Subtropical mouse-tailed bats use geothermally heated caves for winter hibernation

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We report that two species of mouse-tailed bats (Rhinopoma microphyllum and R. cystops) hibernate for five months during winter in geothermally heated caves with stable high temperature (20°C). While hibernating, these bats do not feed or drink, even on warm nights when other bat species are active. We used thermo-sensitive transmitters to measure the bats’ skin temperature in the natural hibernacula and open flow respirometry to measure torpid metabolic rate at different ambient temperatures (T_a,16–35°C) and evaporative water loss (EWL) in the laboratory. Bats average skin temperature at the natural hibernacula was 21.7±0.8°C, and no arousals were recorded. Both species reached the lowest metabolic rates around natural hibernacula temperatures (20°C, average of 0.14±0.01 and 0.16±0.04 ml O_2 g^-1 h^-1 for R. microphyllum and R. cystops, respectively) and aroused from torpor when T_a fell below 16°C. During torpor the bats performed long apnoeas (14±1.6 and 16±1.5 min, respectively) and had a very low EWL. We hypothesize that the particular diet of these bats is an adaptation to hibernation at high temperatures and that caves featuring high temperature and humidity during winter enable these species to survive this season on the northern edge of their world distribution.

1. Introduction

Torpor and hibernation are common physiological adaptations used by mammals to conserve energy. These behaviours have been studied mostly in the context of adaptation to negative energy balance and extended periods of water and food shortage, and have been described in species from desert and tropical habitats. In recent years, different ecological interactions were found to affect the use of torpor and hibernation [1–5]. The Rhinopomatidae (mouse-tailed bats) are a monotypic family of subtropical insectivorous bats inhabiting semi-arid and warm regions in Asia and Africa. Two species, the greater mouse-tailed bat (Rhinopoma microphyllum) and the lesser mouse-tailed bat (Rhinopoma cystops) are medium-sized insectivorous bats with body masses of approximately 25 g and 12 g, respectively, and are both well adapted to arid environments [6,7]. Rhinopoma microphyllum and R. cystops inhabit the dry and warm regions of Israel, which is the northern edge of their world distribution [8]. These species have limited tolerance to low ambient temperatures and it has been suggested that they are unable to perform deep torpor or hibernation [6].

We have previously found that during summer, R. microphyllum exhibit complete sexual segregation, inhibiting warm and dry caves (28–32°C). We also found that lactating females remain almost normothermic during the day and perform long foraging bouts during the night, while males and non-lactating females use daily torpor during the day and perform short foraging bouts during the night [9,10]. During late summer (August) both species accumulate large amounts of body fat, sometimes reaching 50% of their body mass, a phenomenon typical for hibernators. This increase in body fat is achieved by switching diet preference during summer (mid-July) from coleopterans and heteropterans to mainly fat-rich winged carpenter ants [11]. This fat-rich food...
contains a high fraction of saturated and mono-unsaturated fatty acids (SFA and MUFA, respectively), but almost no polyunsaturated fatty acids (PUFA) [12] which are considered important for hibernation success at low temperatures [13–17]. As a result, mouse-tailed bat pre-winter body fat is lacking in PUFAs and is extremely saturated [11,12], which is a-typical for hibernators.

During late October, both mouse-tailed bat species move to caves in which they remain throughout the winter [12]. Based on our observations of no foraging activity during the winter months, and the accumulation of large amounts of saturated body fat before winter [11,12], we hypothesized that mouse-tailed bats hibernate during winter at high ambient temperatures. To test these hypotheses, we monitored skin and hibernaculum temperature of free-ranging mouse-tailed bats during winter, and examined the effect of ambient temperature on energy expenditure and water loss under controlled conditions in these two species.

2. Material and methods

(a) Winter hibernacula

A winter colony of both R. microphyllum and R. cystops was discovered during a field survey on 2003 on a cliff by the Sea of Galilee (32° 46′ N 35° 32′ E, 100 m below sea level). The cave is a wet karstic cave in Eocene limestone formed by a phreatic and hypogenic dissolving process in a confined aquifer. The dissolving has created a maze network of mainly horizontal branched tunnels with some halls and typical domes in which the bats hang. The temperature in this cave is relatively high and constant due to geothermic activity (speleological data from the Israeli Cave Research Unit, The Hebrew University, Jerusalem). From 2003 to 2013, we visited this cave three to eight times a year, and counted the bats directly by observation or photography. We also acoustically identified and counted bats emerging from this cave during winter nights, using Pettersson D900 (Pettersson Elektronik, Sweden) and ANABAT bat detectors (Titley Scientific, Australia). During 2003 and 2004, we placed paper sheets on the cave floor beneath the roosting bats for faeces collection.

(b) Cave and skin temperature

We use thermal sensitive transmitters to record skin temperature (Tsk) in hibernating mouse-tailed bats. Skin temperature of small mammals (including bats) was validated and is considered to be a good predictor for body temperature, and is used in numerous studies to measure the use of torpor and hibernation in free-ranging small mammals including bats [18–20].

Nine adult R. cystops (five females and four males) were captured during daytime (15 January 2012) in their natural hibernacula as described previously. The bats were brought to the laboratory, marked individually with bat rings (Porzana, UK, for R. microphyllum—4.2 mm, for R. cystops—2.6 mm) and placed in a custom-made wooden cage in a temperature-controlled room at 20 °C, which resembles the ambient temperature of the bats’ natural hibernacula. An animal was considered in torpor when its metabolic rate decreased under 0.7 ml O2 g−1 h−1 [21] and/or was performing intermittent breathing patterns. TMR of the bats was measured using an open-flow respiriometer. Bats (all fasted at least 2 days in the laboratory and probably much longer in their hibernacula) were weighed using electronic scales (Micron, China, ±0.01 g) and introduced individually into a metabolic chamber (Perspex chambers; 250 ml for R. microphyllum and 210 ml for R. cystops). O2 consumption and CO2 production were measured by gas analyser (FoxBox, Sable Systems Int., USA). Dry air passed through the metabolic chamber at a constant flow of 100 ml min−1. Data were collected at 5-s intervals using a PC and ADAMview software (Advantech, USA). After placing a bat in the chamber, the chamber was immersed in a temperature-controlled water bath at 20 °C, reflecting natural hibernacula temperature.

To detect the influence of ambient temperature on TMR the metabolic rate of each bat was measured at various temperatures on 2 consecutive days, each starting with 120 min of acclimation to 20 °C. On day 1, TMR was recorded at 19 °C, 18 °C, 17 °C and 16 °C for 120 min each. We did not reduce Tb below 16 °C as at this temperature the bats started to get stressed and as this temperature was reported as lethal to this species [6]. On the second day, TMR was recorded at 20 °C, 25 °C, 30 °C and 35 °C (33 °C is the highest temperature we recorded in the summer roosts [9]) for 120 min each. The experiment was stopped when a bat aroused from torpor, i.e. no apnoea cycles were detectable and CO2 levels in the chamber rose above 0.7%.

For data analysis alone the last 30 min of each temperature were used. VO2 ml O2 g−1 h−1 was calculated according to Withers [22]. For comparisons of TMR, we used the average value of VO2 for the last 30 min of measurement at each temperature.

During November and February 2013, 10 R. cystops were measured for TMR as described above at 20 °C. At the end of each measurement Tsk was taken from a hairless area of the dorsal side, by an infra-red thermometer GM300 (Benetech, China). We avoided invasive procedures as these are protected species in Israel.

At the end of the 2-day experiment, we prepared the bats for release back to nature: bats were hand-fed daily with a syringe for two weeks with 1 ml of squeezed darkling beetle larvae (Zophobas morio) enriched with high nutrient food for pets (Recovery, Royal Canin). The bats were fed in order to increase their weight which, we assumed, will increase their chance for survival in nature. The bats were returned to the hibernacula in late March. Two of the bats used in the experiments were recaptured in good
shape 1 year later. We assume that no harm was caused to the bats from the captivity period.

(d) Evaporative water loss
For EWL measurements an additional 10 adult bats (R. microphyllum, three males and two females; R. cystops three males and two females) were captured in February 2013 in their winter hibernacula as described before. The bats were placed in individual Perspex metabolic chambers (250 ml for both species) with constant air flow of 100 ml min$^{-1}$ of a CO$_2$ free, dry air from a cylinder. Air supply to the animals was controlled by an eight-channel gas controller and monitor (Flow bar-8, Sable Systems Int.). The air flowed to an eight-channel gas multiplexer (V5, Sable Systems Int.) that selected channels sequentially for sampling. Air samples were passed through a water vapour analyser (RH-300, Sable Systems Int.). To make sure the bats were hibernating during the measurements, we also measured O$_2$ and CO$_2$ levels in the air sample: the air coming out from the RH-300 was dried with a drierite (W. A. Hammond, USA) column and passed through an O$_2$/CO$_2$ analyser (FoxBox, Sable Systems Int.). Data regarding water vapour, O$_2$ and CO$_2$ were collected every 5 s using Expedata software (Sable Systems Int.). EWL was calculated using Lighton’s 10.11 equation [23].

3. Results
In the winters of 2003–2013, we counted 200–500 individuals of R. cystops and 50–500 of R. microphyllum in the observed winter roost. Rhinopoma microphyllum was often found in clusters while R. cystops always maintained a distance of forearm and tail from each other. During all our visits, the bats’ eyes were opened and they were able to swiftly fly (within seconds) in response to disturbance. Bats were making audible calls, which were detectable before entering the cave during both day and night. In contrast to the summer roosts, in the hibernacula no fresh faeces were observed on the cave floor or on the collection paper sheets positioned under the clusters of bats at any point of their stay there. However, much fresh urine was absorbed onto these sheets.

Six other species of insectivorous bats were identified visually and acoustically in the same cave during winter: Rhinolophus ferrumequinum, R. blasii, R. hipposideros, Miniopterus schreibersii, Taphozous perforatus and Myotis capaccini. Unlike all of these latter species, which were observed emerging from the cave to feed on winter nights and whose faeces were found under their roosting spots, R. cystops and R. microphyllum remained inside the cave on relatively warm nights (greater than or equal to 20°C), when many aerial insects were active.

During the study we found another five caves with winter colonies of Rhinopoma in Israel, four of them along the Syrian–African rift valley and all of which are warm and humid. This area is geologically active and contains many hot springs and underground warm-water cisterns.

(a) Cave and skin temperature
While ambient temperatures outside the cave fluctuated considerably during winter from 4 to 22°C (figure 1), the temperature inside the cave remained relatively constant at about 19°C in the outer parts and at about 22°C in the inner parts of the cave (figure 1). Relative humidity in the cave was approximately 100%.

$T_{sk}$ of all bats recorded was 1–3°C above average cave temperature (table 1). All bats exhibited sporadically short events of higher $T_{sk}$. These events were more common during the first days after transmitter attachment and always lasted less than 40 min (figure 2).

(b) Torpid metabolic rate
After the mouse-tailed bats were introduced into the metabolic chamber at 20°C they reduced their metabolic rate within 2 to 25 min and entered torpor. $T_{sk}$ of torpid bats at 20°C was 22.3 ± 1.7. The torpid bats performed typical cycles of apnoea followed by a short ventilation period. These cycles were temperature-dependent. Both species
showed the longest cycles around natural hibernacula temperature of 20 °C with an average of 14 ± 1.6 min for *R. cystops* and 16 ± 1.5 min for *R. microphyllum* (figure 3), and with a maximum cycle length of 28 min.

The two species differed significantly in their torpid metabolic rates (TMRs) at different temperatures (two-way repeated measure ANOVA $F = 7.9$, $p < 0.001$). *R. cystops* had significantly lower TMRs at the lowest measured temperature of 16 °C (figure 4, post hoc with Holm–Sidak method: difference of means $= 1.59$, $t = 7.1$, $p < 0.001$), and *R. microphyllum* had significantly lower TMRs at the highest measured temperature of 35 °C (figure 4, post hoc Holm–Sidak method: difference of means $= 0.345$, $t = 2$, $p = 0.04$).

Average TMR at 20 °C was 0.14 ± 0.01 and 0.16 ± 0.04 ml O$_2$ g$^{-1}$ h$^{-1}$ for *R. microphyllum* and *R. cystops*, respectively (figure 4b). In *R. microphyllum*, TMR increased significantly at 16 °C, while in *R. cystops* it increased significantly at 35 °C. Six out of eight *R. microphyllum* started arousing from torpor when the ambient temperature was lower than 17 °C, and only two remained torpid. However, TMR of these two individuals was significantly higher than TMR of *R. cystops* at the same temperature (post hoc with Holm–Sidak method: difference of means $= 0.345$, $t = 2$, $p = 0.04$).

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**Figure 2.** Skin temperature ($T_{sk}$) of four *Rhinopoma cystops* during January–February 2013 (black circles). Grey line, cave temperature (average of four sensors).

**Table 1.** Forearm length, body mass, monitoring period and skin temperature of nine hibernating *Rhinopoma cystops* during winter 2012.

<table>
<thead>
<tr>
<th>no.</th>
<th>sex</th>
<th>start</th>
<th>end</th>
<th>mass (g)</th>
<th>forearm (mm)</th>
<th>average $T_{sk}$ (°C)</th>
<th>min $T_{sk}$ (°C)</th>
<th>max $T_{sk}$ (°C)*</th>
</tr>
</thead>
<tbody>
<tr>
<td>339</td>
<td>F</td>
<td>15 Jan</td>
<td>19 Jan</td>
<td>11.20</td>
<td>55.3</td>
<td>22.02</td>
<td>20.54</td>
<td>24.96</td>
</tr>
<tr>
<td>379</td>
<td>F</td>
<td>15 Jan</td>
<td>19 Jan</td>
<td>11.60</td>
<td>55.8</td>
<td>21.2</td>
<td>20.35</td>
<td>23.5</td>
</tr>
<tr>
<td>499</td>
<td>F</td>
<td>15 Jan</td>
<td>19 Jan</td>
<td>11.90</td>
<td>57.9</td>
<td>22.57</td>
<td>19.5</td>
<td>23.73</td>
</tr>
<tr>
<td>538</td>
<td>M</td>
<td>15 Jan</td>
<td>6 Feb</td>
<td>10.90</td>
<td>57.7</td>
<td>21.21</td>
<td>19.51</td>
<td>29.09</td>
</tr>
<tr>
<td>738</td>
<td>M</td>
<td>15 Jan</td>
<td>31 Jan</td>
<td>14.90</td>
<td>59</td>
<td>23.18</td>
<td>19.78</td>
<td>25.48</td>
</tr>
<tr>
<td>877</td>
<td>F</td>
<td>15 Jan</td>
<td>6 Feb</td>
<td>10.40</td>
<td>55.2</td>
<td>21.22</td>
<td>19.49</td>
<td>23.6</td>
</tr>
<tr>
<td>918</td>
<td>F</td>
<td>15 Jan</td>
<td>6 Feb</td>
<td>11.70</td>
<td>56.9</td>
<td>21.11</td>
<td>19.09</td>
<td>27.4</td>
</tr>
<tr>
<td>938</td>
<td>M</td>
<td>15 Jan</td>
<td>15 Jan</td>
<td>15.20</td>
<td>60.8</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>957</td>
<td>M</td>
<td>15 Jan</td>
<td>6 Feb</td>
<td>13.50</td>
<td>59.5</td>
<td>21.03</td>
<td>19.41</td>
<td>25.2</td>
</tr>
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</table>
difference of means = 1.59, t = 7.1, p < 0.001). When ambient temperature was raised above 20°C, while TMR of both species increased, at these temperatures that of R. cystops was significantly higher than that of R. microphyllum, and reached normothermic values at 35°C of about 0.91 ± 0.2 ml/O2 h (figure 4).

We found significantly lower TMR in R. microphyllum at 20°C in the 2013 group (see below, EWL experiment) compared with the 2012 group at the same time of the year (0.14 ± 0.01 versus 0.087 ± 0.01 ml O2 g⁻¹ h⁻¹, t-test t = −5.19, p < 0.001). This may be related to the fact that the first group was kept in the laboratory for a few days before measurements in low humidity and constant noise from the climate chamber compressor, which might stress the bats. No significant difference between the years was found in R. cystops (t-test, p = 0.8).

Q₁₀ values for the torpid mouse-tailed bats were higher than 2 in both species (table 2).

c) Evaporative water loss
Total EWL at hibernacula temperature (20°C) was 0.29 ± 0.05 mg H₂O(h g⁻¹) for R. microphyllum and 0.38 ± 0.1 mg H₂O(h g⁻¹) for R. cystops. There was no significant difference in total EWL between the species (t-test t = −1.5, p = 0.16). We suggest that the main channel for EWL in mouse-tailed bats is cutaneous, as most of the time the bats were in apnoea, with their mouth and nostrils shut.

4. Discussion
Our results show that both R. cystops and R. microphyllum hibernate during winter. During hibernation, the bats showed intermitted breathing, with bouts of ventilation and apnoea, as reported in several other hibernating rodents, bats and marsupial species [24]. During the ventilation and apnoea, uptake and clearing of O₂ and CO₂ was rapid and greatly reduced respectively, and we assume that as reported in other species, blood oxygen and CO₂ tension change accordingly [24]. The fact that apnoea cycles length changed with temperatures suggests that breathing bouts are correlated with metabolic demands, and most probably with blood gas levels.

Even though these two species have the option to hibernate in cold caves nearby, they prefer to hibernate in a geothermally heated cave with warm and a stable ambient temperature of 19–23°C. This behaviour suggests that this Ta is of advantage for the mouse-tailed bats during their winter hibernation, which is indeed supported by our findings that lowest TMR, and hence highest energy conservation, and longest cycles of apnoea are achieved around 20°C. It is possible that the existence of these geothermally heated caves enables mouse-tailed bats to extend their distribution northwards along the Syrian–African rift valley. In contrast to the outmoded assumption that hibernation is associated with low temperatures, we present an example of a bat that is not only able to hibernate at high temperatures, but prefers to hibernate at high ambient temperature and is able to maintain low

Figure 3. An example of oxygen consumption VO₂ ml O₂ g⁻¹ h⁻¹ of Rhinopoma microphyllum (a) and Rhinopoma cystops (b) in the laboratory at different ambient temperatures (20–35°C at 5°C intervals, 120 min at each temperature). Dashed line, ambient temperature, solid line, oxygen consumption. Peaks represent ventilations between apnoeas.
Table 2. Q10 values (± s.d.) of Rhinopoma microphyllum and Rhinopoma cystops.

<table>
<thead>
<tr>
<th>temperature range</th>
<th>R. microphyllum</th>
<th>R. cystops</th>
</tr>
</thead>
<tbody>
<tr>
<td>20 – 30°C</td>
<td>2.5 ± 0.5</td>
<td>3.5 ± 1.3</td>
</tr>
<tr>
<td>25 – 35°C</td>
<td>4.0 ± 0.8</td>
<td>3.1 ± 1.2</td>
</tr>
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</table>

R. microphyllum, which may explain its wider distribution in Israel: during summer it is found at higher altitudes and in larger areas of the Mediterranean region [26]. Kulzer [6] reported that mouse-tailed bats die at ambient temperature of 15°C, and that when their Tb is below 19°C, their re-warming rate is significantly low in comparison with other bat families. Based on our previous work on summer torpor and activity Tsk [9] and on the present observations on hibernation Tsk in mouse-tailed bats, we suggest that mouse-tailed bats defend torpor body temperature of about 20°C, and start thermoregulating if Tb drops below 19°C. This finding is unusual for hibernators as for most hibernators, the minimum Tb is limited by the freezing point of body fluids (approx. 0°C), which prevents a further drop of Tb [27]. For the mouse-tailed bats, using geothermally heated caves and keeping body temperature at this relatively high level will have adaptive significance, since it will significantly reduce the energetic cost of arousals, and therefore, the total cost of hibernation.

We suggest that mouse-tailed bats started arousing and increased TMR at 16°C owing to their body fatty acid composition. We previously found that towards the end of summer, during the pre-hibernation period, mouse-tailed bats feed mainly on queens of carpenter ants [11]. These queen ants are an extremely poor source of PUFA (0.5%) and rich in SFA (approx. 44%) and MUFA (approx. 55.5%) [12]. We also found that this extremely saturated lipid profile is reflected in the mouse-tailed bats’ pre-hibernation tissue, which is, to the best of our knowledge, the most saturated ever recorded in a mammal [12] and differs from the typical PUFA-rich food preference and body composition of other hibernating mammals [17]. High levels of dietary PUFA in pre-hibernating mammals are known to positively affect torpor and hibernation, for example, by increasing depth and duration of torpor bouts [14,15,28], but the function of these fatty acids during hibernation is still unknown [29,30]. Since mouse-tailed bats fat is saturated, unlike other hibernators, it should restrict their ability to hibernate at low temperatures.

During hibernation, hibernating mammals are motionless and their eyes are closed, while mouse-tailed bats hibernate with their eyes open, instantly react to stimuli, and swiftly become active after being disturbed, even when their body temperature is still far below normothermy (approx. 37°C). This can be explained by the relatively high Tb of mouse-tailed bats during hibernation. We observed mouse-tailed bats actively flying when their body temperature was still low (approx. 23°C) and argue that they can perform many basic functions at relatively low Tb (see also [9]). Quantitative data on locomotor performance at low Tb in torpid marsupials suggest that they can run at Tb far below 20°C [31]. The ability to react fast to threat may be especially important for a small mammal hibernating at a cave entrance in a subtropical winter. Unlike winters in temperate regions, in a subtropical climate other mammals, reptiles and birds of...
prey are present and active during the winter and might be a threat to the hibernating bats. Therefore, vocal communica-
tion between individuals like we heard when entering the
hibernacula and a fast response may be crucial for survival
and adds another adaptive significance of hibernation at
high temperatures.

Why do these bats hibernate during the Israeli temperate
winter? This is especially interesting as other bat species
inhabiting the same cave remain active and forage. A possible
explanation is that for a subtropical bat at the northern edge
of its distribution, the Mediterranean winter is too cold to be
active and to survive so they hibernate in geothermally
heated warm protected caves. However, another subtropical
bat, *T. perforatus*, inhabits the same cave during winter but
remains active. This may suggest that other factors influence
the use of torpor in these species. One possibility is that in
contrast to the active bat species, the mouse-tailed bats in
northern Israel are diet-specialists. During early summer
they consume mainly coleopterans and heteropterans,
which are scarce during winter, and from July they feed
almost solely on winged ants, which are absent during the
winter months [11]. Other factors, like predation risk, were
suggested as possible contributors to the use of torpor and
hibernation [1], but these remain to be studied.

We did not record any periodic arousals during hiber-
nation in any of the mouse-tailed bats in their natural
hibernacula. We expected to find more than few such arou-
sals during the 25 days of *Tsk* recording. In other temperate
zone bats hibernating at ambient temperature around 15°C
and above, arousals appear almost every day [32–35]. One
exception is the large (60 g) subtropical insectivore bat
*Hipposideros terebensis*, hibernating at relatively warm hiber-
nacula around 20°C. In this bat, torpor bouts lasted from
1.6 to 19 days, and arousals and foraging bouts are observed
throughout winter (70% of torpor bouts were shorter than 10
days) [36]. We monitored mouse-tailed bats *Tsk* for 25 days
and did not record a single arousal in any of the eight bats
recorded. Nevertheless, we did record sporadic increases of
3–8°C in body temperature up to 25–29°C for a very short
duration (20–60 min, figure 2 and table 1). Based on these
findings, we suggest that mouse-tailed bats do not perform
arousals, or that they perform unusual, extremely long
torpor bouts for hibernation in high ambient temperatures.
Except for the energy saving, reducing arousal frequency
can reduce possible oxidative stress or other damage to the
brain and other tissues due to hypoxia during arousals
(reviewed by [37,38]).

In contrast to other hibernating bats [32,36,39] mouse-tailed
bats remain in their hibernacula all winter long and avoid forag-
ging or drinking. During our study the mouse-tailed bats were
never observed drinking water, neither during warm winter
nights above 20°C nor during the summer, suggesting that
they are very efficient at conserving water. It was previously
suggested that hibernating mammals lose water through EWL
until a specific threshold at which they must arouse to drink
[40–42]. According to this hypothesis, if mouse-tailed bats are
very efficient in reducing water loss during hibernation, this
might significantly contribute to reducing arousals during
hibernation or even to avoiding them. Indeed, mouse-tailed
bats possess a very low density of capillaries in their skin,
which reduces EWL [43]. Accordingly, we found that the total
EWL of mouse-tailed bats is exceptionally low, even under
the zero relative humidity conditions we used in the laboratory.
As cave relative humidity is close to 100%, the values of EWL in
wild hibernating mouse-tailed bats should be even lower and
close to zero. Even though most of the water loss is through
the skin, we suggest that during apnoea in which nostrils are
closed, pulmonary water loss should be greatly reduced. It
was previously suggested in other bat species that during bat
apnoea the glottis is closed and prevents water loss, but there
is contradicting evidence to this theory [41,44,45]. Mouse-
tailed bats have distinctive valves in their nostrils (figure 6).
During apnoea these valves are shut and only flutter (open
and shut rhythmically with diaphragm movement) during
the ventilation cycles between the apnoeas. This results in
greater total EWL than during apnoea (figure 6). We suggest
that in mouse-tailed bats the nostril valves function analogi-
cally with the spiraculum of the insects’ trachea [46] and

Figure 5. Body temperature and metabolic rate in hibernating mammals in the temperature range of 10–30°C (black filled circles, data from [21]). Open squares, ambient temperature and TMR measured in *Rhinopoma microphyllum* on 2012, black square, on 2013. Grey triangles, ambient temperatures and TMR measured in *Rhinopoma cystops* on 2012. (Online version in colour.)
contribute to reducing pulmonary water loss. We observed these nostril valves in another two arid zone bat species; Taphozous nudiventris and T. preforatus. In Israel, these two species occupy the same habitats as mouse-tailed bats, and we suggest this might be a common mechanism for reducing water loss in arid zone bats.

In summary, both species of mouse-tailed bats enter a very efficient hibernation, which they perform in geothermally heated, stable microclimate of warm hibernacula, maintaining their body temperature above 20°C. Unlike other hibernators, we observed no periodic arousals or periods of normothermy during hibernation, and even though it is possible that the recording period was too short to record such arousals, we suggest that their ability to function at low T_b, combined with their efficient water economy reduces the need for periodic arousals in these subtropical hibernating species. Their pre-hibernation diet in Israel, and as a result their body fatty acid composition, may contribute to their hibernation success, but at the same time we hypothesize it forces them to maintain their body temperature above 16°C. Hibernating in the moderate Israeli winter raises questions regarding the selective forces and adaptive significance of using hibernation in this genus, and remains to be studied. The finding that mouse-tailed bats use specific caves with constant high temperature and humidity during winter, enabling these species to survive on the northern edge of their distribution, highlights the importance of protecting such caves for the conservation of these species.

Ethics statement. All procedures were carried out under permit no. 2009/31867 from the Israel Nature Reserves and Park Authority (NPA) and the Ethics Committee license no. L-09-002.

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