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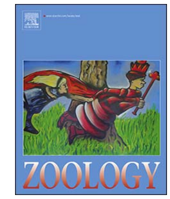


# Thermoregulation of a temperate reptile in a forested habitat

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ABSTRACT

A major focus in zoology is to understand the phenotypic responses of animals to environmental variation. This is particularly important when dealing with ectotherms in a thermally heterogenous environment. We measured body temperatures of a free-ranging, medium sized temperate reptile, the tuatara, *Sphenodon punctatus*, to investigate its thermal opportunities and the degree to which the animal actively regulates its body temperature. We found high variation in body temperature between individuals, but this variation could not be attributed to sex or body size. However, variation among individuals in timing of burrow use did affect body temperature and in one of the years studied tuatara were found to be more effective in their thermoregulation when sharing a burrow with a seabird (*Pachyptila turtur*). The strength of this study is that it includes both biotic and behavioural components of the thermal environment of a temperate reptile, areas which are often missing from thermal studies that focus on the abiotic aspects.

## 1. Introduction

The role of the thermal environment has received increased attention due to the current phenomenon of global warming. Thermal environments have numerous impacts on ecology and can affect the potential range of a species resulting in contractions or expansions. Indeed observations of range shifts in parallel with climate change dating from the mid-1700 s have been recorded for many European birds, butterflies, herbs, and trees (Parmesan, 2006). While the thermal environment has impacts on all species it has a more immediate effect on ectotherms, as their internal body temperature is dependent on the environment. However, ectotherms may not be wholly limited by the ambient temperatures, and may attempt to regulate their body temperature using behavioural mechanisms to a particular ‘set-point’ temperature that coincides with the ideal or optimal temperature for organism function (reviewed in Cabanac, 2006).

Thermophysiology and habitat use of squamates (snakes and lizards) are relatively well understood, but phylogenetic patterns of habitat use and thermoregulation among reptiles has received little attention. Tuatara *Sphenodon punctatus* (Fig. 1) represent a distinct lineage of reptiles (Order Rhynchocephalia (sensu Gauthier et al., 1988)) that diverged from their sister group (the squamates) approximately 230 mya (Rest et al., 2003). Although tuatara are ecologically similar to insectivorous lizards, they have many morphological and physiological differences, and they exhibit activity at low temperatures, unusual among modern reptiles (Barwick, 1982; Walls, 1983; Thompson and Daugherty, 1998), and they share burrows with nesting seabirds (Newman, 1987). Cohabitation with a seabird represents a non-traditional heat source and therefore a potential thermal advantage for individuals (Corkery et al., 2014a).

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). 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 the 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). More recent detailed laboratory studies on thermoregulation of tuatara revealed the preferred temperature range of tuatara to be 19.5 - 23.1 °C and that tuatara adjust their basking behaviour in response to the thermal quality of their habitat (Besson and Cree, 2010; Corkery et al., 2014b).

However, to our knowledge, only limited long term data are available for tuatara body temperatures in their natural surroundings and there has been some controversy in the past over whether tuatara actively thermoregulate or not. For example, tuatara may thermoregulate to different degrees depending on the amount of food they had consumed the night before (Saint Girons, 1980). Walls (1983) looked at the

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**Fig. 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 = 215 mm (mean: 197 ± 2 mm) and mass = 355 g (mean: 270 ± 8 g). Photographer: Ilse Corkery.

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, although their investigation was limited to a week in August (winter in the southern hemisphere). Investigations into the sharing of burrows with seabirds revealed that birds increase the thermal quality of a burrow (Corkery et al., 2014a).

It remains largely unknown how weather conditions, burrow microclimate and conspecifics work together to affect the body temperature of this unique reptile over long periods of time and over different seasons. We recorded body temperatures of free-ranging individuals, ambient air temperatures, timing of activity and microhabitat selection during spring, summer and autumn over a period of three years. Using these data, and previously quantified thermal preferences of captive animals (Besson & Cree, 2010), we explored the degree to which tuatara were able to regulate their body temperatures in a highly variable thermal habitat.

## 2. Methods

### 2.1. 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). It was conducted over three successive field seasons (October 2008 – March 2011) in an area called Keepers Bush, which consisted of regenerating coastal forest. There was a total of 10 fieldtrips, each covering a two to three-week period in the: austral spring; September (n = 1), October/November (n = 3); summer, January (n = 3); and autumn, March (n = 3). These periods were selected as part of a larger study because they are biologically important months for tuatara reproduction (see Cree et al., 1992).

The tuatara is a medium sized reptile, up to 450 mm total length and 500 g in females, and up to 600 mm total length and 1 kg 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, 1982). Tuatara inhabiting forested areas are active throughout a 24 hour period (Gillingham and Miller, 1991). On Stephens Island, the tuatara use burrows that have been constructed by fairy prions (*Pachyptila turtur*), a small Procellarid seabird (length 25 cm, weight 90 – 175 g). Male tuatara will defend territories containing multiple burrows while female tuatara have smaller territories, usually centred on a single burrow (Gillingham et al., 1995; Moore et al., 2009a). Tuatara are seasonally monogamous within a year but show polygyny and polyandry across years (Moore et al., 2009b). The size of an individual male tuatara affects his ability to hold territory, with larger individuals more successful in aggressive encounters and thus overlapping with more female territories (Moore et al., 2009a).

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)). Body condition was calculated for each individual, defined as the residuals from a regression of log-transformed mass/log-transformed SVL (eg. Schulte-Hostedde et al., 2005). 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 (Fig. 1). 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 and the iButtons remained attached for a period of 5 - 10 days. This method of obtaining body temperatures was first tested within a laboratory setting. Temperatures from the iButton were found to be comparable with an internal thermocouple and infrared thermometer and therefore accurately represent a reptile's internal body temperature (Supplementary material, Table 1).