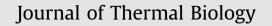
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Black or white? Physiological implications of roost colour and choice in a microbat



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ABSTRACT

Article history: Received 19 April 2016 Accepted 15 July 2016 Available online 17 July 2016 Although roost choice in bats has been studied previously, little is known about how opposing roost colours affect the expression of torpor quantitatively. We quantified roost selection and thermoregulation in a captive Australian insectivorous bat, Nyctophilus gouldi (n = 12) in winter when roosting in black and white coloured boxes using temperature-telemetry. We quantified how roost choice influences torpor expression when food was provided ad libitum or restricted in bats housed together in an outdoor aviary exposed to natural fluctuations of ambient temperature. Black box temperatures averaged 5.1 °C (maximum 7.5 °C) warmer than white boxes at their maximum daytime temperature. Bats fed ad libitum chose black boxes on most nights (92.9%) and on 100% of nights when food-restricted. All bats used torpor on all study days. However, bats fed ad libitum and roosting in black boxes used shorter torpor and spent more time normothermic/active at night than food-restricted bats and bats roosting in white boxes. Bats roosting in black boxes also rewarmed passively more often and to a higher skin temperature than those in white boxes. Our study suggests that N. gouldi fed ad libitum select warmer roosts in order to passively rewarm to a higher skin temperature and thus save energy required for active midday rewarming as well as to maintain a normothermic body temperature for longer periods at night. This study shows that colour should be considered when deploying bat boxes; black boxes are preferable for those bats that use passive rewarming, even in winter when food availability is reduced.

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1. Introduction

Roost choice is particularly important to small insectivorous bats as they have a large surface area to volume ratio and therefore experience high heat loss at low ambient temperatures (T_a). To minimize energy loss, many insectivorous bats use torpor, an effective energy-saving strategy characterized by a marked reduction in metabolic rate (MR) and body temperature (T_b) (Hock, 1951; Geiser, 2013; Stawski et al., 2014; Ruf and Geiser, 2015). Heterothermic mammals use torpor for a variety of reasons (Geiser and Brigham, 2012), including decreases in available resources (Buffenstein, 1985; Speakman and Racey, 1989; Song and Geiser, 1997; Coburn and Geiser, 1998), to deal with seasonal variations in T_a (Dietz and Kalko, 2006; Stawski and Geiser, 2010), and even to permit reproduction in adverse conditions (Grinevitch et al., 1995; Willis et al., 2006; Stawski, 2010; McAllan and Geiser, 2014).

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Although torpor can reduce energy expenditure by up to 99% from that of normothermic values (Geiser and Stawski, 2011), at the end of a torpor bout animals must rewarm to normothermic T_b and the energetic cost of this process, as well as thermoregulation at normothermic T_b , increases with decreasing T_a (Ruf and Geiser, 2015). Thus, the microclimate of a roost can greatly impact the energy expenditure of bats not only at rest and during torpor, but also during the rewarming process.

Bats are known to inhabit a wide range of roost types, such as caves, tree hollows, peeling bark, or leaves to suit varying thermoregulatory, reproductive, and ecological needs (Vonhof and Barclay, 1996; Callahan et al., 1997; Chruszcz and Barclay, 2002; Stawski et al., 2014). For example, the opportunity to roost with other bats appears to be the limiting factor in roost choice for reproductive, cavity-roosting bats (Willis and Brigham, 2007), while hollow entrance size is an important determinant for many Australian tree-roosting species (Goldingay, 2009). Roost choice has direct effects on torpor expression in Rafinesque's big-eared bats (*Corynorhinus rafinesquii*), significantly affecting the number of torpor bouts used per day (Johnson and Lacki, 2013). Therefore the wide range of roost types used by different species of insectivorous bats and other small endotherms can greatly influence an individual's daily energy budget and use of torpor due to their

Abbreviations: T_b, Body Temperature; T_{skin}, Skin Temperature; T_a, Ambient Temperature; T_{box}, Box Temperature; DEE, Daily Energy Expenditure; TMR, Torpor Metabolic Rate; RMR, Resting Metabolic Rate; MR, Metabolic Rate; TBD, Torpor Bout Duration

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differing thermal properties (Stawski et al., 2008; Willis et al., 2008; Doucette et al., 2011). Torpor can also vary amongst individuals based on habitat characteristics and resource availability (Encarnação et al., 2012).

Differences in thickness of bark (Nicolai, 1986), tree colour and the position of the sun are all important considerations for treeroosting bats when deciding where to roost. Some bats prefer more thermally unstable microclimates while others select for cool and/or well-buffered microclimates depending on sex, season, food availability or reproductive status (Law, 1993; Turbill, 2006; Boyles, et al. 2007: Stawski et al., 2008). A cool roost may save bats more energy during periods of deep or prolonged torpor, whereas a warm roost will be beneficial when bats must remain normothermic. Bats are known to choose a cooler and more stable T_a during winter when food availability is low in order to expend comparatively less energy than at high T_a (Speakman and Rowland, 1999). A thermally unstable roost may be cooler at night and in the morning, but as T_a increases animals could take advantage of an increasing roost temperature to passively rewarm to normothermia from torpor (Turbill et al., 2003) and save energy during the rewarming process.

Bat boxes are a commonly used method for providing cost-effective, easily maintained roosting habitat for bats. Boxes are often introduced, for example, into urban areas where roosting trees are compromised or rare, to provide roosts for displaced colonies, to facilitate roosting and thus foraging in crop areas for pest control, or in natural areas that have experienced wildfires, tree thinning, or other situations which have resulted in elimination of bat roosts (Brittingham and Williams, 2000; Smith and Agnew, 2002; Flaquer et al., 2006). However, bat boxes are often painted without consideration to colour, which could dramatically alter the internal temperature of the box/microclimate, and in turn greatly affect the physiology and, importantly, consequent energy use by bats. Some bats from the Northern Hemisphere select dark-coloured roost boxes over lighter ones when given the option (Kerth et al., 2001; Lourenço and Palmeirim, 2004). However these studies were conducted in warm and/or mild climates and thus the physiological implications of roost colour in winter remains unclear. During winter, bats may be more inclined to reduce MR and T_b to minimal levels and thus may not prefer dark boxes when food availability is low. To our knowledge, how roost colour choice may benefit bats in terms of their energy use and savings has not been quantified. It has been suggested that some bats may select dark roosts in autumn/winter, such as burnt trees in wildfire-affected areas (pers. observ; Doty et al., 2016), but the physiological reasons for doing so are uncertain.

The species used in our investigation, Gould's long-eared bat (*Nyctophilus gouldi*), is a small (~10 g) vespertilionid bat that hibernates in south-eastern Australia, and often expresses short bouts of torpor even during spring and summer (Geiser and Brigham, 2000; Turbill, 2006). The torpor metabolic rate (TMR) of these bats can be reduced to an average of 0.06 ± 0.04 ml O₂ g⁻¹ h⁻¹ at T_a 7.0 ± 0.1 °C, which is only 0.58% of the resting metabolic rate (RMR) at a minimum average T_a of 5.9 °C (Currie et al., 2014). *Nyctophilus gouldi* roost under bark, in hollows or cracks of trees (Lumsden et al., 2002; Churchill, 2009; Webala et al., 2010) and orientate themselves in the roost towards the sun (Turbill et al., 2003), effectively exposing themselves to maximum daytime temperatures.

To gain a better understanding as to why bats actively choose dark roost boxes and if bats from the Southern Hemisphere maintain similar roost choice patterns as those from the Northern Hemisphere, we measured the thermal properties of opposing bat box colours, black and white. We also determined the roost preference and skin temperature (T_{skin}) of non-reproductive *N. gouldi* to quantify any physiological differences when roosting in boxes

with potentially different thermal properties. We tested four hypotheses: i) black bat boxes will be warmer than white bat boxes, ii) when fed *ad libitum*, bats will prefer to roost in black boxes in winter because they will save energy whilst rewarming from torpor, and normothermic bats will require less thermoregulatory heat production due to a higher box temperature, iii) when food-restricted, bats will prefer to roost in white boxes in winter in order to reach deeper torpor and save more energy, and iv) box colour choice during the day will be an influencing factor for time spent normothermic at night.

2. Materials and methods

2.1. Experimental protocol

Roosting behaviour and physiological correlates of torpor use in *N. gouldi* were quantified during the Austral winter at the University of New England in Armidale ($30^{\circ}30'S$ 151°39'E) in NSW Australia, a cool-temperate area surrounded by grazing land and open eucalypt forest. Bats were captured in nearby forest using harp traps (© Faunatech Austbat, Australia) and mist nets (© Ecotone, Poland). They were housed in an outdoor aviary for 12 days and (i) offered mealworms (*Tenebrio molitor* larvae) *ad* libitum and water *ad* libitum for the entire duration of Treatment 1 (June 2014) or (ii) food-restricted (water *ad* libitum for the entire treatment and mealworms *ad* libitum only on days 0, 4 and 8) during Treatment 2 (July 2015).

We report data from seven *N. gouldi* in 2014 (Treatment 1; 4 females body mass 10.5 ± 1.3 , 3 males body mass 10.1 ± 0.3 ; mean body mass for both sexes 10.3 ± 1.0 g) and five *N. gouldi* in 2015 (Treatment 2; 5 males; body mass 10.0 ± 0.7 g). The following methods are identical for both treatments. To measure T_{skin}, temperature-sensitive radio-transmitters (~0.5 g, LB-2NT, Holohil Systems Inc., Carp, Ontario, Canada) were glued using a latex adhesive (B-520; Factor2; Lakeside, Arizona) to the mid-dorsal skin region after removing a patch of fur. Before attachment, transmitters were calibrated in a water bath between 5.0 °C and 40.0 °C using a precision thermometer (0.1 °C resolution); pulse rate was regressed against transmitter temperature (r² > 0.99) to derive T_{skin} of bats.

After transmitter attachment, bats were released in an aviary $(2 \times 2 \times 5 \text{ m})$ on campus. Bats were released together to encourage natural roosting behaviours, allowing them to roost communally or solitarily. Six single-chambered plywood boxes (3 Black, 3 White; $25 \times 45 \times 7$ cm) were painted with acrylic paint (White Knight, Villawood, NSW), dried and hung alternating in colour on the wall of the aviary and were exposed to as much direct sunlight as possible throughout the day as dictated by the layout of the aviary, thus facing in a north-northeast orientation. The boxes were therefore exposed to natural fluctuations in T_a and could warm or cool based on T_a and the position of the sun. Weather during both experimental periods was mostly sunny and without rain. To measure box temperature (T_{box}), a temperature data logger (+0.5 °C, DS1921G, iButton Thermochron, Maxim Integrated Products Inc., Sunnyvale, CA, USA) was fitted at the top of each box and covered in mesh to prevent interference from direct contact with bats. External T_a (ambient air temperature outside of the roost) was measured using a temperature data logger (± 0.1 °C, DS1922L, iButton Thermochron, Maxim Integrated Products Inc., Sunnyvale, CA, USA) placed in the aviary and in the shade, shielded from solar radiation. The T_{skin} was recorded in 5-min intervals using a multichannel remote receiver/logger and antenna (Körtner and Geiser, 2000) positioned near the aviary. Data from the receiver/logger were downloaded to a laptop computer at the same time each day. Each morning at 08:00 h, the location of the bats in Download English Version:

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