Heterothermy in a Small Passerine: Eastern Yellow Robins Use Nocturnal Torpor in Winter

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Torpor is a controlled reduction of metabolism and body temperature, and its appropriate use allows small birds to adapt to and survive challenging conditions. However, despite its great energy conservation potential, torpor use by passerine birds is understudied although they are small and comprise over half of extant bird species. Here, we first determined whether a free-living, small ∼20 g Australian passerine, the eastern yellow robin (*Eopsaltria australis*), expresses torpor by measuring skin temperature (T_s) as a proxy for body temperature. Second, we tested if skin temperature fluctuated in relation to ambient temperature (T_a). We found that the T_s of eastern yellow robins fluctuated during winter by 9.1 ± 3.9°C on average (average minimum T_s 30.1 ± 2.3°C), providing the first evidence of torpor expression in this species. Daily minimum T_s decreased with T_a, reducing the estimated metabolic rate by as much as 32%. We hope that our results will encourage further studies to expand our knowledge on the use of torpor in wild passerines. The implications of such studies are important because species with highly flexible energy requirements may have an advantage over strict homeotherms during the current increasing frequency of extreme and unpredictable weather events, driven by changing climate.

Keywords: torpor, thermoregulation, passerines, metabolism, climate change, heterothermy, geographical variation, yellow robin

INTRODUCTION

Endotherms can maintain a high body temperature (T_b) across a range of ambient temperatures (T_a) *via* appropriate adjustment of internal heat production. However, the energetic costs to thermoregulate outside of the thermal neutral zone can be expensive (Mckechnie and Lovegrove, 2002; Angilletta et al., 2010). To deal with these energetic costs, many endothermic species use torpor, a controlled reduction in metabolism and typically T_b (Namekata and Geiser, 2009; Ruf and Geiser, 2015). Torpor is used as a strategy to overcome energetically challenging periods such as cold (Maddocks and Geiser, 2007; Romano et al., 2019; Wolf et al., 2020), reduced food/water or foraging opportunities (Nicol and Andersen, 1996; Nord et al., 2009; Smit et al., 2011) or even hot conditions (Reher and Dausmann, 2021), and its use varies considerably among avian taxa (Geiser, 2021). Some evidence of intra-specific variation in torpor patterns along latitudinal or elevation gradients (Geiser and Ferguson, 2001; Dunbar and Brigham, 2010; Zervanos et al., 2010; Stawski and Geiser, 2011) suggests that T_a may play a major role in torpor expression in passerines, but only

little information on geographical variation is available for birds (Chaplin, 1976; Sharbaugh, 2001). Although some potential costs may occur at low T_bs on a cellular level (Nowack et al., 2019), the use of torpor may reduce predation risk by increasing antipredator behavior (but see Amo et al., 2011; Turbill and Stojanovski, 2018), and in small diurnal birds can reduce metabolic demands by as much as 50% (Cooper and Gessaman, 2005) and may increase survival by 58% (Brodin et al., 2017).

The use of torpor for energy conservation is common in a range of small mammals (e.g., Ruf and Geiser, 2015; Nowack et al., 2020) and in several non-passerine bird species such as hummingbirds and nightjar relatives (Hiebert, 1992; Körtner et al., 2000; Shankar et al., 2020). In contrast, the extent of the use of torpor by passerines, a group which includes over half of extant birds species, is understudied (Mckechnie and Lovegrove, 2002). Despite evidence for large nocturnal T_b reduction dating back to the late 1950's [e.g., in Redpoll *Carduelis flammea* and tree sparrow *Passer montanus*, Steen (1958)], and further anecdotal evidence of nocturnal torpor in multiple species in the 1970's [Crimson chat (*Epthianura tricolor*), red-capped robin (*Petroica goodenovii*), white-fronted honeyeater (*Phylidonyris albifrons*) and banded whiteface (*Aphelocephala nigricincta*); Ives (1973), white-backed swallow (*Cheramoeca leucosternum*); Serventy (1970)], little progress has been made in the field. Some small passerine species have been reported to use torpor under controlled conditions: Golden-collared manakins [*Manacus vitellinus*; Bucher and Worthington (1982)], dusky woodswallows [*Artamus cyanopterus*; Maddocks and Geiser (2007)], rifleman [*Acanthisitta chloris*; Mcnab and Weston (2018)], and malachite sunbirds [*Nectarina famosa*; Downs and Brown (2002)] dropped their T_b to 27–30°C at T_aS of 19.5, 6, 11, and 5°C, respectively. The rifleman has also been reported to decrease metabolic rate to as low as 21% of its expected basal metabolic rate (Mcnab and Weston, 2018). Torpor under controlled environment has also been reported in species adapted to very cold conditions. The black-capped chickadees (*Poecile atricapilla*) from Alaska reduced T_b by about 8°C in both winter and summer when exposed to T_a −30°C, and actively rewarmed (Sharbaugh, 2001). Metabolic rate reduction has also been observed in scarlet-backed Flowerpecker (*Dicaeum cruentatum*), which reduced metabolic rates by over 70% during torpor vs. non-torpor state (Bushuev et al., 2021). While this evidence supports torpor use in passerine species, it is important to evaluate these functions in the wild. Captive conditions do not represent the complexity of the thermal conditions and ecological complexity (e.g., food abundance, predation risk) experienced in the wild, and laboratory studies may therefore underestimate the use of torpor by wild animals (Geiser et al., 2000; O'connor et al., 2017).

To date, only two passerine species studied in the wild have been shown to express torpor. The T_b of noisy miners (*Manorina melanocephala*) fell by 7°C on average, to a minimum of 33°C during winter in eastern Australia, where night time temperatures frequently drop to near 0°C (Geiser, 2019), and fairy wrens (*Malurus cyaneus*) dropped their skin temperature (T_s) by over 14.5°C, with minimum T_s of 27.4°C recorded at average minimum T_a of about 3°C (Romano et al., 2019). Other passerines species which were studied in the wild remained euthermic, even during challenging conditions [e.g., red-headed finch *Amadina erythrocephala* (Mckechnie and Lovegrove, 2003), five species of tropical montane passerines (Burnett et al., 2019), willow tit *Parus montanus* (Reinertsen and Haftorn, 1984), bronze mannikins *Spermestes cucullatus* (Lovegrove and Smith, 2003), great tits *Parus major* (Nilsson et al., 2020), blue tits *Cyanistes caeruleus* (Nord et al., 2009)]. The lack of extensive studies on torpor use in wild passerines is somewhat surprising, because although evidence is limited, data in the wild and under controlled environment do suggests that some passerine species are capable of large T_b reduction. Moreover, many passerine species are insectivorous, small and diurnal and cannot feed at night when T_as are low. The abundance of insects and other food also typically decreases in winter, therefore, it is likely that many passerine species could benefit greatly from the use of torpor.

The aim of our study was to examine the thermal energetics of a small passerine species, the eastern yellow robin (*Eopsaltria australis*; hereafter "eastern robin"), during winter at a cool temperate climate site in the eastern Australian Northern Tablelands (elevation range 980–1050 m). We determined whether individuals express torpor by measuring the magnitude of T_s reduction and whether this reduction is related with ambient temperature (T_a). Additionally, we discuss our results in comparison with the thermal energetics of a closely related species, the western yellow robin (*Eopsaltria griseogularis*) (hereafter "western robin"), which is the only other member of the genus *Eopsaltria* in Australia (Loynes et al., 2009). The western robin was studied in a Mediterranean climate in WA (Douglas, 2017).

MATERIALS AND METHODS

We captured four adult wild-living eastern robins (2 male, 2 female; mean body mass 19.4 g) during the southern hemispheric winter (July–August) in Imbota Nature Reserve, NSW, Australia (30.58°S, 151.72°E), a 218 ha open *Eucalyptus* and *Acacia* woodland. The population of eastern yellow robins in Imbota included on average nine pairs between 2000 and 2003, but the population likely declined (Debus, 2006) as a result of low reproduction in this region, mainly due to nest predation by Pied Currawongs (*Strepera graculina*) (Debus and Ford, 2012), and eastern robins produce too few independent young to replace adult mortality (Zanette, 2000; Debus, 2006). Additionally, eastern robins appear to be most sensitive to loss, fragmentation and degradation of habitat in rural landscapes (Watson et al., 2001, 2002; Lambeck, 2002), and an intense drought from mid-2017 to 2020 and major fire events in summer 2019 in NSW may deteriorated the quality of the site and caused further population decline. Indeed, during our fieldwork we could not find more than five individual eastern robins on the site.

Average daily minimum and maximum T_as for Imbota in midwinter (July) are 1.3 and 12.2°C, and average summer T_a reach up to 26.3°C (Bureau of Meteorology, 2021). After capture, birds were held in a cotton bag until processed. The birds were weighed to the nearest g with a digital scale (HCB-1002,
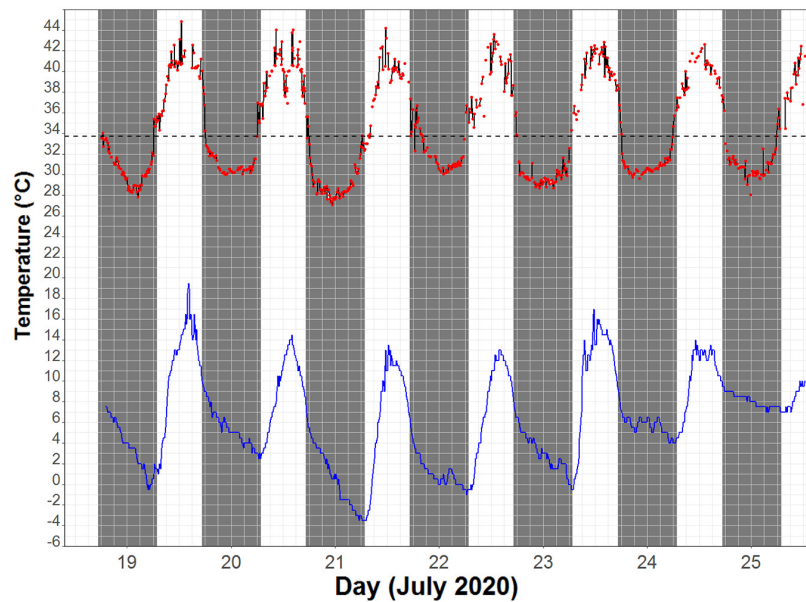
FIGURE 1 | An example of skin temperature (T_s) fluctuation of one individual (red line) and the corresponding ambient temperature (T_a) measured near the roosting site (blue line) over a 7-day period. Black dashed line depicts the torpor threshold (33.7°C), calculated as 5°C below the resting T_s.

Adam highland HCB). Each bird was banded with an individual numbered metal band and a unique combination of color bands. We then attached a temperature-sensitive radio transmitter (LB-2XT, 0.33 g, Holohil Systems Ltd., Canada) directly to the skin, between the shoulder blades using a latex-based adhesive (12% resin, Manfred Sauter GmbH). Transmitters were calibrated in a water bath to the nearest 0.1°C between 25.0 and 40.0°C in ~5.0°C increments with a precision digital thermometer (Model 15-077-8, Fisherbrand, United States) before attachment. T_s of each individual bird was calculated from the interval between two pulses following the calibration curve ($R^2 > 0.98$), and was recorded automatically in 10-min intervals with receiver/loggers fitted with an H-frame antenna (Titley Electronics or Telonics Inc., ARI, United States) placed near the roost site. Transmitters remained attached to the birds for 7–15 days, and we recorded T_s over a total of 30 days. Birds were active during the day and mostly remained within range of the logger. We excluded from the analysis daytime data for one bird, which often was beyond range during the day. We also excluded nights where signal was lost (as a result of bird moving or signal interrupted), which resulted in a total of 7 measurement nights for 3 individuals and 6 measurement nights for 1 individual and a total of 2678 T_s data points.

Air temperature (T_a) was recorded every 10 min using four temperature loggers (iButton DS1922L, 0.06°C resolution, Maxim Integrated Products, Inc., Sunnyvale, CA, United States) placed on the southern (shady) side of trees near the roosting locations. We fitted two separate linear mixed effect models with bird identity as a random effect to explain (1) minimum T_s as a function of body mass and mean T_a and (2) minimum T_s as a function of body mass and minimum T_a as explanatory variables. Second, we also ran a linear mixed effect model with average T_s

range (maximum T_s–minimum T_s), again as a function of body mass and mean and minimum T_a in two separate models. The torpor threshold was defined as a reduction by $>5°C$ below the resting T_s (Schleucher, 2004; Ruf and Geiser, 2015). The resting T_s was calculated as the average minimum T_s during daytime, between 10:00 and 15:00 of two of our studied individuals, which had sufficient daytime measurements to calculate average minimum T_s.
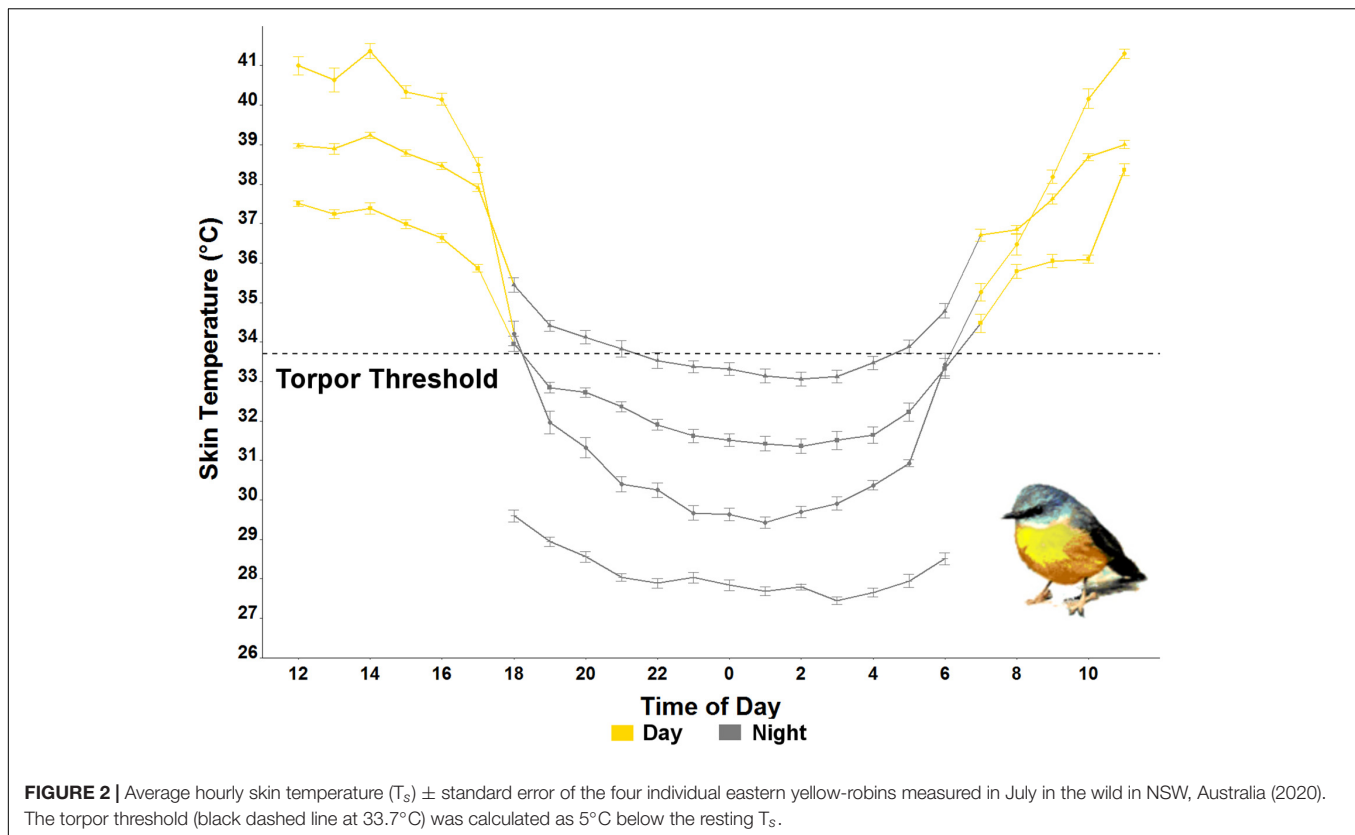
Statistical analysis was conducted using R version 3.6.0 (R Development Core Team).[1] The *R-function lme* in *R* package *nlme* was used for the mixed effect models (Pinheiro et al., 2020). Data are presented as the mean ± s.d. of individual mean daily values.

RESULTS

The average daytime T_a (between sunrise and sunset) at our study site for the eastern robin was 9.5 ± 4.3°C (range −3.5 to 19.5°C) and average night-time T_a was 4.0 ± 3.1°C (range −3.5 to 10°C). The average maximum and minimum T_a recorded were 14.3 ± 2.2°C and 1.3 ± 3.1°C, respectively. T_a dropped below 0°C on three days (**Figure 1**). Rain (21 and 7 mm) occurred only on 2 days (26 and 27 July), and coincide with T_s measurements of only one bird. We therefore did not analyze the effect of rain on torpor use in this study.

The T_s of eastern robins decreased from an average maximum T_s of 39.6 ± 3.1°C (range 44.8–34.0°C), 0.3 ± 0.3 h after sunset (19:10 h), to average minimum T_s of 30.1 ± 2.3°C (range 26.0–34.6°C). The torpor threshold was set at 33.7°C based on average

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[1] http://www.R-project.org/

FIGURE 2 | Average hourly skin temperature (T_s) ± standard error of the four individual eastern yellow-robins measured in July in the wild in NSW, Australia (2020). The torpor threshold (black dashed line at 33.7°C) was calculated as 5°C below the resting T_s.

resting T_b of 38.7°C, which is similar to a rest phase T_b of 38.9°C found previously in birds from the order Passeriformes (Prinzinger et al., 1991). Torpor bout duration (TBD) during which the T_s remained below the torpor threshold lasted for 10.3 h on average, with a maximum individual TBD of 14 h. Rewarming of T_s (the time in the morning where T_s was only followed by higher T_s for at least six consecutive measurements) started −2.6 ± 0.9 h relative to sunrise (06:45 h), when the average T_a was 2.1 ± 2.9°C. Minimum T_s was reached at 00:36 h on average (range between 21:21 and 02:41; **Figure 2**). Average individual daily fluctuations of T_s were 9.1 ± 3.9°C (range: 3.4–17.1°C), with maximum daily T_s range of 17.1°C recorded on 20 July (11:21 h), when the T_s of one individual dropped to 27.1°C (at a T_a of 0.5°C), the absolute minimum recorded (**Figure 1**).

The average minimum T_s, and average daily range of T_s of the eastern robin were significantly affected by average T_a ($T_s = 28.01 + 0.34T_a$, $df = 22$, $t = 3.18$, $P < 0.01$; $T_{srange} = 2.37 - 0.05T_a$, $df = 19$, $t = -2.25$, $p < 0.05$, respectively), and by minimum T_a ($T_s = 29.82 + 0.18T_a$, $df = 22$, $t = 2.21$, $P < 0.05$; $T_{s\ range} = 2.13 - 0.03T_a$, $df = 19$, $t = -2.30$, $p < 0.05$, respectively), but were independent of body mass at capture ($p > 0.05$).

DISCUSSION

We provide new evidence that the eastern robin, a small ∼20 g Australian passerine, uses nocturnal torpor and reduces its night-time T_s during winter to as low as 27.1°C, with TBD lasting over

10 h on average. At the time rewarming began, T_as were still low, on some days below 0°C, and rewarming commenced almost 3 h before sunrise (**Figure 1**), suggesting endogenously controlled rewarming to prepare for the active phase of morning foraging (Hiebert, 1992).

Although our measurements are based on only four individuals and T_s was used to quantify their thermal biology, we contend that our data are meaningful. All individuals showed a similar, highly predictable daily T_s change and while there is some gradient between core T_b and T_s (Lovegrove and Smith, 2003), T_s is very close to core T_b in small birds, variation being less than 2°C in the 50 g common poorwill (Brigham, 1992), and not exceeding 4°C even in an 80 g owl (Smit and Mckechnie, 2010). In comparison to a rest phase T_b of 38.9°C in birds from the order Passeriformes (Prinzinger et al., 1991), T_s reduction in our study is on average 8.7°C, with maximum reduction of 12.9°C. Moreover, if T_a was influencing the measurement T_s significantly, we would expect to see T_s fluctuate closely with T_a. Instead, T_s started to increase when T_a was still low (about 2°C on average) and even falling (**Figure 1**). Therefore, even with a small error from the T_s measurements, the data clearly show that the birds used nocturnal torpor.

The magnitude of nocturnal T_s drop during torpor increased with decreasing mean and minimum T_a. This relationship was previously found in other passerine species (Reinertsen and Haftorn, 1983; Nord et al., 2009, 2011; Romano et al., 2019) and supports the assumption that the controlled reduction of T_s aims to conserving energy during energetically expensive periods,
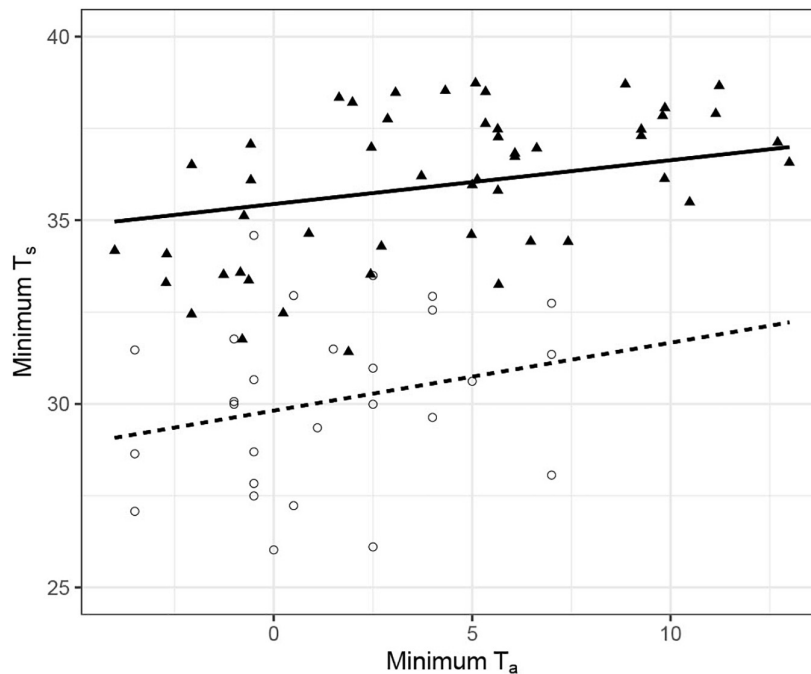
FIGURE 3 | The relationship between minimum skin temperature (T_s°C) and ambient temperature (T_a°C) in the eastern ($N = 4$; open circles, dashed line) and western ($N = 7$; filled triangles, solid line) yellow robin. Lines were fitted with a linear mixed effect model with minimum T_s of robins from east and west population separately, in relation to minimum T_a and bird identity as a random effect. Data for the western yellow robin was extracted from Douglas (2017). Like eastern robins (details of statistics in the text), the minimum T_s of the wester robins were significantly affected by minimum T_a ($T_s = 35.44 + 0.11T_a$, $df = 40$, $t = 2.86$, $P < 0.01$).

such as high energy expenditure required for thermoregulation. A reduction of energy expenditure by 10–20% was demonstrated in several captive avian species when exposed to T_a 0–10°C, with T_b reduction of 3–11°C [mountain chickadees *Poecile atricapillus*, and juniper titmice *Baeolophus ridgwayi* (Cooper and Gessaman, 2005); willow tit *Parus montanus* (Reinertsen and Haftorn, 1984)]. Captive noisy miners *Manorina melanocephala* reduced metabolic rate by ~40% when they were measured under T_as of 0–15°C, with a T_b drop of only 4°C (Geiser, 2019). To calculate the predicted metabolic reduction in our studied eastern robins, we followed the equation for metabolic rate $M = C'$ (T_b-T_a) (Snyder and Nestler, 1990), where M = metabolic rate and C' = thermal conductance. C was set as 0.186 following Douglas (2017) for western robin, a closely related species of similar size as the eastern robin, because our birds were in steady-state torpor and thermal conductance under such conditions is strongly related to body mass (Schleucher and Withers, 2001; Geiser, 2004) and is often steady below TNZ over a wide range of T_a [but may deviate under extreme conditions; Fristoe et al. (2015)]. Based on these calculations, we estimated that the metabolic rate of a 20 g eastern robin during torpor was about 4.9 ml O_2 g^{-1} h^{-1} at T_a = 0.5°C compared to predicted metabolic rate of over 7 ml O_2 g^{-1} h^{-1} at the same T_a if the bird remained euthermic. Our calculated MR of torpid birds is still above BMR of eastern robin (3.28 ml O_2 g^{-1} h^{-1}; Bech et al., 2016), but this is often the case during nocturnal torpor in small passerines (e.g., Maddocks and Geiser, 2000). Importantly, the calculation predicts that the eastern robin reduced MR during torpor by

about 24% derived from the average minimum T_s reduction, compared to its rest-phase T_s of 38.7°C. This prediction is appropriate here because eastern robins maintained a T_b-T_a differential of >25°C *via* thermoregulation during torpor, unlike many torpid mammals, which when thermoconforming, can have T_b-T_a differentials of often <1°C (Geiser, 2021). When the minimum recorded T_s of 27.1°C was used for the calculations, the MR was reduced by about 32%.

Our data suggest torpor use by eastern robins as an energy saving strategy. Although our study only report data from four individuals, it clearly demonstrates that eastern robins are capable of such energy savings through thermal flexibility. However, we do not argue that our results apply to the whole species. Over its entire range, local conditions are key elements in driving physiological strategies, and we therefore expect some variance in thermal energetics among geographically separated species and/or populations. Indeed, the western robin, a closely related species to the eastern robin (mean body mass 18.5 g), and the only other member of the genus *Eopsaltria* in Australia (Loynes et al., 2009), remained euthermic in Dryandra woodland National Park (mean T_s 35°C), with a Mediterranean climate, lower elevation site (228 m) in WA during winter (Douglas, 2017). The minimum T_s recorded of the western robins were about 5°C higher on average than that of the eastern robins. The variation in the thermal energetics between the western and eastern robins cannot be explained by the acute exposure to different T_a because night-time T_a in Dryandra dropped similarly to our study site, to a minimum T_a of −3.95°C (**Figure 3**). The

two robin species are also very similar in external appearance and size, excluding body mass as a potential explanation for the observed differences in thermal biology. The climate in Dryandra is mild relative to Imbota (i.e., winter T_a rarely drop below 0°C; Bureau of Meteorology, 2021). Therefore, a potential explanation for these differences may be that long-term thermal adaptation to the conditions in the occupied habitat may drive geographical variation in physiological traits, likely to minimize the potential costs accompanying the use of torpor. Similar differences have been observed between captive bred and wild-caught feathertail gliders (Geiser and Ferguson, 2001) and between captive woodchucks originate from different populations (Fenn et al., 2009).

Although the western robins did not express torpor like the eastern robins in our study, we do not argue that western robins, or any other passerine species which were studied in the wild and did not express torpor, are not capable of some form of heterothermy to conserve energy. Scarlet-backed flowerpeckers *Dicaeum cruentatum*, for example, which were studied in captivity for 3 years, appear to express torpor only in years with poor food quality (Bushuev et al., 2021). Other species have been considered homeothermic for decades until they were studied at the relevant conditions that trigger the use of torpor [e.g., mouse lemurs *Microcebus murinus* and *M. myoxinus*; (Ortmann et al., 1997)] and there are many other examples. Therefore, western robins, although they may not use torpor routinely as a means to balance their daily energy budget, still may express torpor under challenging conditions, such as drought or extreme cold, to increase the probability of survival.

Our study provides evidence for torpor expression in a small ∼20 g passerine, and suggests plasticity in the expression of torpor, in response to local environment. The resulting flexibility in energy requirements allows animals to optimize energy conservation to increase fitness and has the advantage over strict homeotherms during the current increasing frequency of extreme and unpredictable weather events, driven by changing climate. Indeed, despite range reduction and extreme climatic events, eastern yellow robins manage to survive in a marginal reserve and perhaps torpor expression permits them to overcome these energetically challenging periods and maintain fitness. The question that remains to be answered is whether individuals that previously did not encounter extreme climatic events, or local climatic changes, are able to apply thermal strategies to adjust to new environmental conditions. Resolving these questions is important in light of climatic changes that are expected to change local conditions for populations, but also for translocation conservation programs (Cooper et al., 2018), which need to consider the physiological limits of introduced species.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author.

ETHICS STATEMENT

The animal study was reviewed and approved by the University of New England Animal Ethics Committee (Authority No. AEC20-009).

AUTHOR CONTRIBUTIONS

YA-R and FG formulated the idea and designed the study. YA-R, CB, and JM performed the fieldwork. YA-R performed the data analysis with advice from JM. YA-R wrote the manuscript with advice from all other authors. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2021.759726/full#supplementary-material

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