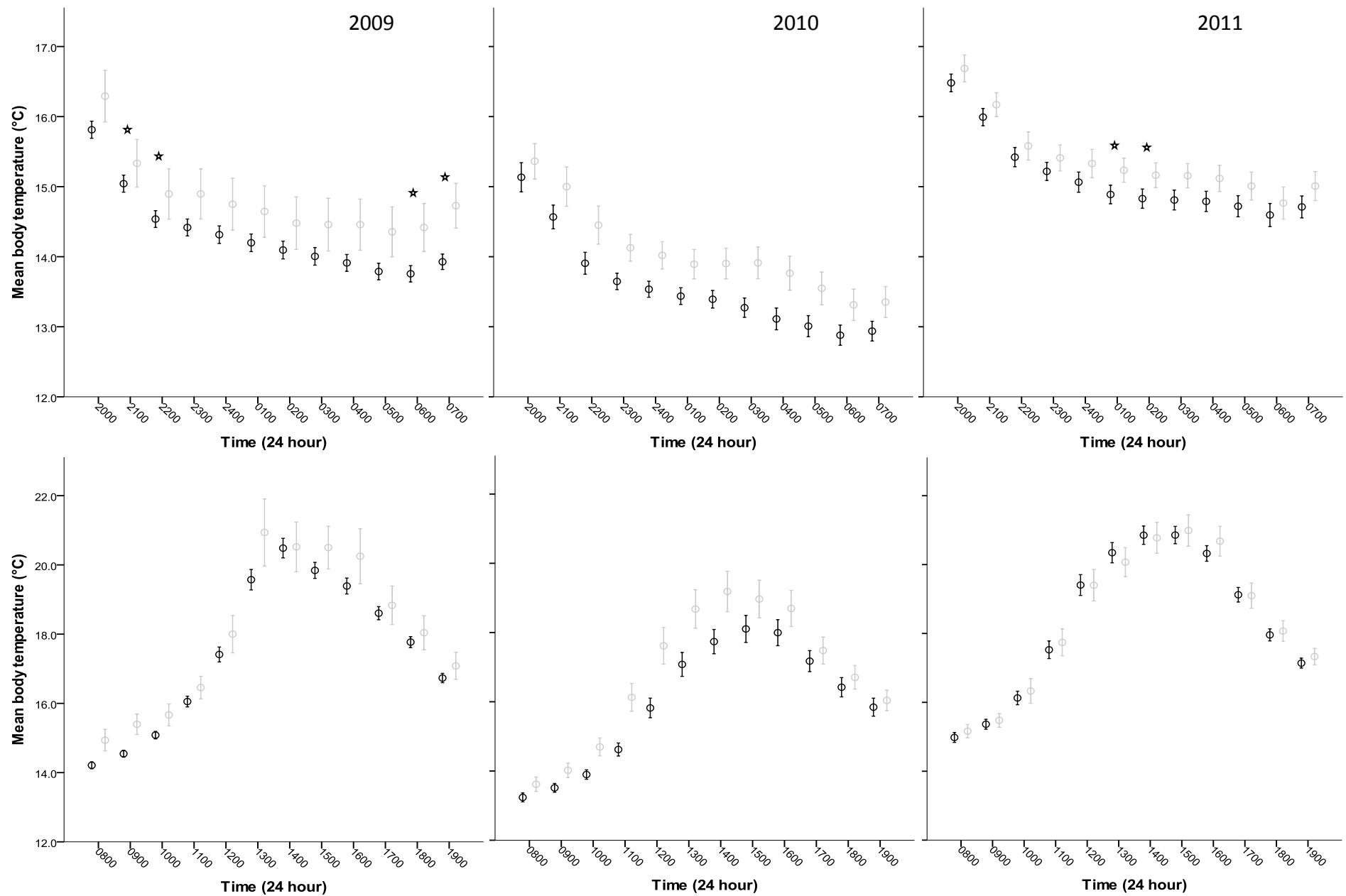*Figure 4. Mean hourly temperature ± 1SE during January 2009, 2010 and 2011. Grey circles represent tuatara cohabiting with birds and black represent tuatara that are the sole occupants of their burrow. Stars indicate significant differences (P ≤ 0.005) between the two groups. Top row = 2000 – 0700 hours, bottom row = 0800 – 1900 hours.*

5.5 Discussion

Thermoregulation in tuatara has been described in terms of basking behaviour; movement by tuatara into sunspots is the only way that tuatara can get their body temperatures up into their preferred temperature range, as temperatures in the shade may never reach 19.5°C or higher (chapter 2). However, tuatara are active at temperatures as low as 4.5°C (chapter 2). To my knowledge these results provide the first evidence for the impacts of cohabitation with birds affecting the thermal physiology of a reptile. This study shows that when tuatara share a burrow with a bird their body temperature is higher for between one and fifteen hours in a day. This result accords well with intuition, that is, an endotherm produces heat and therefore raises surrounding air temperatures providing a heat source for an ectotherm.

Mean ambient temperatures were 11 - 12°C in October over the three years studied and in only one of the three years was preferred body temperature able to be achieved. These environmental temperatures are far below the preferred range of tuatara (19.5 – 23.1°C), therefore any additional opportunity to maintain a higher body temperature could be valuable at this time of year. Birds enable tuatara to maintain up to 1.8°C higher body temperature through the night for several months of the year, October to January (Austral spring to summer). During the night, tuatara sharing a burrow with a bird had the most obvious thermal benefits, with significantly higher temperatures from 1900 to 0800 hours in October (in two years). However, there were also significant differences at midday. Those tuatara that were warmer during the night may be able to raise their body temperatures faster when basking due to a higher base rate than those tuatara without a bird in their burrow. Similarly, in January, the trend was for tuatara with a bird in their burrow to have a higher mean hourly T_b, but this was rarely significant. Relative environmental temperatures were cooler in October than January (chapter 2) which could explain why thermal differences were less pronounced in January, as all burrows including those without seabirds were warmer than those in October. There were some differences in the results between the three years which could be related to differences in yearly temperatures. For example, in October 2009 the mean differences in body temperature between tuatara cohabiting with birds and those without a bird in their burrow was much lower for most of the day compared to 2008 and 2010. Mean environmental temperatures (CliFlo data base; NIWA, 2011) were similar in the October/November period over the three years, but minimum monthly temperatures were higher in 2009 than in either 2008 or 2010. January 2011 had higher mean temperatures than either 2009 or 2010 and the difference in mean body

temperature between tuatara cohabiting with birds and those occupying empty burrows was less pronounced in this year. Thus, it is possible that thermal benefits from cohabiting with a seabird may only be fully exploited in years with low environmental temperatures.

On Stephens Island, males engage in prenuptial displays and mating during January to March, and although spermatocytogenesis is believed to occur year round, spermiogenesis is maximal in February, abortive in May, arrested in August and incipient in October (Saint Girons & Newman, 1987, Cree *et al.*, 1990). Females lay their eggs in October/November. Therefore, having a burrow in which a bird resides, enabling higher temperatures in October/November could have reproductive implications. Higher temperatures for females could sustain higher levels of activity, i.e. leaving the forest to dig a nest and lay eggs, and higher temperatures for males could facilitate the onset of spermiogenisis. In January, ambient temperatures are warmer, with mean temperatures around 14 to 15°C and environmental conditions regularly permit T_{set} to be reached, therefore the difference in burrow temperatures due to the presence of a chick may be relatively minor. However, if warmer burrows reduce the amount of time required for active thermoregulation, they would potentially allow greater amounts of time to be dedicated to mating behaviours.

There appeared to be differences in the body temperatures of males versus females but this was only significant for two out of the three years in October. This small difference was also only significant when there was no bird in the burrow. This indicates that the presence of a bird in the burrow had a stronger influence on temperature which masked the slightly higher temperature of male tuatara. This would be interesting to tease out further as sex was not significant in other tests on the influence on body temperature (chapter 2). No significant difference was observed in body temperature between males and females in January.

Tuatara with a bird in their burrow had significantly higher d_e- d_b values than those without a bird in their burrow in October, (- 0.3 ± 0.1°C and - 0.7 ± 0.1 °C respectively and in January, 0.4 ± 0.2°C and -0.1 ± 0.1°C respectively), which could mean that the presence of a bird in their burrow enabled them to thermoregulate more effectively. However, all values are close to zero, indicating that tuatara cohabiting with birds are still closer to thermoconformers than thermoregualtors.

The next step would be to determine whether these temperature differences are biologically relevant for tuatara. In ectotherms, an increase in body temperature increases metabolic rate and may increase rates of digestive processes (McConnachie & Alexander, 2004). The primary effect of increasing body temperature during digestion seems to be a marked reduction in the time required for digestion rather than an energetic saving or increased efficiency of digestion (Wang et al., 2002). Tuatara are nocturnal predators, hunting and consuming their prey during the coldest hours of the day, therefore having a burrow warmer than ambient temperatures to retreat to at night could be extremely beneficial in terms of reducing the time it takes to digest food. Refuge temperatures may be important to reach high enough T_b to complete digestive and physiological processes related to the previous night's activity (Kearney & Predavec, 2000). Tuatara are sit and wait predators, and will consume prey such as weta as they come past, but they often retreat to their burrow to consume/digest large prey items (Fraser, 1993; pers. obs.). This behaviour may be primarily concerned with conspecific and predator avoidance but if tuatara remain within the burrow post-feeding, they may obtain thermal benefits for digestion.

An increase in metabolic rate could also lead to higher growth rates for tuatara. It has been shown that temperature of diurnal refuge may affect growth and food intake in Eublepharid nocturnal geckos (Autumn & DeNardo, 1995). Tuatara on Lady Alice Island reach the inferred size of maturity about 2-3 years earlier than on the colder, more southern Stephens Island (Castanet et al., 1988). Thermal benefits for the tuatara could also have reproductive implications. Tuatara take at least ten years to reach sexual maturity and have a low reproductive output. Tuatara eggs have a soft, parchment-like shell. It takes the females between one and three years to provision eggs with yolk, and up to seven months to form the shell. It then takes between 11 and 16 months from the time the eggs are laid to the time they hatch. The rate of reproduction in tuatara is the lowest of any reptile (Cree et al., 1992). Mating occurs in February/March and nesting intervals between two and nine years are known (Cree et al., 1992, Mitchell et al., 2010). The reasons for the variance in nesting frequency between females are still unclear but are possibly linked to their thermal environment and available resources such as food, and the interaction between these, for example, the conversion of energy into reproduction.

It has been previously noted that the presence of seabirds during this annual period from October to January provides tuatara with supplementary protein in the form of eggs and chicks which, particularly for breeding tuatara, may have a direct survival value (pers. obs.,Walls, 1981).

However, a seabird burrow which acts as an enhanced thermal refuge may in fact be a renewable resource for tuatara. By returning to their burrows before the coldest night temperatures, tuatara can escape low air temperatures and hence are able to conserve their heat during the night in the warmer burrow. If some individuals within a population could potentially exploit these thermal refugia, then that could lead to a fitness advantage. Fairy prions like most seabirds display natal philopatry (Greenwood & Harvey, 1982), meaning that they return year after year to the same area, and even to the same burrow (chapter 4). Tuatara also maintain the same territories for many years (Moore et al., 2009b). Therefore, burrows containing a seabird could potentially be a reliable resource that is constant year after year.

However, during prion breeding seasons, tuatara were found more often in burrows unoccupied by birds (Newman, 1987), and in our study approximately 50% of tuatara shared a burrow with a bird (in October 2009), therefore some other costs may outweigh any thermal benefits. Intense competition between prions and tuatara for space was evident in the single-chambered burrows (Walls, 1978). If both optimal and suboptimal patches are equally accessible, then only optimal patches should be selected, but if optimal patches are difficult to exploit, then the costs of finding or reaching optimal patches might outweigh the benefits from these patches (Tracy & Christian, 1986). Interference from the fairy prions may mean that optimal patches, i.e., warmer burrows are more difficult to "exploit".

Our results show for the first time that the presence of a seabird within a burrow has direct transferrable thermal benefits to a reptile. It would be useful to repeat these investigations with both larger sample sizes and over more years with varying weather patterns to evaluate annual variation, sex specific advantages and fitness consequences. Overall, mean body temperatures in October were only significantly higher for tuatara with a bird in their burrow for two out of the three years and in January for one out of the three years, but when hourly data were investigated, there were significant differences in all three years for October. It is therefore important to look beyond mean values to see what is actually happening at discrete time points. Although occupying a fairy prion burrow may not be necessary for survival, it seems to constitute an important and possibly advantageous microhabitat for some portion of the population. Different ecosystem engineers such as other species of seabirds create similar habitats, but a cost/benefit analysis for different associations may not reveal similar flow on thermal effects for tuatara. Measurement of inter-island variation, ideally including other species of procellariiforme seabirds would be useful to reveal the importance of seabirds for

tuatara thermoregulation and to reveal the full range of the cost/benefit balance between this reptile and seabirds.

5.6 References

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CHAPTER SIX

Categorizing the tuatara-fairy prion association: Thesis summary and applications

6.1 Introduction

Understanding the mechanisms and conditions underlying species interactions is a key challenge for ecosystem conservation (Stachowicz, 2001). The classification of interactions has also become useful in terms of conservation efforts, for example, in the identification of obligate mutualisms necessary for the functioning of a particular species or community. Using both field and laboratory data, I investigated factors that influenced the dynamics of an unusual vertebrate association, the cohabitation of tuatara and fairy prions in a burrow. The fairy prion is a seabird that comes to land only for the breeding season and the tuatara is a burrowing reptile, active primarily at night in a temperate climate. Several features of species' biology such as distribution and abundance of symbiotic partners, the availability of alternative partners or resources, the need for services provided and/or the abiotic setting in which the interaction occurs, may contribute to the maintenance of a positive or negative association. In other words, rather than being fixed attributes of species interactions, benefits and costs can vary over both time and space. I measured the effects that this association had on tuatara thermoregulation, and demonstrated the difficulty in applying that information to categorize a complex interaction. Understanding the effects that management actions have on interspecific associations is a priority for individual species recovery, for example, the Recovery Plan for Tuatara (Gaze, 2001) considers small nesting seabirds to be a habitat feature that is favourable for the long term survival of tuatara. The results of this thesis addressed questions fundamental to conservation, within the broad field of restoration ecology and by specifically enhancing the understanding of the tuatara-fairy prion association and how abiotic factors such as temperature and humidity can influence how this association is categorized. Further, these results can be used to improve species monitoring and to develop future research into how climatic change may interact with habitat availability to influence the full range of natural outcomes of a given association.

6.2 Summary of major findings

The major findings from the previous four data chapters are briefly summarised as follows:

1) **Chapter Two – Behaviour not morphology determines thermophysiology**

   The body temperatures of tuatara were monitored with the use of thermal data loggers during Austral spring, summer and autumn. The environment on Stephens Island only permits preferred body temperature to be reached for more than three hours a day in January (mid Austral summer). Tuatara are not precise thermoregulators for much of the day or year. The mean body temperature for tuatara on Stephens Island was always within 1°C of mean environmental temperature. Males and females did not differ in mean body temperature or effectiveness of thermoregulation, and body size did not predict body temperature or cooling rates, but larger animals heated faster than smaller animals. Burrow location and depth influenced burrow temperature. Variation between individuals in timing of burrow use affected body temperature. The presence of a bird in a burrow increased humidity within the burrow, and body temperature of tuatara. Thus, behaviour (burrow use) and burrow selection have greater influences on a tuatara's body temperature than an individual's sex or size.

2) **Chapter Three – Behavioural thermoregulation under hydric and digestive constraints in juvenile tuatara**

   A thermal gradient was used to test for differences in burrow selection under differing humidity levels and digestive states within laboratory conditions. Juvenile tuatara tended to exhibit a preference for warmer temperatures regardless of digestive state, humidity or time of the day. However, a clear diel trend in thermoregulatory behaviour was evident, with tuatara selecting higher temperatures during the day. Under the dry treatment, tuatara selected higher temperatures on the gradient. During the night tuatara were outside their burrows more often and moved about the gradient more frequently. Greater numbers of tuatara were recorded outside their burrows under the wet treatment compared to the dry. Digestive state had no discernable effect on either temperatures selected, or burrow use under captive conditions.

3) **Chapter Four – The fairy prions' breeding behaviour in relation to the tuatara: How a bird responds to a large reptilian burrow-mate**

The successful incubation of an egg to hatchling stage was not correlated with the presence of a tuatara in the burrow, although predation of prion chicks by tuatara has been documented in the past. Arrival time at the burrow was dependent on timing of dusk, but also with the presence of a tuatara at the burrow. Fairy prions cohabiting with a tuatara had later arrival times at their burrow than individuals which were the sole occupant of their burrow. Tuatara did not affect activity levels at the burrow in either September or October, but the presence of a tuatara at the burrow reduced the amount of time that adult birds spent at the burrow with their chick in January. Both a resident tuatara and random visits from tuatara almost halved the time fairy prions spent at the burrow.

4) **Chapter Five – Sharing a burrow with a seabird increases the body temperature of a reptile**

Tuatara that occupy burrows containing a fairy prion are able to maintain up to 1.8°C higher body temperature through the night for several months of the year. For two out of the three years studied, tuatara cohabiting with fairy prions were significantly warmer for mean hourly body temperature between 1900 and 0800 hours in October. The presence of a bird had no significant effect on the amount of time spent within the preferred temperature range (19.5 – 23.1°C), but did influence the effectiveness of thermoregulation by allowing tuatara to maintain higher mean temperatures than individuals without a seabird occupied burrow. In January, there was an overall trend for tuatara cohabiting with a bird to have warmer temperatures although this was not statistically significant for most of the time.

6.2 Categorizing the tuatara fairy prion association

I examined the interactions between tuatara, *Sphenodon punctatus* and fairy prions, *Pachyptila turtur* by combining spatial, behavioural, and temperature data to provide the most complete picture of this unique association to date. These data plus existing knowledge was combined in an attempt to categorize the association (Fig. 1)
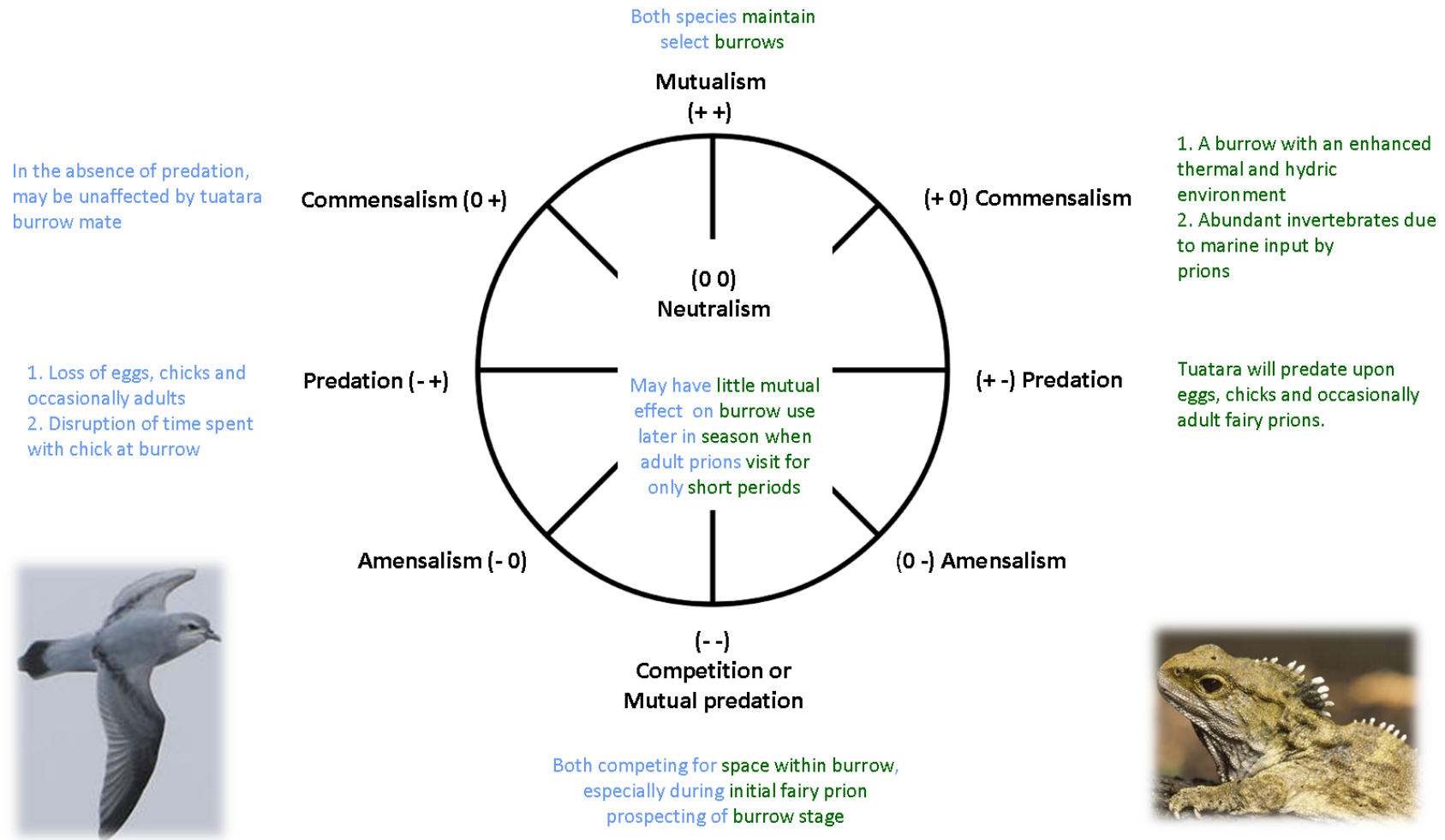
Figure 1. Species interactions compass relative to the tuatara-fairy prion association.

Firstly, evidence that this relationship is best described as a mutualism as it has been historically listed in biology textbooks (Marshall-Cavendish-Corporation, 2000, Jenkins & Page, 2010) is tenuous. However, both species do maintain and defend particular burrows (pers. obs., Harper, 1976, Moore *et al.*, 2009). Several aspects of their biology contribute to negative interactions for both. Tuatara will prey upon the eggs and chicks of the fairy prions and occasionally adults (Newman, 1978, Walls, 1978, Markwell, 1998). In January when fairy prions are feeding their chick they may spend less time at the burrow due to the presence of a tuatara (chapter 5), thus a tuatara may act like a parasite within the fairy prions living space. Both species are competing for a limited resource, the confined space of a burrow, and conflict can occur, adult fairy prions are capable of driving tuatara out of the burrow, and fairy prions when incubating are often disrupted by tuatara, as is evident from the loud squawking from within burrows which often occurs upon entry by a tuatara (pers. obs., Wright, 1963, Gaston & Scofield, 1995).

However, in instances where individual tuatara do not prey upon either the eggs or chicks the association could well be one of commensalism. The tuatara benefit from an enhanced thermal and hydric environment (chapters 2 and 4), have an abundance of invertebrates to prey upon due to increased nutrient addition from the fairy prions (Mulder & Keall, 2001), and the birds themselves may remain unaffected. This scenario may be most likely in October/November when adult birds remain within the burrow incubating their egg and are able to defend themselves against tuatara. It is also during this period that tuatara are most likely to obtain thermal benefits. Environmental temperatures in the October/November period when adults are incubating eggs are a lot cooler than when chicks are present in burrows in January (chapter 2). Thus, increased burrow temperatures in comparison with above ground temperatures would be more pronounced during October/November. In January, the positive effects of this association for tuatara may diminish as increased above ground ambient temperatures, ensure that all burrows are warmer than in October. It is at the chick stage that fairy prions are most vulnerable to attack by tuatara, as adults are able to defend themselves and protect the eggs in many instances (Gaston & Scofield, 1995).

When the benefits from this interaction decrease for the tuatara, such as when air temperatures increase and invertebrates are plentiful throughout their habitat (Walls, 1981), this association may even tend toward neutralism. The tuatara and fairy prions may effectively coexist despite the presence of the other and without significantly impacting upon each other. Thus, what at first glance may be a relatively simple cohabitation, it may actually be categorized as five out of

the six broad categories that describe the effects of two or more species on each other depending on time of year. It is now recognized that commensal and mutualistic associations are dynamic; they form and dissolve under different conditions of predator risk, resource levels, competition and many other factors (Dickman, 1992). In this instance, the dynamics of the association are mainly affected by the level of predation exerted by the tuatara, by the transition in benefits experienced by the tuatara, and by differing levels of competition over the main resource, the burrow. Overall, this may be a passive association as a result of both species selecting similar habitats (burrows) but the outcome of the cohabitation can be expected to change over both space and time.

6.4 Conservation implications

The behavioural and thermal results of this research can be applied toward conservation management of tuatara in many ways. For example, translocation is one of the most commonly used tools in New Zealand conservation, and over 400 translocations of 40 taxa (primarily birds) were carried out by 1995 (Armstrong & McLean, 1995). Translocations aimed at restoring tuatara to parts of their former range have occurred since the mid-1990s (Mitchell *et al.*, 2008). The knowledge that the thermal environment in parts of the tuatara's extant range is challenging and that burrow selection and burrow use behaviour is a strong determinant of thermoregulatory behaviour, at least within a dense population, must thus be factored in when making decisions about appropriate tuatara habitat for translocations. The physiology of an animal ultimately determines the range of environmental conditions under which it can survive. However, thermoregulatory behaviour represents an important component of non-genetic adaptive capacity of the ectotherm to differing thermal regimes, that also has potential to mitigate the impact of ongoing climate change (Gvoždík, 2011). One of the long term objectives of the Tuatara Recovery Plan is to reinstate tuatara as a component of healthy ecosystems throughout their pre-human range (Gaze, 2001). Relatively simple assessments of the thermal environments in areas proposed for translocations combined with knowledge of tuatara's thermoregulatory behaviour could be used to predict the success of translocations. However, extant populations do not cover all thermal environments of past tuatara, such as areas in the South Island, and tuatara thermoregulate to different extents under differing thermal scenarios, at least under controlled laboratory conditions (Besson & Cree, 2010).

In addition to thermal constraints, (for example, on Stephens Island environmental temperatures are never warm enough to permit tuatara to reach their preferred body temperature range in September or March, chapter 2), natural populations of tuatara restricted to offshore islands are also often limited by the availability of fresh water. This situation will perhaps increase in importance with the potential for more frequent droughts in the future (Ministry-for-the-Environment, 2011). The fact that tuatara are more active and leave their burrows more often under humid conditions may mean that tuatara in arid conditions may be more vulnerable if they are unable to forage to the same extent. Tuatara are sit and wait predators (Daugherty & Cree, 1990), but invertebrates such as weta are also affected by drought. For example on Middle Island off New Zealand, tusked weta were reduced to very low numbers after a significant drought in 1993-1994 (New, 2008) and ground weta are most often out on calm, warm and humid nights (Johns, 2001). Water loss may be the over-riding factor which reduces nocturnal and daytime activity during warm or dry periods, or indeed the factor which governs the number of days that an animal can repeatedly bask (Barwick, 1982). Burrows occupied by seabirds are more humid than an empty burrow (chapter 2, Towns, 1992). Thus, the buffering role of seabird burrows as a humid retreat could increase in significance within the tuatara habitat in times of drought.

Knowledge of how tuatara use their landscape and how burrow depth and location affects both the temperature of the burrow and associated body temperature is also useful for captive facilities. Tuatara select microhabitats with respect to temperature (chapter 3) and in colder areas, deeper burrows and those located in open areas are important thermal buffers (chapter 2). Location of burrow also affects basking opportunities as tuatara bask close to their burrow entrance. Captive management is increasingly recognised as having potential to contribute to well-rounded species recovery programmes (Connolly & Cree, 2008). Properly executed, captive management may (i) allow production of animals for reintroduction into the wild (Kleiman, 1989, Mallinson, 1995); (ii) provide an insurance policy to ensure survival of the species (Leus, 2011); (iii) provide a source of animals for research assisting conservation in the wild (Ryder & Feistner, 1995); and (iv) facilitate advocacy and education (Rahbek, 1993, Balmford et al., 1995). Providing adequate habitat in the form of suitable burrows and basking sites will contribute to optimizing health and reproduction.

Seabirds may fulfil keystone roles at the sites at which they occur. Burrow nesting seabirds are often ecological drivers of the terrestrial ecosystems where they breed (Smith, 1976, Mulder & Keall, 2001, Markwell & Daugherty, 2002, Miskelly *et al.*, 2009). During natural catastrophes where populations are decimated it is essential to understand the basic biology of the species, e.g. where populations come from, numbers, ability to recover, etc. Restoration projects on islands in particular, are often based around seabirds, and hence a knowledge of their abundance and behaviour could be especially valuable in conservation projects (Markwell, 1997). For example, a new translocation of seabirds might be vulnerable to predation in areas where tuatara are especially strong in numbers. This may shift the balance of this association to one solely of predation.

6.5 Directions for future research

This research has answered many questions regarding the thermal ecology of tuatara and the association between tuatara and fairy prions, but throughout the course of this research, many new questions have arisen. The groundwork has now been laid for more complex, advanced questions of interspecific interactions and evolutionary ecology of tuatara that may expand on the work presented in this thesis.

6.5.1 How does this interaction change with different seabird species?

To understand whether the balance of this reptile-seabird interaction was unique to Stephens Island, it would be useful to investigate how tuatara and other seabirds coexist on other islands. This would enable us to determine whether different species of seabirds, for example, larger seabirds such as Flesh-footed shearwaters *Puffinus carneipes,* and Bullers shearwaters *Puffinus bulleri*, result in a shift in the type of biological interaction, such as to outright competition. Tuatara on Aorangi Island (northern New Zealand) with a high incidence of eye damage were those that were cohabiting with Bullers shearwaters (Tyrrell *et al.*, 2000). Tuatara are mainly visual hunters (Wojtusiak, 1973, Meyer-Rochow, 1988), and any loss or impairment of vision may reduce the ability to feed, which would have implications for breeding behaviour and success (Tyrrell *et al.*, 2000). A better understanding of the factors affecting tuatara-seabird interactions would enable predictions based on population dynamics (size, density, etc.,) that could have applications for the long term viability of small, captive, or translocated populations.

The interchangability of burrowing seabirds as partner species for tuatara has not been examined in detail and may be critical in the long-term conservation efforts of this species.

6.5.2 Do long periods of droughts affect thermoregulation in tuatara?

Tuatara are often restricted to islands on which there are no standing bodies of freshwater (e.g. Stephens Island, (Moore *et al.*, 2007). In periods of drought, humidity may play a greater role in determining habitat selection and timing of activity. Water loss may be the over-riding factor which governs the number of days that an animal can repeatedly bask or which reduces activity during warm periods. With current rates of climate change, predicted future droughts and increased variability in weather patterns (Ministry-for-the-Environment, 2011), water may well become a limiting factor for tuatara. Under sustained drier conditions, tuatara may become more reliant on humid seabird burrows. The effects may also differ between different size classes, with smaller animals more vulnerable to water loss; for example, the rate of water loss is proportional to surface area in the snake, *Elaphe climacophora* (Gans *et al.*, 1968). A higher vulnerability of juveniles to potential future droughts could have impacts on recruitment into a population.

6.5.3 How does density affect the thermoregulation of tuatara?

My investigations were solely restricted to Stephens Island where the largest population of tuatara exist, and thus where tuatara are easily observed. As basking opportunities may be density-dependent, it is important for greater generalisation and application of results to compare the thermoregulatory behaviour in areas that are ecologically similar, but which vary in tuatara density. For example, in Zealandia (wildlife sanctuary with a predator-proof fence in Wellington, NZ), tuatara inhabit an area that is roughly the same in both latitude and weather to Stephens Island, but they are present in much lower densities. Only 200 individuals were released into the 225 ha Zealandia sanctuary (Miller *et al.*, 2009), compared to ~50 000 tuatara on 150ha Stephens Island (Gaze, 2001). A strategy of precise thermoregulation may require a precise use of the habitat (Adolph, 1990), which may only be possible when competition for space is lowered. Tuatara usually bask close to the entrance of their burrow (pers. obs., Saint Girons *et al.*, 1980). This may be especially important in the early morning, before they have sufficient time to heat up (chapter 2) and when locomotor performance may be low. Thus, when

free from the constraints of conspecific competition, tuatara may in fact use their thermal habitat more selectively.

6.6 Summary

I provided new knowledge revealing that environmental conditions matter when determining the kind of interaction between two or more species. This is particularly timely in light of scenarios of global climate change that predict increased temperatures, changes in water availability and increased variance (Stachowicz, 2001). Both categorizing interactions between species of high conservation value and attempting to understand the costs and benefits associated with this interaction can aid conservation efforts. In the future it is predicted that habitat-ameliorating positive interactions will grow in importance as global environmental stress increases (Stachowicz, 2001). These results can be used to develop future research into how climatic changes in temperature and rainfall may interact with habitat availability to influence the full range of natural outcomes of the tuatara-fairy prion association.

6.7 References

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Appendix 1: Comparison of internal and external body temperature measurements

Table 1. Hourly body temperatures of a male (SVL 272mm, mass 770g) and female tuatara (SVL 213mm, mass 400g) recorded externally with a datalogger (iButton attached to the tail) and infra-red thermometer, and internally with a thermocouple

Tuatara	Time (hrs)	Datalogger (°C)	IRT (°C)	Thermocouple (°C)
MALE	1100	22.5	23.0	22.8
	1200	23.0	22.8	22.9
	1300	23.0	23.2	23.0
	1400	23.5	23.2	23.3
	1500	23.5	23.4	23.6
FEMALE	1000	18.5	18.2	18.5
	1100	21.0	21.0	21.2
	1200	22.0	22.0	22.1
	1300	22.5	22.4	22.6
	1400	23.0	22.8	23.0