

RESEARCH ARTICLE

Does the New Zealand rockwren (*Xenicus gilviventris*) hibernate?Brian K. McNab^{1,*} and Kerry A. Weston²

ABSTRACT

In this study, we examined the thermal physiology of the endangered New Zealand rockwren (*Xenicus gilviventris*), a member of the Acanthisittidae, a family unique to New Zealand. This family, derived from Gondwana, is thought to be the sister taxon to all other passerines. Rockwrens permanently reside above the climatic timberline at altitudes from 1000 to 2900 m in the mountains of South Island. They feed on invertebrates and in winter face ambient temperatures far below freezing and deep deposits of snow. Their body temperature and rate of metabolism are highly variable. The rockwrens in our study regulated their body temperature at ca. 36.4°C, which in one individual decreased to 33.1°C at an ambient temperature of 9.4°C; its rate of metabolism decreased by 30% and its body temperature then spontaneously returned to 36°C. The rate of metabolism in a second individual twice decreased by 35%, nearly to the basal rate expected from its mass without a decrease in body temperature. The New Zealand rockwren's food habits, entrance into torpor and continuous residence in a thermally demanding environment suggest that it may hibernate. However, for that conclusion to be accepted, evidence of its use of torpor for extended periods is required. Acanthisittids are distinguished from other passerines by the combination of their permanent temperate distribution, thermal flexibility and a propensity to evolve a flightless condition. These characteristics may principally reflect their geographical isolation in a temperate environment isolated from Gondwana for 82 million years in the absence of mammalian predators.

KEY WORDS: Acanthisittidae, Flightless condition, Gondwana, Poor-will, Rifleman, Torpor

INTRODUCTION

The question whether a passerine hibernates raises the broader question whether any bird hibernates. That the common poor-will (*Phalaenoptilus nuttallii*) hibernates is widely accepted, originally based on observations of Jaeger (1948, 1949), 72 years ago, of torpid individuals found along a canyon wall in southern California. They, like other caprimulgids (Brauner, 1952; Marshall, 1955; Bartholomew et al., 1957, 1962; Howell and Bartholomew, 1959; Dawson and Fisher, 1969; Ligon, 1970; Lane et al., 2004; McKechnie et al., 2007; Ruf and Geiser, 2015), readily enter torpor, but that does not guarantee that they hibernate.

Confusion between torpor and hibernation often occurs (McNab and O'Donnell, 2018). Not all examples of torpor represent hibernation, even though hibernation is based on an extended period of torpor. Hummingbirds in the tropics, for example, do not hibernate, even though they go into torpor at night, reflecting a day of intense flight and a small body mass. Short-term torpor and hibernation represent extremes along temporal and thermal continua. The existence of an extended period of torpor is the basis for judging whether a species hibernates, as the name implies, in winter.

Three poor-wills were kept from autumn to spring in a large shed, after which they were released (Marshall, 1955). They were exposed to ambient temperatures (T_a) from −5 to 22.5°C. The longest period of continuous torpor in an individual was 4 days. One was said to have ‘...hibernated every morning...’ and ‘...a bird in deep hibernation at dawn would have been active through the previous evening before midnight’ (Marshall, 1955, p. 132). In a summary of torpor periods of birds, Ruf and Geiser (2015) reported that the longest period in a poor-will was 120 h (5 days), whereas the next longest period was 16 h in another caprimulgid, the European nightjar (*Caprimulgus europaeus*). This is not hibernation; it is short-term torpor.

Recent observations by Woods et al. (2019) demonstrated that free-ranging poor-wills in Arizona were often torpid for 4–7 days. These birds roosted in a series of sites that faced south and southwest. The length of torpor decreased with an increase in T_a and with a solar input reflecting the orientation of roosts to the sun. One individual, when shaded, remained in torpor for 45 days, although with periodic increases in skin temperature. This incident represents hibernation under controlled conditions. The question is: how often would this occur in unmodified conditions?

The thermal dependence of torpor is seen in the tricolored bat (*Perimyotis subflavus*). This bat is distributed in eastern North America from southern Canada to central Florida. In one study in Kentucky, half of the individuals became euthermic after ca. 40 days of continuous torpor at a cave temperature of 10°C (Davis, 1965). In northern Florida, half became active after 4 days of continuous torpor at a cave temperature of 16°C (McNab, 1974). The conversion in this bat from hibernation to short-term torpor reflects a decrease in latitude and, therefore, an increase in cave temperature. A commitment to hibernation can only occur in environments that are constantly cold. It cannot occur in the thermally variable environments in which the poor-will was studied.

Torpor length in the poor-will has a temperature sensitivity similar to that in the tricolored bat. Poor-wills in Arizona appear to sit at an intermediate position along the short-term torpor/hibernation continuum. Presumably, torpor length of poor-wills in Arizona would increase during a cold, cloudy period. Can poor-wills tolerate extended periods of torpor in a constantly cold climate, or do they require a sustained food input obtained during short periods of activity? If so, does that determine a northern limit to their distribution in winter?

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The suggestion that a passerine may hibernate is completely unexpected. Some passerines go into torpor (McKechnie and Lovegrove, 2002; Schleucher, 2004): principally small, tropical insectivores and frugivores. Temperate swallows enter torpor (Lasiewski and Thompson, 1966; Serventy, 1970; Prinzinger and Siedle, 1988) in response to the unreliability of flying insects as food. Swallows, however, avoid harsh winters through migration to warm temperate and tropical environments. A similar behavior is found in temperate swifts, hummingbirds and most caprimulgids. An Australian passerine, the white-browed babbler (*Pomatostomus superciliosus*), goes into shallow torpor (body temperature, $T_b > 37^\circ\text{C}$), which it usually avoids by communal roosting in enclosed nests (Douglas et al., 2017).

In contrast, the rifleman (*Acanthisitta chloris*), a sedentary passerine endemic to New Zealand, has a flexible approach to cold conditions (McNab and Weston, 2018). It readily enters torpor at T_a between 10 and 25°C , when T_b decreases to 27°C , after which it spontaneously arises from torpor.

The T_b of some cold-temperate passerines, especially tits and finches, can be forced to 34°C . That requires an exposure to T_a from -15 to -30°C (Steen, 1958; Reinertsen, 1983). For example, it took an exposure to -15°C for 3–4 h, while withholding food, to reach T_b between 34 and 35°C in the willow tit (*Parus montanus*) (Reinertsen and Haftorn, 1983, 1984). This combination of conditions is unlikely to be encountered in its nocturnal shelters. T_b of black-capped chickadees (*Parus atricapillus*) decreased to 34°C when exposed to a T_a of 0°C for 4–6 h. However, they were unable to arouse to their normal T_b at room temperature (Chaplin, 1976). Furthermore, '[w]hen the [tits and finches] had become acclimated to constant cold (-10°C) and were supplied food, none entered into a hypothermic state' (Reinertsen, 1983, p. 276).

The highly endangered New Zealand rockwren (*Xenicus gilviventris*) and the rifleman are the only surviving members of the Acanthisittidae, the New Zealand 'wrens.' This passerine family is a line derived from Gondwana (Ericson et al., 2002; Worthy et al., 2010) and considered to be the sister taxon to all other passerines (Hackett et al., 2008; Selvatti et al., 2015; Mitchell et al., 2016). Acanthisittids are not related to the Northern Hemisphere wrens (Troglodytidae), which belong to the suborder Passeri (oscine passerines), whereas the acanthisittid belong to the suborder Acanthisitti. Of the eight known species of acanthisittids, four of the six extinct species were flightless, with the evolution of a flightless condition occurring at least three times (Worthy et al., 2010; Mitchell et al., 2016; McNab and Weston, 2018). The rockwren is a weak flier.

The New Zealand rockwren lives above the climatic timberline in the mountains of South Island. Its altitudinal distribution is from 1000 to 2900 m, where in winter it encounters very low T_a and several meters of snow. Active nests of rockwrens have been found buried in snow banks. This species does not descend to lower altitudes in winter in spite of its food habits of a predominant preference for invertebrates. How can this combination of characteristics and conditions be tolerated and to what extent do they reflect the environment in which they evolved in the absence of mammalian predators?

A limited number of measurements on the thermal biology of New Zealand rockwrens were made, the results of which are reported here. The aim of this study was to determine the characteristics of the energy expenditure of the New Zealand rockwren.

MATERIALS AND METHODS

Study species

The rockwren, *Xenicus gilviventris* Pelzeln 1867, is small (14–20 g) with limited flight and is a permanent resident above the timberline.

Its diet is composed predominantly of insects, although it also includes the berries and nectar of subalpine shrubs.

Study area

Six rockwrens were captured using mist nets during the austral summer (26 February to 10 March 2016) at the Homer-Gertrude Cirque (ca. 1000 m a.s.l.; 44.76°S , 168.00°E), Fiordland National Park, South Island, New Zealand. The habitat is composed of extensive boulder fields, rocky bluffs and snow tussock (*Chionochloa* sp.), and alpine scrub. Following capture, birds were transferred to the nearby Knobs Flat Research Station, in the lower Eglinton Valley, Fiordland National Park.

Experimental protocol

Measurements of energy expenditure were made in the laboratory between 19:00 h and 01:00 h, 5–7 h after capture when the rockwrens were inactive and post-absorptive. The oxygen consumption of two wrens was measured at the same time when contained in separate temperature-controlled chambers of 1.5 l. They were exposed to T_a from 5 to 31°C . Room air was drawn through the chambers, and the exiting air scrubbed of carbon dioxide and water. The flow rate of the air stream was measured by a TSI 4140 flow meter (TSI Instruments Ltd), and varied from ca. 105 to 350 ml min^{-1} , depending on the oxygen consumption of an individual. The oxygen content of the air exiting the flow meter was measured by a two-channel S-3A/II Applied Electrochemistry oxygen analyzer, with its electrical outputs sent to a two-channel NGI strip-chart recorder. Measurements usually lasted for 1.5–2 h or until a steady-state oxygen concentration was obtained, steady-state being defined as a constant oxygen content in the air exiting the chamber lasting for >20 min. Three or four measurements, each at a different T_a , were made on each individual in a night. At the end of each temperature exposure, body mass was measured, as was cloacal temperature with a thermocouple. The morning after measurement, the birds were released at their place of capture.

Rate of metabolism (\dot{V}_{O_2} , in $\text{ml O}_2\text{ g}^{-1}\text{ h}^{-1}$) was calculated from the equation:

$$\dot{V}_{\text{O}_2} = \frac{\text{fr} \times 60 \times \Delta\text{O}_2}{(0.7907) \times M} = \frac{75.88 \times \text{fr} \times \Delta\text{O}_2}{M}, \quad (1)$$

where fr is flow rate (ml min^{-1}), 60 (min h^{-1}) converts the units from minutes to hours, 0.7907 is the mean proportion of oxygen-free gas in the atmosphere, ΔO_2 is the difference of the oxygen content between the atmosphere and the gas exiting the chamber, and M is mass (g) (McNab, 2006). This relationship was corrected to standard conditions of pressure (760 mmHg) and temperature (0°C) by the TSI flow meter.

Capture, handling and short-term maintenance in captivity followed approved methods outlined by the Department of Conservation, New Zealand, under approval AEC 292.

RESULTS

T_b and \dot{V}_{O_2} were measured. A very large variation occurred in T_b (Fig. 1A). Whereas the T_b of most cool- to cold-temperate passerines during their resting period is between 39 and 42°C (McNab, 1966), it was usually between 36 and 37°C in the rockwren. Individual 1 had a T_b of 36.4°C at T_a between 20 and 30°C (Fig. 1A). At a T_a of 9.4°C , its temperature decreased to 33.1°C from which it spontaneously returned to 36.0°C within half an hour of being exposed to 30.1°C . The high variability in T_b in this species does not represent a failure of temperature regulation. A failure is illustrated by a decrease of T_b

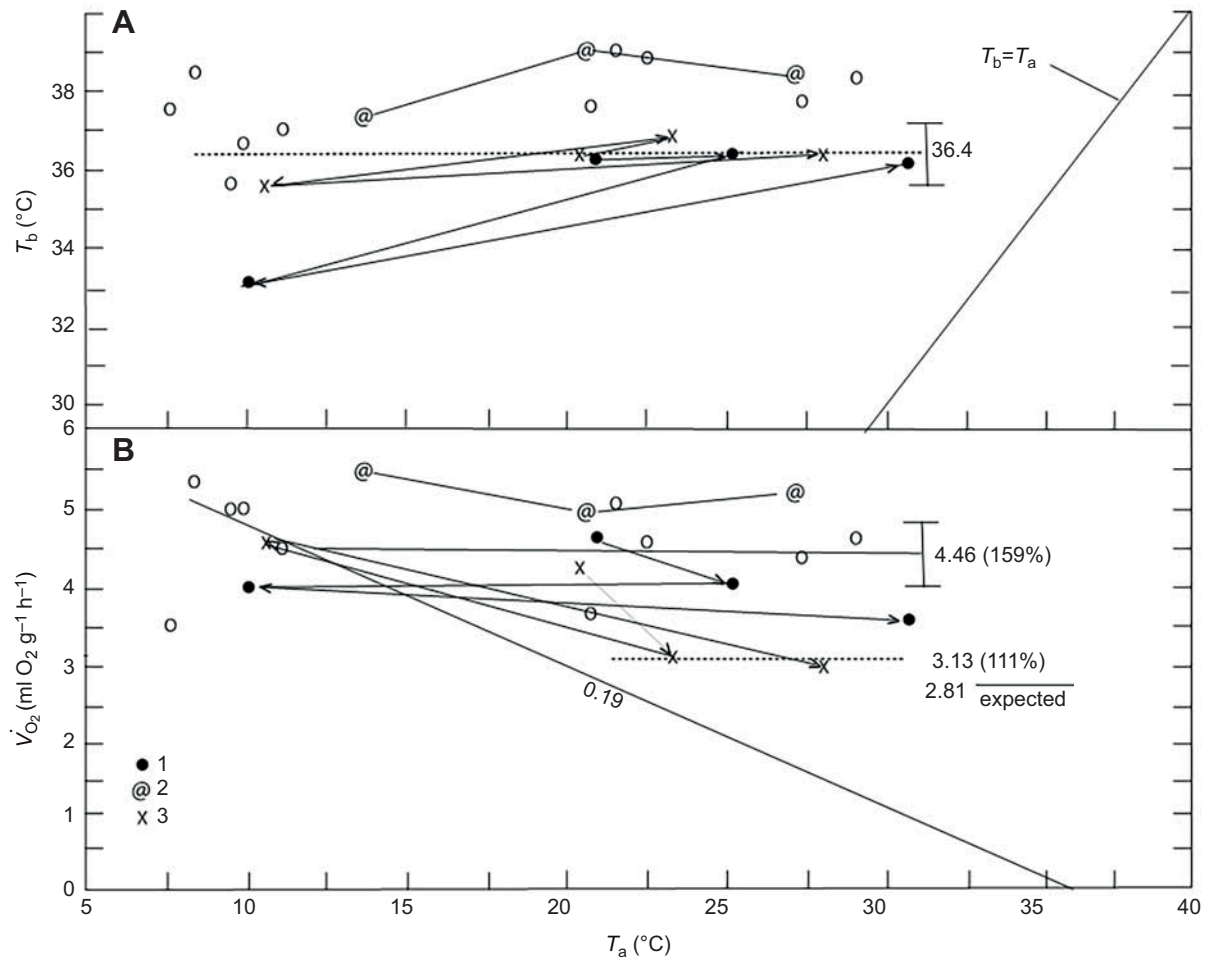


Fig. 1. Body temperature and rate of metabolism in six New Zealand Rockwrens (*Xenicus gilviventris*). (A) The body temperature (T_b) of rockwrens as a function of ambient temperature (T_a). An estimate of regulated T_b is indicated. (B) Rate of metabolism (\dot{V}_{O_2}) as a function of T_a . T_b and \dot{V}_{O_2} of two individuals (1 and 2) are connected in sequence of measurement. Because of distinctive measurements of metabolism in individual 3, they are identified. Two estimates of basal rate of metabolism are indicated and compared to the value expressed from body mass.

with a decrease in T_a without an ability to arise from torpor, which was not seen here. Some of the variability was associated with activity, as in individual 2 (Fig. 1A). The variation in T_b makes it difficult to estimate the rockwren's regulated T_b . At a T_a between 12 and 30°C, an estimate of mean T_b is $36.4 \pm 0.15^\circ\text{C}$ ($n=9$).

As expected from the variation in T_b , \dot{V}_{O_2} was highly variable (Fig. 1B). \dot{V}_{O_2} variability in this species was so great that it is difficult to estimate a basal rate of metabolism. The mean rate at T_a between 20 and 30°C was $4.44 \pm 0.075 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$ ($n=8$). This mean is 158% of the basal rate expected from mass, which was $15.3 \pm 0.23 \text{ g}$ ($n=21$) (McNab, 2009). This is unlikely to be a good estimate of basal rate, especially as several individuals had much lower rates.

Another estimate of basal rate can be derived from the four low measurements, which are correlated with T_b that are typical for this species and not representative of a thermal depression. Two of these measurements in one individual (individual 3) decreased by about 35% to 3.01 and 3.25 $\text{ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$ (Fig. 1B). T_b did not decrease in this individual. Here, the estimate equals $3.29 \pm 0.198 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$ ($n=4$), which is 117% times the expected basal rate. Whatever the best estimate of basal rate, it is high. Thermal conductance equals $0.19 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1} \text{ }^\circ\text{C}^{-1}$, which is 112% of the value expected from mass (Aschoff, 1981).

The detailed pattern of T_b and \dot{V}_{O_2} in individual 1 are described as a function of T_a and time in Fig. 2. Its T_b was usually ca. 36.5°C . But

when exposed to 9.4°C , its immediate response was an increase in \dot{V}_{O_2} to compensate for the increased temperature differential with the chamber, after which the rate decreased by ca. 30%, reflecting a decrease in T_b to 33.1°C . The decrease in rate continued with a time lag when exposed to 30.1°C . At the end of the experiment, T_b had increased to 36.0°C .

DISCUSSION

The New Zealand rockwren has a highly variable T_b and rate of metabolism at all T_a between 5 and 31°C . The variability is such that it is difficult to define the characteristics that are usually used to describe the energetics of an endotherm: a regulated T_b and basal rate of metabolism. A similar condition occurs in the rifleman (McNab and Weston, 2018), its only living relative. What is striking is that the rockwren has these physiological characteristics while having a high basal rate, although its level is not clearly defined. In contrast, a similarly sized (14.9 g) Northern Hemisphere troglodytid wren, the Carolina (*Thyrothorus ludovicianus*), has a basal rate equal to 1.54 times the rate expected from its body mass, has a mean T_b equal to 39.4°C with some variation, and does not enter torpor (Eberhardt, 1994). This difference emphasizes the physiological uniqueness of New Zealand 'wrens'.

The rockwren's entrance into torpor is a regulated state, as it is in the rifleman, which is demonstrated in both species by the ability of

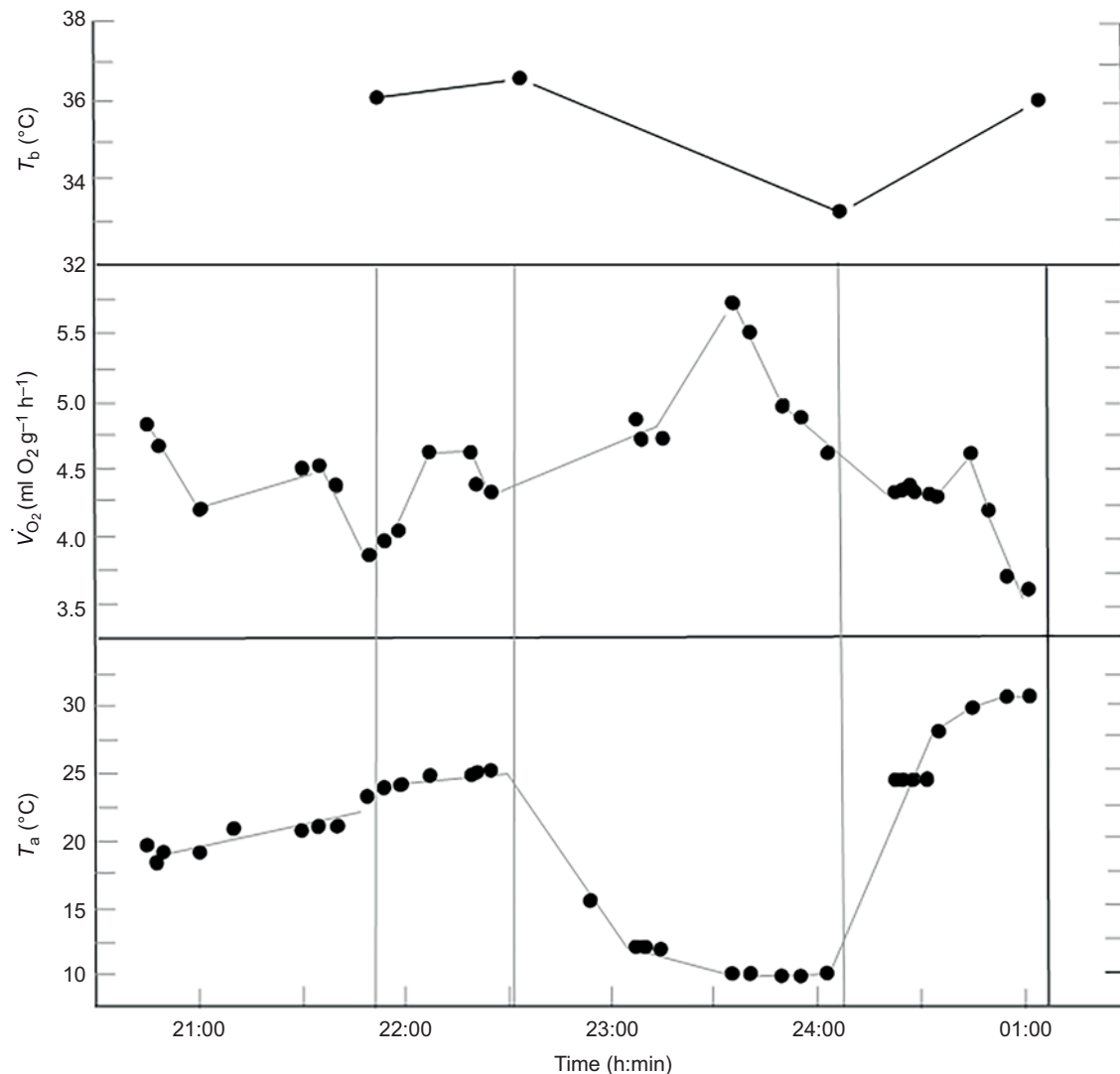


Fig. 2. T_b , $\dot{V}O_2$ and T_a as a function of time in individual 1.

T_b to spontaneously arise to normal levels. These species have a pattern in energetics that is distinctive in passerines committed to a permanent residency in a temperate environment.

Their thermal behaviors are very different from those found in finches, tits and the white-browed babbler. The behaviors of the two New Zealand wrens differs. Unlike the rockwren, the rifleman is found at altitudes from sea level to 1000 m in forested environments. It gleans an insect diet from surfaces, especially tree trunks, cool weather not likely disrupting its food supply for an appreciable period. There is no evidence to suspect that the rifleman hibernates, although measurement of nest temperature in winter may clarify that conclusion.

The rockwren's commitment to the cold environmental conditions that it confronts in winter, in combination with its thermally vulnerable food habits, entrance into torpor and sedentary lifestyle, make it a likely candidate for hibernation. These characteristics differ from those of finches and tits, which are granivorous, with a food supply available throughout the year, unlike the invertebrate diets of the rockwren and rifleman.

Evidence of an extended period of torpor is required to conclude that the rockwren hibernates, which we think likely. Given its highly endangered status, however, acquiring enough appropriate data will

be difficult. A continuous measurement of the temperature in an occupied nest during winter may distinguish between the occurrence of short-term torpor and hibernation in the rockwren. Unlike the poor-will, which exploits a thermally complex environment in winter, the thermal environment in winter faced by the rockwren is unforgiving.

What is clear is that the acanthisittids are physiologically distinctive, with a thermal behavior unknown in any other passerine family restricted to temperate environments, especially when coupled with their repeated propensity to evolve a flightless condition. The extinct members of the family probably were also thermally flexible, given the behavior of their two living relatives, their small masses and flightless status. The extent to which these characteristics emerged from the family's unique phylogenetic position is unclear, unless it reflects a thermal flexibility not found in other temperate passerines. Their thermal flexibility may be a response to residence on a temperate landmass that has been independent of Gondwana for over 82 million years in the absence of mammalian predators, although a mouse-sized, terrestrial mammal of unclear relationship was present in the Miocene (Worthy et al., 2006). The occurrence of this family in the Early Miocene suggests that this family, as well as several others, reflects a vestige of a

Gondwanan ancestry in New Zealand (Worthy et al., 2010; Mitchell et al., 2016).

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: B.K.M., K.A.W.; Methodology: B.K.M.; Formal analysis: B.K.M., K.A.W.; Investigation: B.K.M., K.A.W.; Resources: B.K.M.; Writing - original draft: B.K.M., K.A.W.; Writing - review & editing: B.K.M., K.A.W.; Funding acquisition: K.A.W.

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