Frequent nocturnal torpor in a free-ranging Australian honeyeater, the noisy miner

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Abstract

Torpor in birds is considered to be far less common than in mammals. This is particularly true for passerine birds for which knowledge of torpor expression is scarce, although almost all are small, have high energy expenditure and could profit energetically from using torpor. To assess whether the extent and diversity of avian and especially passerine torpor expression and heterothermy may be currently underestimated because of limited long-term data on free-ranging birds, core body temperature fluctuations were quantified over ~ 4.3 months in a medium-sized honeyeater, the noisy miner (*Manorina melanocephala*, ~ 75 g), in an open woodland during the cold season in eastern Australia. Miners used shallow nocturnal torpor frequently (63% of days), torpor bouts lasted on average for 6.5 h (maximum 13.5 h) and, unlike during hypothermia, torpor was terminated by endogenous heat production for rewarming. Body temperatures (T_b) ranged from a maximum of 43.5 °C to a minimum of 33.0 °C, often fell by 7 °C at night, and the overall mean T_b was 38.7 ± 0.7 °C. The data show that yet another passerine bird, widely viewed to be homeothermic, expresses torpor in the wild for energy conservation. Considering the size of miners, it seems probable that many other, especially smaller birds, use a similar approach at least in winter to enhance the chance of survival in the face of high energy expenditure and low food availability.

Keywords Birds · Energy conservation · *Meliphagidae* · Passerines · Torpor · Winter

Introduction

Avian and mammalian endothermy allows the regulation of a high and constant body temperature (T_b) to maximise bodily functions over a wide range of ambient temperatures (T_a). However, to achieve this, the animals must produce large amounts of internal heat to compensate for heat loss from the body to the environment especially during cold exposure (Withers et al. 2016). Heat loss is also strongly affected by body size because relative surface area and body mass are inversely related. This can be problematic for birds and mammals, the majority of which are small, and therefore have to compensate for heat loss from the body surface by internal heat production that requires the intake of large amounts of

food to fuel a high metabolic rate (MR). For insectivorous, frugivorous and nectarivorous species that must cope with seasonally fluctuating food supplies, this is not always possible. Therefore, many small endotherms are not permanently homeothermic (i.e. maintain a constant high T_b) but rather are heterothermic (i.e. have a fluctuating T_b) and use torpor for energy conservation, often during times of food shortage and/ or cold exposure. Torpor is characterised by a substantial and controlled reduction in MR (often by ~ 50 to 95%) and T_b (often by ~ 5 to 35 °C) and may last for several hours (daily torpor) and up to several weeks (hibernation or multiday torpor), interrupted by periodic arousals (McKechnie and Lovegrove 2002; Ruf and Geiser 2015).

Both birds and mammals can use torpor (Bartholomew et al. 1957; Dawson and Hudson 1970; Prinzinger and Siedle 1988; Körtner et al. 2000; Brigham et al. 2000; Schleucher 2001; Downs and Brown 2002; McKechnie and Lovegrove 2002; Geiser et al. 2006; Ruf and Geiser 2015; Woods et al. 2019). However, it is widely believed that torpor in small birds is far less common than in small mammals because birds can migrate to avoid adverse conditions and food shortages, whereas most small mammals cannot. This

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argument is based on the assumption that all birds use long-distance migration, which is of course not the case. Many Australian birds, for example, are sedentary or nomadic and since the Australian continent is characterised by low rainfall, high evaporation rates and prolonged periods of drought and low primary productivity, food is likely to be periodically limited, in addition to the usual seasonal challenges. Sedentary birds that rely on insects, nectar or fruits, in particular, must deal with energetic bottlenecks under such conditions, and since they do not migrate, they must use appropriate physiological and behavioural adaptations to survive (Doucette et al. 2011; Douglas et al. 2017). Moreover, torpor and migration are not mutually exclusive as torpor can have an important role during migration stopovers to save energy and maximise energy availability for flight (Carpenter and Hixon 1988; Hiebert 1993).

Although not restricted to these taxa, torpor in birds is best known for the nightjar relatives (*Caprimulgiformes*), which contain the only known avian hibernator (Withers 1977; Brigham 1992; Woods et al. 2019), and the hummingbirds (*Trochiliformes*) (McKechnie and Lovegrove 2002). However, data on torpor in free-ranging birds remain scarce (Brown and Downs 2004; McKechnie and Mzilikazi 2011). Interestingly, more than half of all extant bird species belong to the order *Passeriformes* (> 5000 species), and most of these are small. Nevertheless, data about torpor use in the passerines, especially in the wild where torpor is often more pronounced than in captivity (Geiser et al. 2000), are restricted to only a few (< 1%) species (McKechnie and Lovegrove 2002). In comparison, 25–50% of the > 5000 mammalian species are estimated to express torpor (Geiser et al. 2018). Torpor in passerines appears to be rather shallow, with T_b in many species falling from around 41 to 42 °C to near 30 °C; a minimum T_b of ~ 25 °C was observed in sunbirds (Downs and Brown 2002; McKechnie and Lovegrove 2002; Maddocks and Geiser 2007). From an evolutionary point of view, Australian passerines are an interesting group with regard to torpor as many species are endemic, and the majority of passerines appear to be the result of a massive Australian radiation (Ford 1989), and therefore are especially likely to be physiologically adapted to the aridity and low productivity of the continent.

The aim of my study was to provide the first long-term data on the T_b fluctuations in a free-ranging medium-sized honeyeater, the noisy miner (*Manorina melanocephala*, Meliphagidae). Data on captive individuals suggest that the species does not enter torpor because they reduced T_b by only up to ~ 4 °C at night (Maddocks 2001). However, the regular nocturnal reduction of T_b made the species a likely candidate for torpor expression in the wild. Honeyeaters are one of the most successful Australian bird families. Noisy miners are largely insectivorous but also eat fruits and nectar. They are abundant, live in family groups in eastern Australia and because of their aggressive nature can displace other small bird species (Ford 1989; Lindsey 1992; Barati et al. 2016).

Methods

Ten noisy miners were captured as by-catch during netting of other birds using mist nets at Imbota Nature Reserve (30° 35′ S, 151° 44′ E; elevation approximately 1000 m), an open eucalypt woodland on the New England Tablelands, on the morning of 10 and 11 May 2001. Birds were transported to the University of New England, were weighed to the nearest 0.1 g using an electronic balance and were implanted with calibrated, waxed (Paraffin/Elvax, Minimitter, USA) iButtons (Thermochron DS1921G, resolution 0.5 °C). The iButtons provided readings every 90 min for a maximum of 128 days from 10/11 May to 15/16 September (i.e. 2048 readings, most of which were taken during the Austral winter). The waxed iButtons weighed 3.4 g, which is about 4% of the birds' body mass at capture. iButtons were disinfected in 70% ethanol and were implanted intraperitoneally under general isoflurane/oxygen anaesthesia as described (Rojas et al. 2010). Following implantation, a topical anaesthetic (Xylocaine, AstraZeneca Pty Ltd., North Ryde, NSW, Australia), Betadine Antiseptic Liquid, and Leuko Spray Bandage (BSN medical Pty Ltd., Clayton, Vic, Australia) were applied to the suture site. Birds were fitted with a ring for identification, allowed to recover for several hours and released in the afternoon at the site of capture. Released birds were observed, were well coordinated and flew immediately to their family group. Three of these miners were recaptured on 20 and 24 September 2001, iButtons were removed as described above and, after recovery, birds were released at the capture site. To assess whether iButtons could have had a negative effect on miners during winter, 'control' body masses are presented for comparison. These previously unpublished body mass data, provided by Dr. Paul McDonald, were obtained from miners netted for a behavioural ecology study on this species conducted from 2011 to 2014 in similar habitat on the New England Tablelands (Barati et al. 2018), but not implanted with loggers.

During the experimental period, sunrise time ranged from 05:40 to 06:50 and sunset from 17:00 to 17:51. The T_a (air) was measured in 90-min intervals at the capture site using a calibrated iButton (DS1921G, 0.5 °C resolution) mounted in the shade 1 m above the ground.

Torpor was defined as a reduction in T_b by > 5 °C below normothermic, resting T_b (Ruf and Geiser 2015). This fall of T_b for definition of torpor seems better suited to describe its occurrence than a single absolute value for a torpor threshold because the normothermic resting T_b of bird species varies from about 35 to 41 °C (McKechnie and Lovegrove 2002).

As the most frequent T_b readings were between 40.5 and 42.0 °C (present study), resting T_b of miners in the thermoneutral zone was reported to be 41.5 °C (MacMillen 1985) and resting T_b was measured to be 40.9 °C (winter) and 41.4 °C (spring) in a captive study on the species (Maddocks 2001), I defined a fall of T_b to or below 36.0 °C as torpor occurrence for this species. This fall of T_b is also much greater than the ± 2.0 °C T_b range recently defined as homeothermy (Hetem et al. 2016). Torpor occurrence was calculated as torpor expression/day, i.e. days with one and two bouts of torpor were counted as one event. Torpor bout duration (TBD) was calculated as the time at or below 36.0 °C, which seems appropriate considering the large falls of T_b (Fig. 1). Timing of torpor entry and arousal was calculated for TBD of 180 min or longer in July, when torpor was most frequent and pronounced, and therefore such an analysis provides the most meaningful information; if more than one torpor bout was observed/day, the longer bout was analysed.

Numeric values are presented as means with 1 SD for the number of individuals (n); N represents the number of measurements. The average T_b with SD was calculated for all measurements although this value should be considered with the bimodal distribution of data in mind. Moreover, the means for T_b are expressed to the nearest 0.1 °C because a rounding to the nearest 0.5 °C resulted in a misrepresentation of data (for example, a mean maximum T_b of 43.0 ± 1.0 °C does not describe the data as well as the reported T_b of 42.8 ± 0.8 °C). The means for times and duration are expressed to the nearest 0.5 h considering the measured intervals. Newer equipment with higher data capacity and better resolution is now available. A heterothermy index (e.g. Smit et al. 2011) was not calculated for the T_b data because it does not distinguish between long and shallow and short and deep torpor bouts, important variables often used for characterising torpor patterns
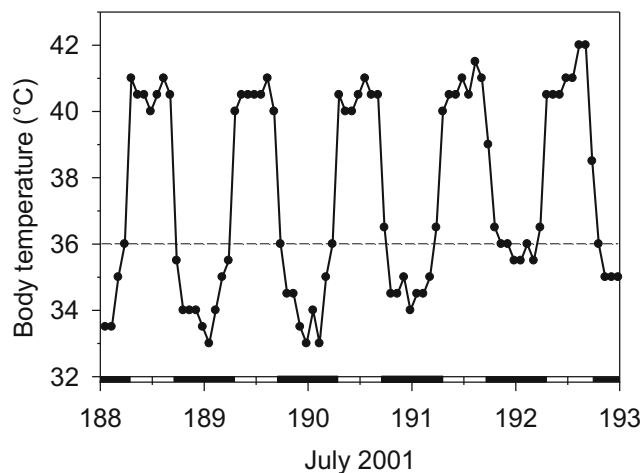
Fig. 1 Body temperature (T_b) fluctuations over 5 days in July (midwinter) in noisy miner #1. Horizontal dark bars indicate night. The broken horizontal line at 36.0 °C represents the torpor threshold. Days on X-axis are Julian days since 1 January

(Brigham et al. 2011; Ruf and Geiser 2015). Least squares regressions were used to assess whether daily mean T_b, daily maximum T_b and daily minimum T_b of each individual is correlated with the daily mean T_a, daily maximum T_a, daily minimum T_a and day length. The mean monthly TBD of the three individuals was regressed against mean monthly mean T_a, mean maximum T_a, mean minimum T_a and the mean monthly day length.

Permits for the work were provided by the University of New England Animal Ethics Committee and the National Park and Wildlife Service of NSW.

Results

The body mass of the three recaptured miners was 76.9 ± 0.5 g (initial capture mass, May), 70.1 ± 6.2 g (recapture mass, September) and the mean mass loss was 6.8 ± 1.0 g. For comparison, body mass of control miners netted in May was 73.3 ± 9.5 g ($n = 48$) and 65.7 ± 12.6 g ($n = 39$) in September, and the mean mass loss was 7.6 g. The T_a measured during the study period ranged from − 4.5 °C (minimum) to 19.5 °C (maximum) and the mean was 7.3 ± 4.6 °C (Fig. 2).

The T_b of miners showed strong daily fluctuations, which clearly shows that they are heterothermic. For example, in miner #1 in July (mid-winter), T_b over 5 days showed predictable fluctuations from maxima of about 40 to 42 °C during the day to minima of around 34 °C during the night (Fig. 1). However, the large daily fluctuations of T_b were not restricted to mid-winter. From May to September, T_b fell predictably by > 5 °C, often on a daily basis (Fig. 2).

Torpor was restricted to night time and mean torpor use for the 3 miners was 63 ± 43% of days. Torpor expression ranged from 0 to 81% (May,), 17 to 100% (June), 42 to 100% (July), 3 to 100% (August) and 0 to 100% (September). The three individuals did not exhibit the same torpor use. Miners #1 and #3 expressed torpor in all months, and in both individuals, two bouts of torpor/day were observed from May to August on certain days, which were interrupted by brief normothermic periods, with T_b increases usually to T_b 36.5 °C. Miner #2, the lightest bird at capture (72.0 g) and recapture (65.2 g), did not express torpor in May and September, and its maximum torpor use (42%) was observed in July. Interestingly, miner #1, the heaviest bird (capture 82.8 g, recapture 77.0 g) expressed most torpor (97% of days and the longest torpor bouts, see below) during the study and its mass loss was the lowest (5.8 g) of the three individuals.

With regard to physiological variables of miners, the mean absolute maximum T_b ($n = 3$, $N = 3$) was 42.8 ± 0.8 °C (individual maximum T_b 43.5 °C), the mean minimum T_b was 34.3 ± 1.3 °C (individual minimum T_b 33.0 °C) or a mean drop by 8.5 ± 0.5 °C. The overall mean T_b was 38.7 ± 0.7 °C ($n = 3$, $N = 6144$). Miner #2 with the least torpor expression

Fig. 2 Fluctuations of body temperature (T_b) in three noisy miners (**a** #1, **b** #2, **c** #3) and **d** air temperature (T_a) over the entire cold season
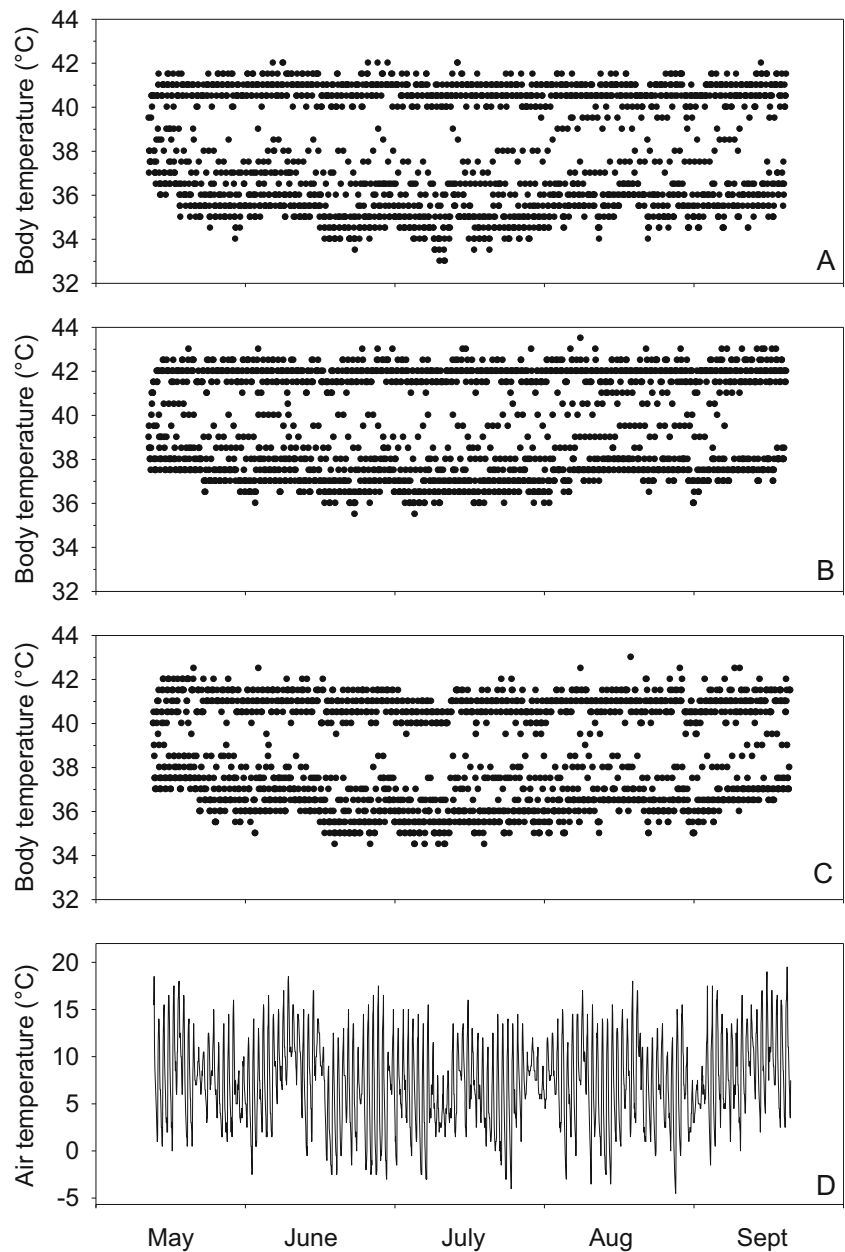

had the highest mean T_b (39.5 ± 2.3 °C) in comparison to miners #1 (38.5 ± 2.6 °C) and #3 (38.5 ± 2.3 °C). Miner #2 also had the highest daily mean maximum T_b (42.4 ± 0.5 °C) in comparison to miner #1 (41.2 ± 0.4 °C) and #3 (41.4 ± 0.5 °C). The T_b minima changed with the season and were lowest in mid-winter (Fig. 2). Interestingly (Fig. 3), the T_bs were either high, most at 40.5 to 42.0 °C (absolute peak at 41.0 °C), or low, most between 35.0 and 38.0 °C (absolute peak at 36.5 °C), with only few values in between (i.e. T_b 38.5 to 40.0 °C). The daily maximum T_b was reached at 10:30 ± 0:30 h and the minimum T_b at 05:30 ± 2:00 h ($n = 3$), whereas the daily maximum T_a was at 15:00 h and the minimum T_a at 07:00 h. Unexpectedly, the daily mean T_b, maximum T_b and minimum T_b of individuals were not strongly correlated with

the daily mean T_a, maximum T_a and minimum T_a. The r^2 for the mean T_b as a function of T_a, regressed separately for the three miners, ranged from 0.17 to 0.27, those for the maximum T_b from 0.14 to 0.23 and those for the minimum T_b from 0.009 to 0.063. When the T_bs for the three miners were plotted as a function of day length most regressions had a higher r^2, ranging from 0.25 to 0.53 (mean T_b), 0.13 to 0.33 (minimum T_b), but only < 0.07 for maximum T_b.

Torpor bout duration (TBD), especially the longest bouts observed, also changed with the season (Fig. 4). In May (austral autumn) and September (austral spring), TBD lasted from 1.5 to 10.5 h, whereas in June/July, most torpor bouts lasted for 7.5 to 13.5 h, although TBDs of 1.5 h were also observed. The TBD for the three miners (Fig. 4) ranged from 0 to 8.5 h
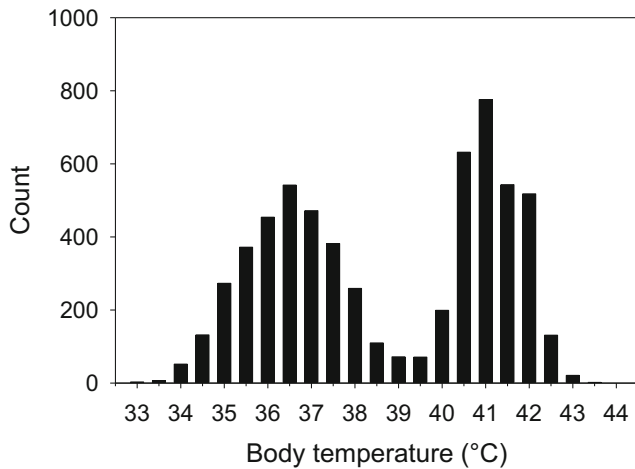
Fig. 3 Frequency distribution of body temperatures (T_b) of the three noisy miners. T_b range for all miners: 35.5 to 42.0 °C, miner #1 range: T_b 33.0 to 42.0 °C, miner #2: T_b 35.5 to 43.5 °C, miner #3: T_b 34.5 to 43.0 °C

(May), 3 to 9.5 h (June), 3 to 11 h (July), 3 to 10.5 h (August), and 0 to 6.5 h (September). For the entire season, mean TBD was 9.5 ± 2.5 h (miner #1), 3.0 ± 1.5 h (#2) and 6.5 ± 3.5 h (#3), and the overall mean TBD was 6.5 ± 3.0 h ($n = 3$). Monthly mean TBD of the three miners was correlated with the monthly mean T_a ($r^2 = 0.73$), monthly maximum T_a ($r^2 = 0.57$), monthly minimum T_a ($r^2 = 0.48$) and mean monthly day length ($r^2 = 0.49$).

Timing of torpor entry and arousal was highly predictable, at least in mid-winter (July) when torpor was most frequent and pronounced. However, as indicated by the TBD data, timing differed among individuals. Torpor entry occurred at $18:00 \pm 0:30$ h, arousal at $04:30 \pm 1:00$ h (miner #1), entry at $22:30 \pm 1:30$ h arousal at $04:00 \pm 6:30$ h (#2), and entry at $19:30 \pm 1:00$ h arousal at $04:30 \pm 3:30$ h (#3). The miner with the latest torpor entry and earliest arousal necessarily had the shortest TBD and vice versa. Interestingly, miner (#2), which
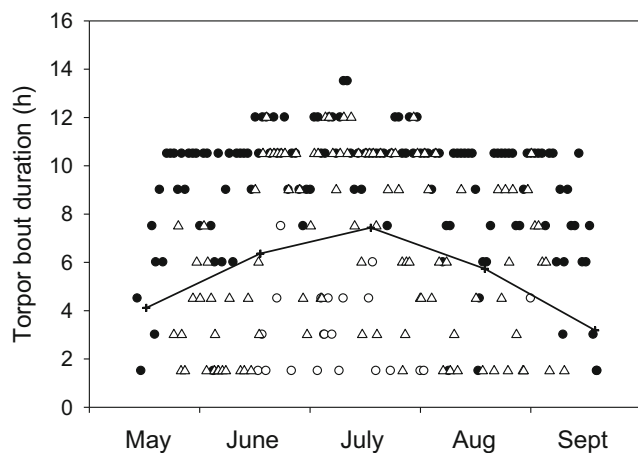
had the largest variance of entry and arousal times, had the shortest TBD. The earliest torpor entry occurred at 17:41 (sunset 17:06) and the latest torpor arousal at 05:41 (sunrise 06:50) was observed for a torpor bout lasting 13.5 h.

Discussion

The data show that yet another passerine bird is heterothermic and regularly expresses nocturnal torpor, likely for energy conservation, during the cold season in the wild. Torpor in noisy miners was frequent and often used on a daily basis, lasted for around 6.5 h on average, and was restricted to the night. However, as in other passerines (McKechnie and Lovegrove 2002), the minimum torpor T_b was relatively high at 33 °C. The maximum difference in T_b between activity and torpor is ~ 10 °C nevertheless, which is much greater than the T_b variation of ± 2 °C defined to be homeothermy (Hetem et al. 2016) and is greater than the fall of T_b by ~ 4 °C measured in captivity (Maddocks 2001). With regard to high T_bs, maximum T_bs of 43.0 to 43.5 °C were reached in miners even in winter, which approximates the T_b maxima observed during heat stress ($T_a \sim 40$ to 50 °C) in Australian passerines (McKechnie et al. 2017).

The noisy miner is yet another bird that in the past was considered to be homeothermic, but clearly expresses shallow torpor in the wild. A published study on the thermal energetics of captive noisy miners did not specifically investigate whether or not miners can express torpor and did not consider this energetically consequential possibility (MacMillen 1985). In several other species, including the rather large tawny frogmouths (*Podargus strigoides*, ~ 500 g) and kookaburras (*Dacelo novaeguinieae*, ~ 350 g), data on thermal energetics of captive birds suggested that these birds are strictly homeothermic, but subsequent field studies have shown that they regularly do use torpor in the wild (see Körtner et al. 2000; Cooper et al. 2008). The incorrect assumption of homeothermy in heterothermic endotherms is not restricted to birds, but includes a number of mammals such as shrews (several species in both the *Crocidurinae* and *Soricinae*) and elephant shrews (*Elephantulus edwardii*), which initially had been classified as homeothermic, but in more detailed studies were shown to use torpor, with a T_b of less than 10 °C in *E. edwardii* (see Geiser and Mzilikazi 2011; Ruf and Geiser 2015). These large discrepancies between thermal biology observations on the same species strongly suggest that the understanding of the diversity of heterothermy in birds and mammals is currently rudimentary and often simply reflects a lack of appropriate experimental work. This gap of knowledge will result in wrong interpretations and predictions, especially with regard to energy use and food requirements, for example, as a function of season or climate change.

Fig. 4 Torpor bout duration (TBD) of the three noisy miners (miner #1 dots, #2 circles, #3 triangles) over the entire cold season. Symbols are for single measurements, lines connect monthly means (crosses)

The body mass loss of the three miners fitted with iButtons was ~9% from the initial capture in May to recapture in September. This raises the question of whether the iButtons or surgery adversely affected the animals. However, as the mass loss of control miners that were not implanted with loggers was actually ~11% over the same time period in the same habitat, it is likely that the decline in body mass in late winter/ early spring is part of a natural seasonal cycle in free-living birds. Pronounced seasonal fluctuations in body mass have even been observed in captivity despite access to ad libitum food in tawny frogmouths, *Podargus strigoides* (Stulberg et al. 2018) and in free-ranging willow tits, *Parus montanus*, which reduced body mass in spring (Koivula et al. 1995).

The available data on only three birds raises the question of whether they are representative. Although the sample size precludes predictions about the entire population, it clearly shows that two of three measured birds used torpor frequently and not only when it was very cold, whereas the third individual used torpor less. It is entirely possible and even likely that not all miners in all habitats exhibit torpor in this way, but the data show that they are physiologically capable of doing so.

Although data on only three individuals are available, to my knowledge, the data set derived from temperature loggers presented here is among the most continuous, complete and extensive for heterothermic birds measured in the field to date. The reliable and extensive data from loggers without missing values permit meaningful calculations even when based on a small number of individuals (see Geiser and Mzilikazi 2011), which has implications for required sample sizes. These reliable and continuous logger data typically differ from those obtained via temperature telemetry especially for small flying species that easily can leave the transmitter reception range resulting in missing data, especially during activity (Cooper et al. 2008). Of course, the drawback of data derived from temperature loggers alone is the lack of behavioural and foraging data, whereas temperature telemetry often provides these as well (Rojas et al. 2010). Therefore, it is desirable to obtain continuous long-term data on behaviour, foraging and thermal biology, as well as other variables, when this is technologically possible.

Miners expressed torpor regularly, but the minimum T_bs at night were relatively high and one may ask whether an average drop of T_b by ~7 °C from rest to torpor does result in substantial energy savings. Measurements on captive miners show that at T_as between 0 and 15 °C, similar to the thermal conditions during the present field study, resting MR at night falls to ~ 60% of that during the day with only a ~4 °C drop in T_b, to a large extent because of a ~40% reduction in thermal conductance at night (Maddocks 2001). Therefore, if the same fall in thermal conductance is assumed to occur in miners in the field, the reduction of T_b by ~7 °C, as regularly observed in the wild, should reduce resting energy expenditure by at least 50% in comparison to that during the day. As torpor lasted for over one quarter of the day on average, this reduction in MR should result in energy savings that are probably large enough to be crucial for winter survival of miners in the wild.

The smallest mass loss (~7%) in miner #1, which used most torpor in comparison to miner #2 expressing least torpor (mass loss ~10%) supports the view that using torpor is energetically beneficial. The reason why miner #2 expressed less torpor may be related to actual or perceived predation risks (Laurila and Hohtola 2005; Andreasson et al. 2019). However, intrinsic factors, such as miner #2 having a higher mean T_b and a ~1 °C higher mean daily maximum T_b than the other two birds, also need to be considered.

The high T_b during torpor in birds and especially passerines has resulted in the view that torpor in birds and mammals may differ functionally. In the avian literature, the nocturnal drop of T_b is often referred to as 'nocturnal hypothermia' or 'facultative hypothermia' suggesting that the mechanisms of T_b and MR reduction in birds and mammals are fundamentally different. However, a detailed examination of the interrelations between T_b and MR during torpor entry and arousal shows the same general patterns during shallow torpor in a passerine and during deep hibernation in a bat (Geiser et al. 2014). Torpor is a controlled energy-conserving process, characterised by a fast initial reduction of MR followed by fast cooling of T_b during torpor entry (as in Fig. 1). Arousal from torpor is characterised by a fast active increase of MR and high heat production followed by a fast increase in T_b (as in Fig. 1). In contrast, during cold-induced hypothermia, which is not controlled, the opposite is observed with a slow reduction of T_b because MR remains high in an attempt to avoid this state, and T_b falls only because heat loss exceeds the capacity for heat production. During the rewarming phase from hypothermia, the increase of T_b is passive (i.e. requires an external heat source) and slow, and MR remains low throughout the process (Geiser et al. 2014). These clear functional differences between torpor and hypothermia do not seem to justify the use of the term hypothermia for describing shallow torpor in birds. Of course, the high, defended T_b in torpid passerines will preclude a wide temperature range over which MR can fall with T_b and thermo-conformation is possible. Passerine birds regulate T_b during torpor at T_b ~25 to 35 °C, in contrast to mammals, many of which regulate T_b during torpor between T_b ~0 and 15 °C (McKechnie and Lovegrove 2002; Ruf and Geiser 2015). At first glance, the relationships of MR as a function of T_a in mammals and birds may therefore appear to differ. However, apart from differences in minimum T_b, there seem to be no basic functional differences in the thermal physiology of torpor in birds and mammals.

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