

Heterothermy in an Australian passerine, the Dusky Woodswallow (*Artamus cyanopterus*)

Tracy A. Maddocks · Fritz Geiser

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Abstract Information regarding passerine heterothermy and torpor is scant, although many species are small and must cope with a fluctuating food supply and presumably would benefit from energy savings afforded by torpor. We studied whether insectivorous Dusky Woodswallows (*Artamus cyanopterus*; ~35 g) enter spontaneous torpor (food ad libitum) when held outdoors as a pair in autumn/winter. Woodswallows displayed pronounced and regular daily fluctuations in body temperature (T_b) over the entire study period. The mean T_b ranged from ~39°C to 40°C (photophase, day time) and ~33°C to 36°C (scotophase, night time). However, on 88% of bird nights, nocturnal T_b minima fell to < 35°C. The lowest T_b observed in air was 29.2°C. However, when a bird fell into water its T_b dropped further to ~22°C; this T_b was regulated for several hours and the bird survived. Our observations suggest that heterothermy is a normal part of the daily thermal regime for woodswallows to minimise energy expenditure. Spontaneous nocturnal torpor in captive woodswallows suggests that torpor in the wild may be more pronounced than recorded here because free-living birds are likely challenged by both low food availability and adverse weather.

Keywords Air · Body temperature · Energy conservation · Shallow torpor · Water

Introduction

The Passeriformes comprise more than half of all extant birds including many small insectivorous species. Passerines like all other birds are endothermic and can regulate a more or less constant high T_b over a wide range of ambient temperatures (T_a) via a high endogenous heat production (Schmidt-Nielsen 1997). Obviously, a high metabolic rate (MR) is energetically expensive and requires a reliable supply of energy in the form of food. Prolonged periods of low T_a can be challenging, as body heat is constantly lost to the environment due to a large $T_b - T_a$ differential. This can be especially problematic for small species because their high relative surface area facilitates heat loss.

Heat loss resulting from exposure to low T_a may cause energetic stress, and the situation is often made worse by reduced food availability. Small-bodied aerial insectivorous birds are likely most vulnerable to the combined impacts of food shortage and cold weather because insect activity declines during cold weather (Racey and Swift 1985). To overcome energetic bottlenecks caused by cold weather and reduced food availability, many small endotherms abandon regulation of a constant high T_b and enter a state of torpor, which, unlike unregulated hypothermia, is characterised by regulated low T_b and MR (Wang 1989; Geiser and Ruf 1995). The reduction of T_b and MR during torpor reduces both thermoregulatory and maintenance energy expenditures and consequently conserves energy during times of actual and potential energetic stress (Geiser 2004).

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T. A. Maddocks · F. Geiser (✉)
Centre for Behavioural and Physiological Ecology,
Zoology, University of New England,
Armidale 2351 NSW, Australia
e-mail: fgeiser@une.edu.au

Present Address:

T. A. Maddocks
Biological Sciences, University of Wollongong,
Wollongong 2522 NSW, Australia

Daily torpor and hibernation are widely employed by small mammals (Wang 1989; Geiser and Ruf 1995; Geiser 2004). In comparison, information regarding torpor by birds is scant. However, it appears that some small insectivorous, nectarivorous and frugivorous birds can use torpor to overcome food shortages and/or inclement weather (Bartholomew et al. 1957; Dawson and Hudson 1970; Prinzing and Siedle 1988; Hiebert 1992; McKechnie and Lovegrove 2002; Schleucher 2004). In many, but not all, of these birds, torpor only occurs after substantial starvation and mass loss, suggesting that torpor is predominantly an emergency strategy rather than a means to routinely balance the daily energy budget. From a taxonomic point of view, avian torpor is known predominantly from the orders Trochiliformes (hummingbirds) and Caprimulgiformes (nightjars) (Dawson and Hudson 1970; Prinzing and Siedle 1988; Brigham 1992; Hiebert 1992; French 1993; Brigham et al. 2000; Körtner et al. 2000; McKechnie and Lovegrove 2002; Schleucher 2004). Surprisingly, knowledge about use of torpor in the Passeriformes is rare considering the diversity of the order (~5,700 species) and its many small insectivorous species (McKechnie and Lovegrove 2002).

As in other parts of the world, passerines form a large part of the Australian avifauna. Recently, it has been proposed that passerines are of Gondwanan origin and, since they arrived in Australia >35 Million years ago (Ericson et al. 2002), should be well adapted to the low primary productivity, aridity and unpredictability of the continent. The insectivorous woodswallows (Artamidae) are an endemic Australian passerine family of diurnal, gregarious and active aerial hunters (Simpson and Day 1993). Although woodswallows exhibit some nomadic or migratory behaviour following migratory insects, their main diet of flying insects makes them especially vulnerable to food shortages and they would presumably profit from entering torpor to help alleviate energetic stress. Whereas anecdotal evidence from field observations suggests that at least some species use torpor for energy conservation (Serventy and Raymond 1973; Geiser et al. 2006), quantitative records of torpor in Australian passerines are entirely lacking.

The purpose of our study was to assess whether the Dusky Woodswallow (*Artamus cyanopterus*), an Australian passerine, displays torpor. We were especially interested in whether woodswallows use torpor on a regular basis when they have free access to food (spontaneous torpor), and aimed to quantify torpor patterns. We predicted that woodswallows are likely to use torpor since they are small and have to compensate via endogenous heat production for a high rate of heat loss. Moreover, they primarily eat aerial insects whose abundance fluctuates both daily and seasonally and whose capture is energetically expensive.

Methods

Two Dusky Woodswallow fledglings (~16 days old, weighing 30.0 and 30.5 g) were captured in January 1998 (Austral summer) about 10 km south-east of Armidale, NSW (30°30'S, 151°40'E). They were weighed to the nearest 0.1 g on the day of capture, and monthly thereafter. After the age of ~23 days, body mass remained stable between 33 and 39 g throughout the experimental period. For the first 2 weeks after capture, they were hand fed at regular intervals on a diet consisting of *Tenebrio* larva and pupae, grasshoppers, and high protein baby food (Farex). After 2 weeks, they were gradually weaned off hand-feeding, and taught to feed themselves. Thereafter, fresh insects (grasshoppers, beetles, moths) were supplied in excess daily. The pair was housed in an outdoor aviary and were exposed to natural photoperiod and temperature fluctuations.

T_b was measured using implanted FM temperature-sensitive transmitters (Sirtrack, NZ). Before implantation, transmitters were coated (Paraffin/Elvax, Mini-Mittter, OR) and calibrated in a water bath ($\pm 0.1^\circ\text{C}$). Transmitters could not be re-calibrated at the end of the study because the batteries were flat. However, we have re-calibrated transmitters of the same model previously and the drift over 2–3 months was usually within 0.5°C and always $< 1.0^\circ\text{C}$. Moreover, the normothermic photophase T_b measured here over time did not differ among months suggesting that temperature drift was negligible. Transmitter pulse rate was regressed against calibration temperature and consequently used to calculate T_b . Transmitters weighed 3.1 g after waxing and were implanted intraperitoneally under Isoflurane/oxygen anaesthesia. Transmitter signals were received using a VHF/UHF scanning receiver (Yaesu, FRG-900) and interfaced with a computer. T_b was recorded every 6 min over a 2.5-month period from April to June (autumn/early winter). T_a was recorded to the nearest 0.2°C every 12 min using a data logger (OTLM Tinytalk II, Hastings) in the aviary. Each day, the average and minimum T_b and T_a during the photophase and scotophase were calculated. Torpor was defined as a reduction of T_b to $< 35^\circ\text{C}$ because this represents a drop of $>5^\circ\text{C}$ in comparison to resting and active daytime T_b of $39\text{--}42^\circ\text{C}$ (Geiser et al. 1996; Schleucher and Prinzing 2006). Linear regressions were fitted using the least squares method and were compared using ANCOVA. Numeric values are presented as mean \pm SD and mean was compared using one-way ANOVA.

Results

Dusky Woodswallows displayed distinct daily fluctuations of T_b over the 2.5-month study period (Fig. 1a–c). T_b was

typically highest ($\sim 39\text{--}42^\circ\text{C}$) during the photophase and was associated with activity. At dusk, T_b decreased by $\sim 0.05^\circ\text{C}/\text{min}$ over a period of ~ 2 h until reaching $\sim 34^\circ\text{C}$ (Fig. 1a–c). The amplitude of the T_b fluctuation was affected by T_a and season. In April, T_b ranged from $\sim 33^\circ\text{C}$ to 41°C over a T_a range of $6\text{--}22^\circ\text{C}$ (Fig. 1a). In May, T_b fluctuated from 29°C to 41°C over a T_a range of $3\text{--}20^\circ\text{C}$ (Fig. 1b). In June, T_b fluctuated from 29°C to 41°C over a T_a range of $4\text{--}18^\circ\text{C}$ (Fig. 1c). Mean normothermic T_b during the photophase was $40.4 \pm 0.1^\circ\text{C}$ (April), $39.0 \pm 0.3^\circ\text{C}$ (May), and $38.6 \pm 0.6^\circ\text{C}$ (June); values did not differ among the 3 months (ANOVA: $F_{2,8}$, $P > 0.05$) and the photophase T_b was not correlated with T_a in all months. In contrast, mean scotophase T_b differed among months and T_b was $36.4 \pm 0.2^\circ\text{C}$ (April), $34.7 \pm 2.5^\circ\text{C}$ (May), and $33.0 \pm 0.5^\circ\text{C}$ (June) (ANOVA: $F_{2,55}$, $P < 0.001$).

Spontaneous shallow torpor ($T_b < 35^\circ\text{C}$) was observed on 88% (42/48 nights, woodswallow 1; 41/46 nights, woodswallow 2) of bird nights, and torpor typically lasted throughout most of the scotophase (Fig. 1a–c). Just prior to dawn (~ 0500 hours), T_b began a gradual increase until it reached $\sim 31\text{--}34^\circ\text{C}$, and then increased to high daytime levels (Fig. 1a–c). The minimum individual T_b recorded were 29.2°C (woodswallow 1; 22 May) and 29.4°C (woodswallow 2; 20 May).

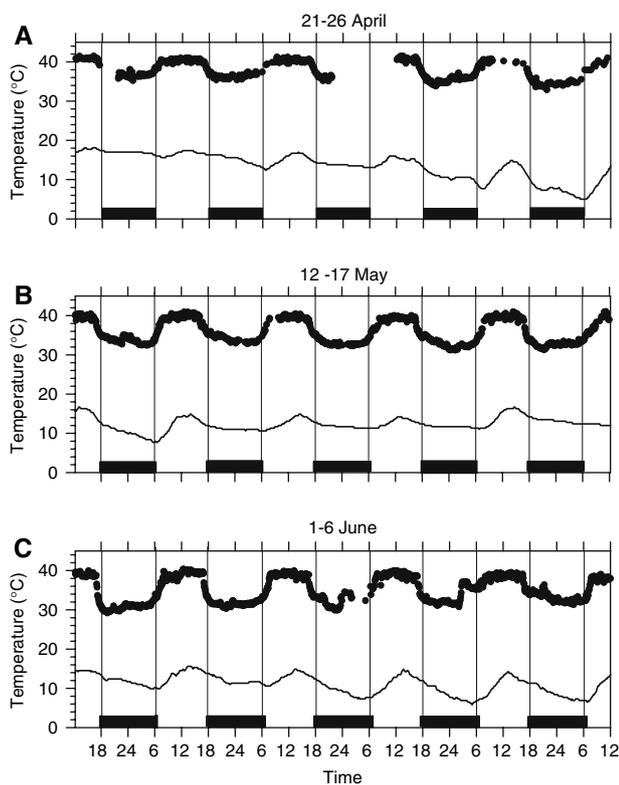


Fig. 1 Measurements of T_b of Dusky Woodswallow (*Artamus cyanopterus*) no.1 over 5 days. T_b (circles) and T_a (solid line) during **a** April, **b** May and **c** June

High T_b ($> 35^\circ\text{C}$) occurred predictably during the photophase and low T_b ($< 35^\circ\text{C}$) during the scotophase throughout most of the 2.5-month measurement period (Fig. 2). As pointed out above, scotophase T_b were lower at times when night T_a were low (e.g. days 22 or 40) in comparison to days when night T_a were high (e.g. days 6 or 12). However, only in May was a significant correlation between T_a and the scotophase T_b observed (woodswallow 1: $T_b = 31.2 + 0.16 T_a$, $r^2 = 0.18$; woodswallow 2: $T_b = 31.1 + 0.19 T_a$, $r^2 = 0.22$).

Nevertheless, scotophase T_b was also affected by season (Fig. 3). In all 3 months, T_b of the two woodswallows showed a bi-modal distribution, with maxima occurring in the photophase and minima in the scotophase, and only a few T_b readings in between. In April, the maximum daily fall of T_b was $\sim 8^\circ\text{C}$ and, in May and June, it was $\sim 11^\circ\text{C}$ over a range of T_a from 2°C to 18°C . In April, the minimum T_b measured were $> 33^\circ\text{C}$, whereas, in both May and June within the same T_a range, the minimum T_b were $< 30^\circ\text{C}$.

The $T_b - T_a$ differential further emphasises a seasonal change of thermoregulation (Fig. 3d–f). During both normothermia and torpor the $T_b - T_a$ differential increased with decreasing T_a . Although the amplitude of the differential was somewhat dependent on T_a , it also was affected by month of measurement. In April, the maximum $T_b - T_a$ amplitude observed between T_a 12 and 18°C was $\sim 7^\circ\text{C}$ (Fig. 3d), whereas in May and June (Fig. 3e,f), the maximum $T_b - T_a$ amplitude observed over the same T_a range was $\sim 10^\circ\text{C}$.

On the morning of 4 June (day 46), woodswallow 2 was discovered in the aviary's water bath. The water was shallow so the bird was able to keep its head above the surface, although its body was submerged. The bird was immediately removed, dried and rewarmed in the laboratory, returned to the aviary ~ 4 h later and apparently suffered no ill effects. Analysis of the T_b data revealed that at 2348 hours, T_b suddenly declined from $\sim 32^\circ\text{C}$ to $\sim 22^\circ\text{C}$ over a period of only 12 min (Fig. 4). We do not know what caused the bird to end up in the water bath, but it is possible that disturbance by a predator, such as a cat or an owl, may have been responsible. T_b fluctuated initially from 21.1°C to 24.2°C over a period of ~ 2 h, then remained relatively steady at $22.7 \pm 0.3^\circ\text{C}$ for ~ 4.5 h. At dawn (0644 hours) a further decline in T_b to $\sim 21.5^\circ\text{C}$ occurred where it remained for ~ 1.25 h before steadily increasing to 23.7°C at 1000 hours when the bird was removed. The T_b of the bird in the water bath was substantially lower than any of the T_b measured during the rest of the study. However, it appears the bird did not become fully hypothermic because it was able to regulate $T_b > 10^\circ\text{C}$ above T_a and defend a more or less constant T_b over several hours.

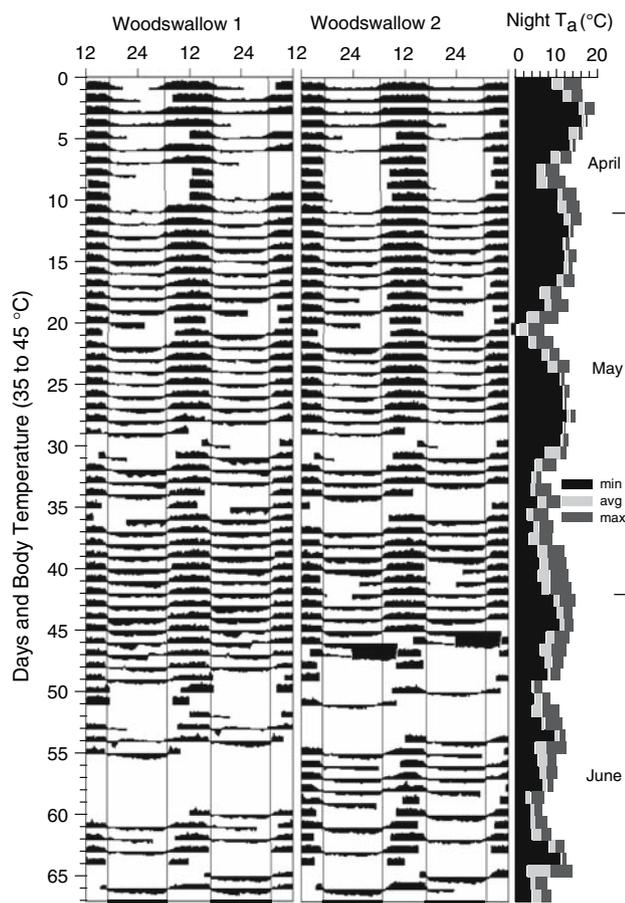


Fig. 2 Double plot of T_b (°C) representing daily fluctuations of T_b for two woodswallows from April to June. Each horizontal line refers to 35°C; positive values indicate T_b above 35°C and negative values indicate T_b below 35°C; the difference between two lines or days is 10°C (i.e. 35–45°C). The double plot shows 2 days per horizontal line starting at midday; day 2 on line one is repeated as day 1 on the following line. The horizontal bar graph on the right shows the minimum (right edge of black bar), average (right edge of light grey bar) and maximum (right edge of dark grey bar) T_a during the scotophase of day 1. Number of days since the beginning of the measurements are shown on the left, months are shown on the right of the graph. Horizontal dark bars at the bottom of the graph indicate the scotophase. Gaps indicate missing data

Discussion

Our study is the first to document regular spontaneous shallow torpor in a captive Australian passerine. Dusky Woodswallows frequently reduced T_b by ~10°C between day and night and the pattern of nocturnal T_b reduction was affected by both season and T_a . Although our results are based on only two individuals they represent long-term continuous measurements and we contend they are representative. The observation of frequent spontaneous torpor in a passerine, without the need of food restriction for torpor induction, suggests that more species than currently accepted are heterothermic.

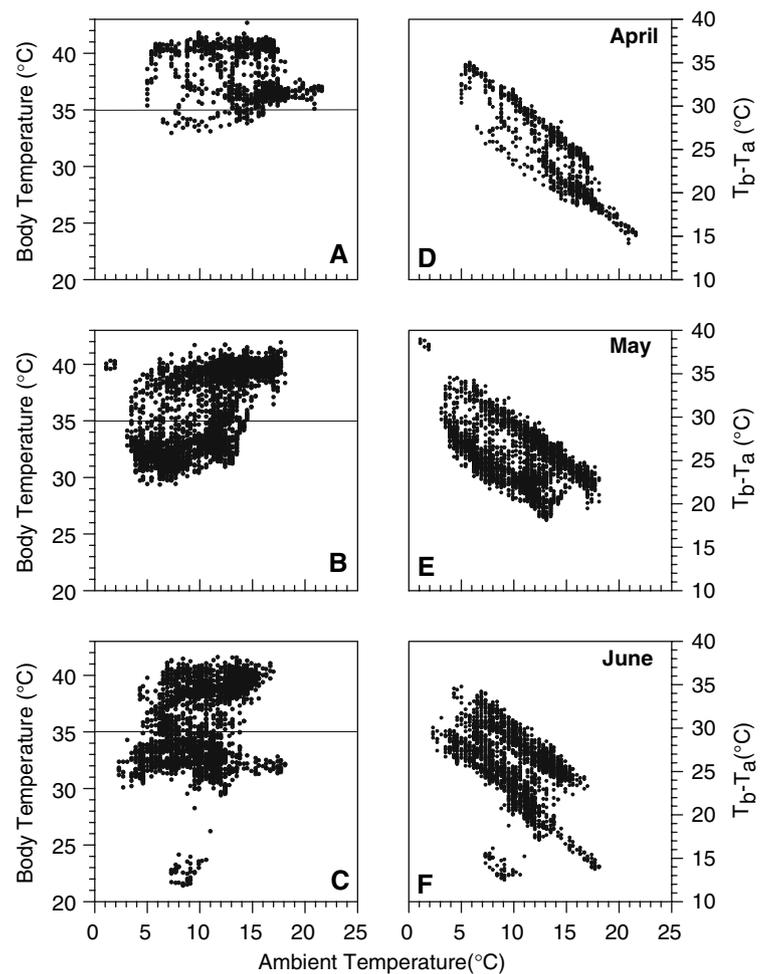
The pattern of torpor by Dusky Woodswallows that we report here is similar to that observed in other diurnal birds such as hummingbirds or martins (Bartholomew et al. 1957; Dawson and Hudson 1970; Prinzing and Siedle 1988; Hiebert 1992; Bech et al. 1997; McKechnie and Lovegrove 2002; Schleucher 2004). Nevertheless, long-term seasonal data on diurnal birds as provided by our study are scant. While other detailed seasonal data of torpor in Australian free-ranging birds have recently become available, these are restricted to the nocturnal Caprimulgiformes (Brigham et al. 2000; Körtner et al. 2000), which obviously differ with respect to timing of torpor. Furthermore, caprimulgiforms also often display two bouts of torpor per day rather than a single nocturnal torpor bout as observed here in the diurnal woodswallows.

It is interesting that the occurrence of torpor in Dusky Woodswallows was highly predictable and did not require food restriction as in many other birds. It is well established that food restriction increases both the occurrence, depth and length of torpor or other forms of regulated heterothermy in both birds and mammals (Hohtola et al. 1991; Geiser et al. 1996; Séguéy and Perret 2005). Moreover, because torpor in captive animals is often less frequent, shallower and shorter than in free-ranging animals (Geiser et al. 2000), it is possible that energetically challenged, free-ranging woodswallows would employ more pronounced torpor than reported here. However, it is also possible that in the wild where woodswallows huddle extensively, pronounced reductions in T_b are not required for energy conservation (Lovegrove and Smith 2003), although during huddling, unlike during torpor, MR can only be reduced to normothermic maintenance levels.

The ability to maintain a steady low T_b under extreme conditions as well as a pronounced thermal tolerance was demonstrated when one woodswallow was submerged in water for several hours. Although the T_b (~22°C) was well below usual nocturnal values in air, it remained relatively stable. The conductivity of water is about 25× that of air (Schmidt-Nielsen 1997) and water saturation eliminates the isolative air layer that is usually trapped between the feathers and the skin of a bird. Thus, maintenance of a stable T_b in cold water (at ~8–10°C) would have required a substantial increase in metabolic rate and shows that the bird regulated its T_b at ~22°C and was not fully hypothermic. Although we do not know whether the bird would have been able to rewarm without external heat, the low T_b suggests that woodswallows may be able to survive extended periods of extremely cold weather and may lower T_b further than regularly observed here when thermally challenged.

Our observation of the pronounced drop of T_b of a woodswallow in the water bath raises the question of whether historical claims by Aristotle that swallows and other

Fig. 3 Body temperatures T_b (a–c) and $T_b - T_a$ differentials (d–f) as a function of T_a (°C) for the two woodswallows during both the photo- and scotophase during April, May and June. The group of very low T_b values in June are the result of immersion in water. The horizontal line at 35°C indicates the threshold T_b for torpor



birds may enter torpor during the cold season, sometimes under ground or in mud, which are now generally discredited as superstitious beliefs, may require re-examination. Torpor has now been observed in several species of passerines including swallows and martins (McKechnie and Lovegrove 2002), as well as in woodswallows, although the response we describe here after immersion in water is the first such record to our knowledge. Moreover, descriptions of torpor in White-backed Swallows *Cheramoeca leucosternum* in a sandbank burrow suggest that it may be of prolonged, rather than of a daily occurrence (Serventy and Raymond 1973; Geiser et al. 2006), implying that deep and prolonged torpor in birds may not be restricted to Poorwills *Phalaenoptilus nuttallii*, contrary to what is currently widely accepted.

Woodswallows are social, often gathering in large flocks. They are known to huddle in groups, a behaviour known to reduce heat loss (McKechnie and Lovegrove 2001). Our birds regularly huddled, and free-ranging woodswallows may huddle in large groups (Simpson and Day 1993), which would reduce thermal conduction and heat loss more effectively (McKechnie and Lovegrove 2001).

The energetic advantage of huddling is substantial and results in a reduction of energy expenditure by up to 50–70% of that of a single birds (McKechnie and Lovegrove 2001). Thus nocturnal torpor, which should result in a reduction in nightly expenditure by ~50% as deduced from the ~10°C fall of T_b , together with huddling, can substantially reduce daily energy and food requirements. Our observations of frequent torpor in woodswallows in the absence of food restriction suggests that, in the wild, torpor will be a common phenomenon for this and perhaps many other birds.

Zusammenfassung

Heterothermie bei einem australischen Sperlingsvogel, dem Rußschwalbenstar (*Artamus cyanopterus*).

Informationen über Heterothermie und Torpor bei Sperlingsvögeln sind selten, obwohl die Individuen vieler Spezies klein sind und mit unsteter Nahrungsverfügbarkeit zurechtkommen müssen und vermutlich profitieren könnten von Energieeinsparungen, wie sie durch Torpor erreicht werden können. Wir untersuchten, ob insektivore

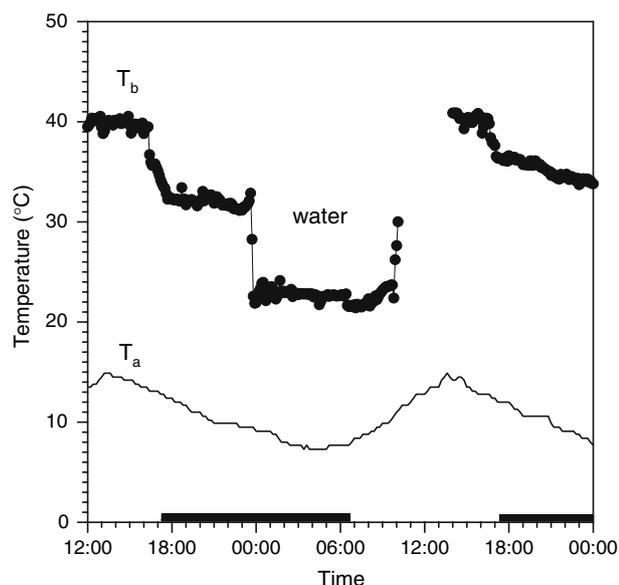


Fig. 4 Body temperature (T_b) of woodswallow 2 during the day it fell into the water bath on 3 and 4 June and ambient (air) temperature (T_a). Note the usual decline of T_b from $\sim 40^\circ\text{C}$ to $\sim 32^\circ\text{C}$ at the beginning of the scotophase. This was followed by a precipitous fall of T_b to $\sim 22^\circ\text{C}$ just before midnight remaining at that level until the bird was removed from the water bath at about 1000 hours. T_b rose when the bird was passively rewarmed and data are missing for ~ 4 h when bird was out of receiver range. The horizontal dark bar indicates night

Rußschwalbenstare (~ 35 g) bei unbegrenzter Nahrungsverfügbarkeit in einen spontanen Torpor fallen, wenn sie als Paare im Herbst und Winter im Freien gehalten werden. Die Rußschwalbenstare zeigten deutliche und regelmäßige tägliche Fluktuationen in ihrer Körpertemperatur über die gesamte Untersuchungszeit. Die mittlere Körpertemperatur betrug ~ 39 bis 40°C tagsüber und ~ 33 bis 36°C nachts. Allerdings fielen in 88% der Vogelnächte die Minima der nächtlichen Körpertemperatur auf unter 35°C . Die geringste in Luft gemessene Körpertemperatur lag bei 29.2°C . Fiel jedoch ein Vogel ins Wasser, erniedrigte sich seine Körpertemperatur weiter auf ungefähr 22°C . Diese Temperatur wurde für mehrere Stunden reguliert, und der Vogel überlebte. Unsere Beobachtungen legen nahe, dass Heterothermie ein normaler Bestandteil der täglichen Thermoregulation des Rußschwalbenstars ist, um das Energieaufkommen zu minimieren. Der spontane nächtliche Torpor bei gekäfigten Rußschwalbenstaren lässt vermuten, dass der Torpor bei freilebenden Vögeln noch deutlicher zutage tritt, weil diese vermutlich sowohl von geringer Nahrungsverfügbarkeit als auch von widrigen Witterungsbedingungen betroffen sind.

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