



The behavioral energetics of New Zealand's bats: Daily torpor and hibernation, a continuum

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ABSTRACT

We examine the impact of behavior on the short-term energy expenditures of the only terrestrial mammals endemic to New Zealand, two bats, the long-tailed (*Chalinolobus tuberculatus*, family Vespertilionidae), and the lesser short-tailed (*Mystacina tuberculata*, family Mystacinidae). Vespertilionidae has a world-wide distribution. Mystacinidae is restricted to New Zealand, although related to five neotropical families and one in Madagascar reflecting a shared Gondwanan origin of their Noctilionoidea superfamily. Both species have highly variable body temperatures and rates of metabolism. They feed on flying insects, which requires them to be torpid in shelters during cold, wet periods. In dry weather *Mystacina* is active in winter at ambient temperatures as low as -1.0°C , foraging for terrestrial invertebrates in leaf litter, even in the presence of snow, and consuming fruit, nectar, and pollen from endemic plants that bloom in winter. The behavior of *Mystacina* expands its presence in a cool, wet, temperate forest in a manner unlike any other bat, another example of the distinctive characteristics of the endemic New Zealand fauna. The use of torpor generally depends on a series of factors, including body mass, ambient temperature, latitude, reproductive cycle, sociality, and fat deposits. These factors result in a diversity of responses that range along a continuum from short-term torpor to hibernation.

1. Introduction

New Zealand has only two endemic, terrestrial mammals, both bats. One is the long-tailed bat (*Chalinolobus tuberculatus*), a member of the world-wide Vespertilionidae. The other is the lesser short-tailed bat (*Mystacina tuberculata*) of the Mystacinidae. A relative, the greater short-tailed bat (*M. robusta*), recently became extinct (O'Donnell et al., 1999; Lloyd, 2001; Hand et al., 2009). The earliest records of Mystacinidae in New Zealand occur in the Miocene (Worthy et al., 2010; Hand et al., 2013, 2015), although members of this family were also found in the Oligocene/Miocene of Australia (Hand et al., 1998, 2005), where they no longer occur.

The Mystacinidae has distinctive characteristics. 1) Based on DNA-hybridization studies (Kirsch et al., 1998) and nuclear gene sequences (Teeling et al., 2003; Rojas et al., 2016), this family is closely related to five families found exclusively in the Neotropics: Thyropteridae, Furipteridae, Noctilionidae, Mormoopidae, and Phyllostomidae. Collectively these families constitute the superfamily Noctilionoidea, which also includes the Myzopodidae in Madagascar (Teeling et al., 2005; Miller-Butterworth et al., 2007) and formerly in Africa (Gennell et al., 2014). This pattern of affiliation and distribution reflects a shared

Gondwanan ancestry. 2) Mystacinidae is one of several taxa endemic to New Zealand that are close to the evolutionary base of their phylogenetic groups, including parrots (Hackett et al., 2008; Wright et al., 2008), passerines (Ericson et al., 2002; Hackett et al., 2008; Mitchell et al., 2016), kiwis (Hackett et al., 2008), the tuatara (Rest et al., 2003), and leiopelmatid frogs (Roelants and Bossuyts, 2005; San Marco et al., 2005). 3) *Mystacina*, unlike other temperate bats, has diverse food habits, including flying insects, terrestrial invertebrates, fruit, nectar, and pollen (Daniel, 1979; Lloyd, 2001). 4) It crawls on the ground and digs burrows in the soil and decaying trees, even in the presence of snow (Daniel, 1979; Jones et al., 2003; Christie and Simpson, 2006). 5) Terrestrial activity is facilitated by folding their wings in thickened flight membranes, which combined with robust hind legs and feet, permits four-appendage walking (Hand et al., 2009).

Chalinolobus, like most vespertilionids, has a diet of flying insects, a food resource that is often unavailable on a seasonal and short-term basis (McNab, 1974; O'Donnell, 2005). In response, this species and other vespertilionids enter torpor, which in the coldest climates, is extended to hibernation. Hibernation in many vespertilionids is associated with a reproductive cycle that requires females to remain torpid to store sperm obtained in fall and winter copulations without

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becoming pregnant until spring. Northern populations of North American tree bats (*Lasiurus*), which have no shelter from cold weather, migrate to warm temperate locations and show a somewhat greater tendency for endothermic energetics (Genoud, 1993). Species that live in warm-temperate and tropical environments use daily torpor, usually in response to the short-term impact of weather on the availability of flying insects (McNab, 1974; Stawski and Geiser, 2010; Stawski et al., 2014). Webb (1998, 1999) and O'Donnell (2001) indicated that *C. tuberculatus* goes into torpor as does its close relative, the congeneric *C. gouldii*, in Australia (Kulzer et al., 1970; Hosken and Withers, 1997; Stawski and Currie, 2016).

We examine the short-term response in summer to the environment that the New Zealand species share, that is when not facing the harshest conditions encountered in winter, or during extended periods of rainfall. How similar are the responses of *Mystacina* and *Chalinolobus* to their shared environment, given their different phylogenetic affinities?

2. Methods

This study was conducted in the lower Eglinton Valley, Fiordland on South Island, New Zealand (44°58'S, 168° 01'E). This region is a cool, wet, temperate environment characterized by extensive mountain ranges covered by a southern beech (*Nothofagaceae*) forest, occasionally with snowfall in the valley (O'Donnell, 2002a).

We captured both species using free-standing harp traps and mist nets on their foraging grounds at dawn during the austral summer (26 Feb. – 10 March 2016) after breeding had finished. Measurements of energy expenditure were made in the laboratory in the morning five to seven hours after capture during the bat's period of inactivity. Individuals were placed in a dark chamber through which room air was drawn. The air exiting the chamber had carbon dioxide and water contents removed, after which flow rate was measured by TSI flowmeters (TSI Instruments Ltd., UK), which corrected the volume of gas to standard conditions of temperature (0 °C) and barometric pressure (760 mmHg). An Applied Electrochemistry (AEI Technologies, Inc., USA) S-3A/II oxygen analyzer continuously measured the oxygen content of the exiting air. A stripchart recorder recorded the electrical output of the analyzer.

Bats were exposed to ambient temperatures between 9 and 34 °C. Measurements always started with an exposure to room temperatures, then exposed to warmer or colder temperatures, returned to room temperature, and again exposed to warm or cold temperatures. An exposure continued until the oxygen consumption was constant for at least 1 to 2 h. A sequence of measurements on an individual in one morning could last up to nine hours. That is, measurements extended approximately for up to 14 to 16 h after capture. At the end of each exposure, rectal temperature was measured by a thermocouple. After the measurements, the bats were released at night where they were captured. Two *Mystacina* were kept for a second day without food to indicate whether their response to ambient temperature differed from that shown on the first day.

Measured rates of metabolism were compared to basal rates estimated from a general mammalian scaling curve (McNab, 2008) and thermal conductances compared to a general mammalian scaling curve (Aschoff, 1981). The basal rates were not compared to a bat scaling curve because the thermal biology of bats is not uniform. Some species are committed to endothermy and have a definable basal rate, whereas others regularly enter torpor and therefore do not defend a basal rate (McNab, 1997).

3. Results

3.1. *Chalinolobus tuberculatus*

The body temperature in six long-tailed bats (mass = 9.0 ± 0.17 g [$n = 35$], the mean number of measurements/individual equaled 5.3)

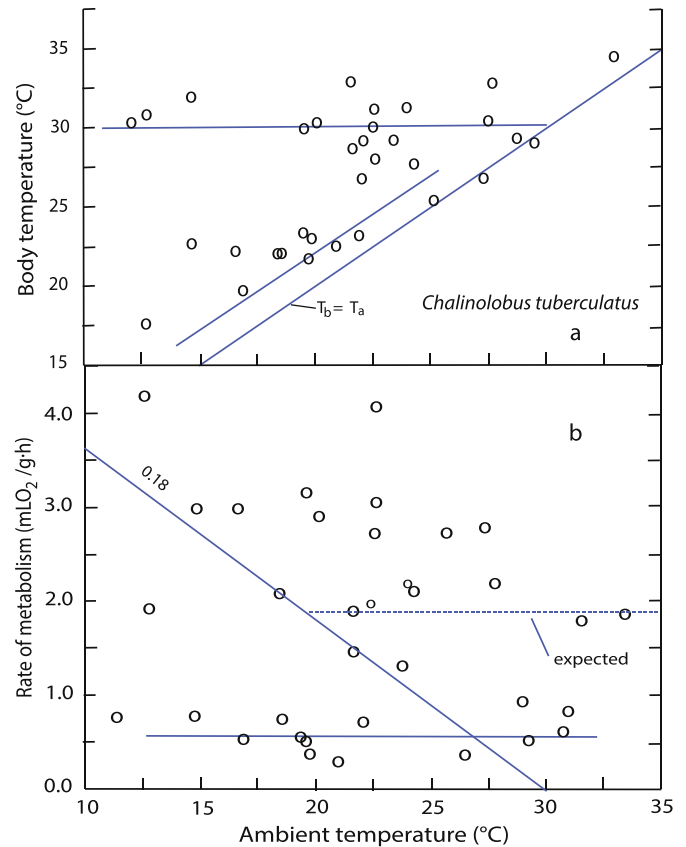


Fig. 1. a) Body temperature and b) rate of metabolism as a function of ambient temperature in *Chalinolobus tuberculatus*.

was highly variable (Fig. 1a). At chamber temperatures between 12 and 25 °C, body temperature either was maintained between 27 and 33 °C, or it decreased to within 3 °C of ambient temperature. There were few intermediate body temperatures at ambient temperatures < 20 °C. A regulated body temperature at intermediate and low ambient temperatures is ca. 30 °C (Fig. 1a).

The rate of metabolism was highly variable, increasing with the variation in body temperature (Fig. 2). At body temperatures near 30 °C, the rate of metabolism varied by a factor of 3:1, some the residual variation in rate increasing with the temperature differential (ΔT)

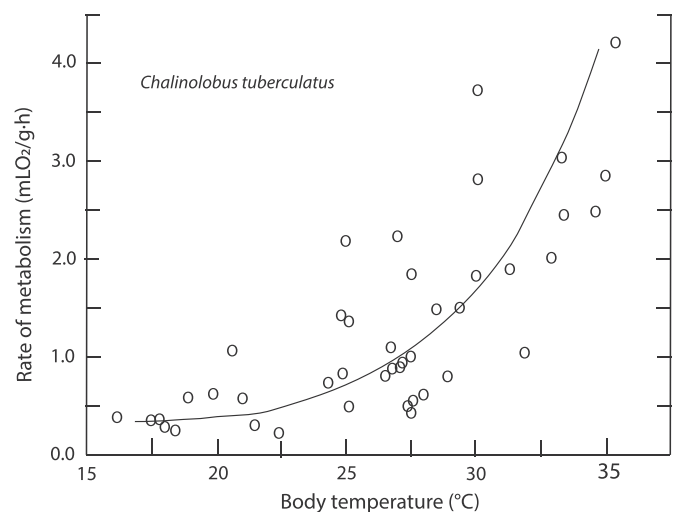


Fig. 2. Basal rate of metabolism as a function of body temperature in *Chalinolobus tuberculatus*.

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