Functional Ecology 1997
11, 585–591

Periodic arousals in hibernating mammals: is evaporative water loss involved?

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Summary

1. Using existing data on the rate of cutaneous and pulmonary evaporative water loss (EWL) for hibernating Little Brown Bats (*Myotis lucifugus*) and on the duration of torpor bouts, body temperature (T_b) and oxygen uptake (V_{O_2}) of Golden-mantled Ground Squirrels (*Spermophilus saturatus*), the rate of EWL was modelled for ground squirrels hibernating at ambient temperatures (T_a) of –2, 2, 4 and 8 °C.

2. Total EWL showed a curvilinear response to T_a, being lowest at 2 °C and increasing with both increasing and decreasing T_a. EWL at –2 °C was about equal to that at 4 °C. The duration of torpor bouts showed the same curvilinear response to T_a and torpor bout duration at –2 °C was similar to that at 4 °C (8·5 *vs* 8·3 days, respectively).

3. At $T_a \geq 2$ °C, where T_b of torpid *S. saturatus* is not metabolically defended, torpor bout duration is significantly related to T_b, V_{O_2} and EWL, with the three variables having similar r^2 values.

4. Using the regression equations generated at $T_a \geq 2$ °C to predict torpor bout durations at –2 °C, where T_b is metabolically defended, shows that the three variables do not have equivalent predictive abilities. T_b and V_{O_2} predicted torpor bout durations of 15·2 and –40·4 days, respectively, compared with observed durations of 8·5 days at –2 °C. EWL predicted torpor bout durations of 8·4 days or only 0·1 days less than that observed at –2 °C.

5. The relation between torpor bout duration and total EWL was insensitive to major variations in cutaneous EWL. Over T_a ranging from –2 °C to 8 °C, a stepwise multiple regression including T_b, V_{O_2} and EWL as independent variables identified EWL as the only variable significantly correlated with torpor bout duration.

6. Our analyses suggest that torpor bout duration may be influenced by EWL, indicating that animals may need to obtain free water when they arouse. An analysis of the structural and temperature characteristics of ground squirrel hibernacula suggests that they may function as a biological condensing tower. Throughout winter, water should evaporate from the warm lower levels and condense in the colder upper regions and so free water may be available to animals when they arouse.

Key-words: Bat, evaporative water loss, hibernation, rodent, torpor bout duration

Functional Ecology (1997) **11,** 585–591

Introduction

Winter presents a severe metabolic challenge to homeotherms. Just as food availability drops to its annual minimum, low ambient temperatures (T_a) increase energy requirements. Many mammals escape this energy bottleneck by hibernating, whereby they reduce body temperature (T_b) usually below 10 °C and metabolic rate to a fraction of that of normothermic individuals. The suppression of metabolic rate through torpor has a clear adaptive value when feeding opportunities are sporadic or non-existent and fat reserves are limited. Hibernators, however, do not exploit the energy savings of torpor to the maximum; all hibernators studied to date arouse periodically (Lyman *et al.* 1982). Although they account for > 75% of the total energy requirement for hibernation (Kayser 1953; Wang 1978; Thomas, Dorais & Bergeron 1990), arousals remain among the least understood of hibernation phenomena.

Although numerous factors have been proposed to account for the occurrence and frequency of arousals, these can be broadly grouped under three principal theories. First, a metabolism theory proposes that the reduction of energy substrates or the accumulation of metabolic wastes forces animals to arouse to re-establish homeostatic conditions (Baumer *et al.* 1971; Mrosovsky 1971; Galster & Morrison 1972). Because metabolic rate decreases as T_a and T_b decline to the lowest level that is not metabolically defended (T_{set}), this theory predicts that the duration of torpor bouts should increase with declining T_a and T_b. This is consistent with observations (French 1982; Geiser & Kenagy 1988).

Secondly, a T_b theory proposes that the torpor/arousal cycle observed in hibernation is possibly: (1) the expression of a natural circadian cycle whose frequency is prolonged by the depression of T_b (Strumwasser 1959; Pohl 1987; see also Lyman *et al.* 1982), (2) the result of reduced neural sensitivity to changes in internal conditions (Geiser & Kenagy 1988), or (3) a result of a temperature-dependent deprivation of non-rapid eye movement sleep while in hibernation (Trachsel, Edgar & Heller 1991). Because chemical, metabolic and neural processes are temperature dependent, and thus depressed by low T_b, this hypothesis also predicts that torpor duration increases as T_b declines.

Finally, a water balance theory argues that hibernators progressively lose body water through evaporative water loss (EWL) until some critical threshold is crossed, forcing animals to arouse (Fisher & Manery 1967; Thomas & Cloutier 1992). Because hibernators closely conform with T_a and because water vapour pressure (WVP) at the body surfaces is temperature-dependent, EWL is less at low than at high values of T_b. As a result, this hypothesis also predicts that torpor duration should increase as T_a and T_b decline. The close concordance between the observed duration of torpor bouts in hibernating *Myotis lucifugus* and those predicted on the basis of EWL has been taken as circumstantial support for a water balance theory (Thomas & Cloutier 1992; Thomas 1995).

Clearly, one of the major obstacles in identifying a 'best fit' theory is the fact that all three predict the same trends in torpor duration. At $T_a \geq T_{set}$, hibernators behave as conforming heterotherms, whereby T_b closely follows T_a. As a result, metabolic, chemical and physical processes taking place within hibernators have similar rates of change with temperature. Because all three hypotheses involve temperature-dependent processes, they predict a similar inverse relation between torpor bout duration and T_a or T_b at $T_a \geq T_{set}$.

However, as T_a drops below T_{set}, hibernators begin to thermoregulate (e.g. Barnes 1989; Geiser, Hiebert & Kenagy 1990) to stabilize T_b (Heller & Hammel 1972). In *Spermophilus saturatus* this occurs when animals are transferred from + 2 °C to –2 °C where V_{O_2} increases dramatically, whereas T_b drops only slightly. Geiser & Kenagy (1988) exploited this divergence in the trends in T_b and V_{O_2} at $T_a \leq 2$ °C to separate the effects of metabolism and T_b on the duration of torpor bouts. Torpor duration decreased by 20% from 2 to –2 °C. Although torpor duration was correlated with T_b over T_a of –2 to 8 °C, including V_{O_2} in a multiple regression increased the amount of explained variance. They concluded that both T_b-dependent and metabolic processes influenced torpor duration.

The fact that torpor duration decreases as T_a drops from 2 °C to –2 °C does not eliminate water balance as a potential cause of arousal. As T_a declines below 2 °C, the difference between T_b and T_a (ΔT) increases (Geiser & Kenagy 1988), resulting in an increase in the WVP gradient (ΔWVP) between the body surface and the surrounding atmosphere. This necessarily leads to an increase in cutaneous EWL below T_{set}. As animals thermoregulate to stabilize T_b they also increase V_{O_2} and pulmonary ventilation (Hammel *et al.* 1968) which increases pulmonary EWL. Because total EWL increases below T_{set}, the water balance theory predicts that torpor duration will decline, a prediction that is consistent with observations.

This paper has two objectives. The first is to model the trends in cutaneous and pulmonary water losses of Golden-mantled Ground Squirrels (*S. saturatus*) hibernating at T_a ranging from 8 °C to –2 °C. The second is to compare T_b, V_{O_2} and EWL in their ability to predict torpor duration accurately over the same range of T_a.

Material and methods

This analysis draws on two databases: one on the rate of cutaneous and pulmonary EWL for the Little Brown Bat (*M. lucifugus*) exposed to varying WVP conditions (Thomas & Cloutier 1992) and another relating the duration of torpor bouts to T_a, T_b and V_{O_2} for Golden-mantled Ground Squirrels (*S. saturatus*; Geiser & Kenagy 1988). Details on experimental conditions are presented in these two papers.

CALCULATIONS OF CUTANEOUS AND PULMONARY WATER LOSSES FOR *S. SATURATUS*

The EWL faced by hibernating *S. saturatus* is the sum of cutaneous and pulmonary losses. Cutaneous EWL for *S. saturatus* was modelled as follows. Thomas & Cloutier (1992) measured total EWL for *M. lucifugus* at 376·3 mg day^{-1} ΔWVP^{-1} (kPa) and evaluated the pulmonary contribution as only 0·3% of the total. We thus took 375·2 mg day^{-1} ΔWVP^{-1} as cutaneous EWL for a 6·4-g bat. The cutaneous surfaces were estimated at 33·89 cm^2 (assuming that bats have similar surface areas to other mammals when their wings are folded; Dawson & Hulbert 1970) and the area-specific cutaneous EWL was calculated as 11·07 mg day^{-1} ΔWVP^{-1} cm^{-2}. Hibernating ground squirrels roll into a nearly spherical posture, so surface area was estimated as that of a 250-g sphere. From this, cutaneous EWL for a 250-g *S. saturatus* is:

$$\text{Cutaneous EWL} = 2124{\cdot}5 \text{ mg day}^{-1}\ \Delta\text{WVP}^{-1}\ (\text{kPa}). \qquad \text{eqn 1}$$

Cutaneous EWL was modelled at T_a of 8, 4, 2 and –2 °C, taking a mean relative humidity of 80% for Seattle's moist coastal climate.

To evaluate the impact of error in our estimates of cutaneous surface area and EWL on our conclusions, a sensitivity analysis was performed, allowing cutaneous EWL to vary from 150% to 33% of our estimated values.

Pulmonary EWL was calculated for a 250-g *S. saturatus* by assuming that air is moved into the lungs, warmed from T_a to T_b and saturated with water, then expelled with no recovery of the water. The amount of air flushed through the lungs in 24 h was estimated using the measured V_{O_2}, an O_2 extraction efficiency of 15% (Schmidt-Nielsen 1984), and a fractional O_2 composition of 0·2095 for air. Thus, we estimated the total daily pulmonary ventilation as:

$$\text{Day volume (1)} = (V_{O_2} \times 24 \times 250)/(0{\cdot}2095 \times 0{\cdot}15 \times 1000). \qquad \text{eqn 2}$$

The saturation deficit for air (mg l^{-1} at 80% relative humidity) moved into the lungs and warmed to T_b was then calculated. Thus, pulmonary losses were estimated as:

$$\text{Pulmonary EWL (mg day}^{-1}) = \text{Day volume} \times \text{Saturation deficit.} \qquad \text{eqn 3}$$

Table 1. T_b, ΔT, V_{O2}, and the duration of torpor bouts for *Spermophilus saturatus* hibernating at T_a values of –2, 2, 4 and 80°C

	T_a (°C)			
Variable	–2	2	4	8
T_b (0C)	0·8	3·6	5·3	9·3
ΔT (0C)	2·8	1·6	1·3	1·3
V_{O_2} (ml $O_2 g^{-1} h^{-1}$)	0·173	0·031	0·038	0·048
Torpor duration (days)	8·52	10·65	8·31	4·63

Temperatures and V_{O_2} are means measured for seven individuals and torpor bouts represent the means for a total of 225 bouts measured for 17 individuals. Data are from the study published as Geiser & Kenagy (1988).

Table 2. WVP characteristics of the air and body surfaces and pulmonary day volumes and saturation deficits affecting cutaneous, pulmonary, and total EWL for *Spermophilus saturatus* hibernating at various T_as values.

	T_a(°C)			
Variable	–2	2	4	8
WVP (air @ 80% r.h.) (kPa)	0·423	0·564	0·650	0·857
WVP (body surface) (kPa)	0·647	0·791	0·890	1·171
Cutaneous EWL (mg day $^{-1}$)	475·88	482·26	509·88	667·09
Day volume (l)^{a}	33·03	5·96	7·18	9·15
Saturation deficit (mg l^{-1})	1·75	1·75	1·85	2·38
Pulmonary EWL (mg day $^{-1}$)*	57·77	10·41	13·27	21·74
Total EWL (mg day $^{-1}$)	533·65	492·67	523·15	688·83

WVP at the body surface, day volume and saturation deficit are based on T_b, ΔT, and V_{O_2} in Table 1.

[*] Calculated from equations 1, 2 and 3 in text

All WVP values are from Weast (1979). Pressures in mm Hg were transformed to SI units (kPa) using the conversion factor 133·32 (Pennycuick 1988).

Results

PATTERNS OF CUTANEOUS AND PULMONARY EWL FOR *S. SATURATUS*

Data on temperatures, V_{O_2} and torpor duration upon which the following analyses are based are presented in Table 1. At $T_a \geq 2$ °C, T_a and T_b vary more or less in parallel. Thus, a 6 °C drop in T_a from 8° to 2 °C results in a 5·7 °C drop in T_b. Across this range animals maintain a ΔT of + 1·3° to + 1·6 °C. Across the same 6 °C drop in T_a, V_{O_2} declines by 35·4%. At $T_a < 2$ °C, however, T_a and T_b diverge. Whereas T_a drops by 4 °C, T_b declines by only 2·8 °C to a minimum of 0·8 °C. Consequently, ΔT increases from + 1·6 °C to + 2·8 °C as T_a drops from 2° to –2 °C. The increase in ΔT is paralleled by a dramatic increase in metabolic rate. A 4 °C drop in T_a from 2° to –2 °C results in a 558·1% increase in V_{O_2}.

The varying T_b and ΔT observed over T_a of 8° to –2 °C act in concert to vary the WVP at the body surface, ΔWVP and cutaneous EWL (Table 2). As T_a drops from 8° to 2 °C, cutaneous EWL declines more or less linearly, dropping from 667·1 mg day^{-1} at 8 °C to 482·3 mg day^{-1} at 2 °C. Below 2 °C, however, increasing ΔT tends to stabilize cutaneous EWL which decreases to 475·9 mg day^{-1} at $T_a = -2$ °C (Table 2).

Pulmonary EWL shows a strong non-linear response to T_a owing to the dramatic increase in V_{O_2} and $T_a = -2$ °C (Table 2). As T_a drops from 8° to 2 °C, pulmonary EWL declines from 21·7 to 10·4 mg day^{-1}. As T_a continues to drop from 2 to –2 °C, the trend reverses and pulmonary losses increase by 555% to 57·8 mg day^{-1}.

Total EWL, representing the sum of cutaneous and pulmonary losses, shows the same non-linear trend. Total EWL is at its minimum at T_a = 2 °C and increases both with increasing and with decreasing T_a (Table 2). At T_a = –2 °C, animals experience EWL similar to that at 4 °C (533·7 *vs* 523·1 mg day^{-1}, respectively). It is noteworthy that this trend parallels the trend in torpor bout duration, where bout durations are roughly equivalent at T_a of 4° and –2 °C (8·3 *vs* 8·5 days, respectively; Table 1).

T_b, V_{O_2} AND EWL AS PREDICTORS OF TORPOR DURATION

The metabolism, T_b and water balance theories all predict that torpor duration is inversely correlated with V_{O_2}, T_b and EWL at $T_a \geq 2$ °C and this was indeed the case (Table 3). T_b, V_{O_2} and EWL explain 53%, 54% and 50%, respectively, of the variance in torpor duration. It is concluded that all three variables perform equally well as predictors of torpor duration at $T_a \geq 2$ °C.

Table 3. Regressions of torpor bout duration (days) on T_b, V_{O_2}, and EWL for $T_a \geq$ 2°C. All regression equations are significant at $P \leq 0{\cdot}001$ (df = 68)

Variable	Torpor bout duration	r^2	Predicted torpor bout duration at $T_a = -2$°C (days)
T_b	$13{\cdot}97 - 1{\cdot}020 \times T_b$	0·53	15·2
V_{O_2}	$21{\cdot}86 - 359{\cdot}942 \times V_{O_2 2}$	0·54	−40·4
EWL	$22{\cdot}85 - 0{\cdot}027 \times \mathrm{EWL}$	0·50	8·4
EWL_{150}	$22{\cdot}98 - 0{\cdot}018 \times \mathrm{EWL}_{150}$	0·50	9·1
EWL_{67}	$22{\cdot}66 - 0{\cdot}039 \times \mathrm{EWL}_{67}$	0·50	7·9
EWL_{50}	$22{\cdot}47 - 0{\cdot}051 \times \mathrm{EWL}_{50}$	0·50	7·4
EWL_{33}	$22{\cdot}13 - 0{\cdot}073 \times \mathrm{EWL}_{33}$	0·50	6·4

To test the performance of the variables below T_a = 2°C, regression equations were used to predict torpor bout durations at $T_a = -2$°C. Note that only EWL predicts torpor bout durations close to the 8·5 days observed at $T_a = -2$°C. EWL_{150}, EWL_{67}, EWL_{50} and EWL_{33} are values of total EWL when cutaneous EWL is varied by 150%, 67%, 50%, or 33% of values predicted by equation 1 in text.

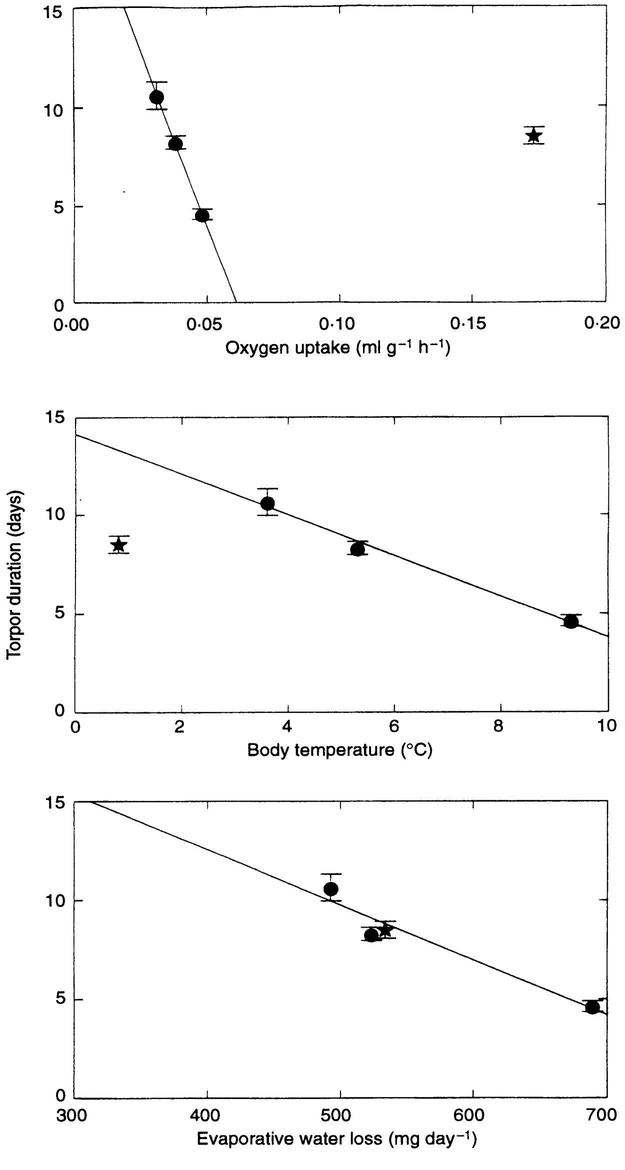

Fig. 1. The relation between the duration of torpor bouts and T_b, V_{O_2} and EWL for *Spermophilus saturatus* hibernating at T_a of −2, 2, 4 and 8 °C. Each line is derived from the regression equations for $T_a \geq 2$ °C (see Table 3). The star indicates the mean torpor duration at −2 °C. Note that only EWL accurately predicts torpor duration at this temperature. Torpor durations are mean ± SE.

Including $T_a = -2$ °C in the analysis results in a marked decrease in the performance of V_{O_2} and T_b. Torpor duration is not significantly correlated with V_{O_2} over T_a of −2° to 8 °C ($r^2 < 0{\cdot}00$, $P = 0{\cdot}93$), whereas T_b explains only 28% of the variance in torpor duration ($r^2 = 0{\cdot}28$, $P = 0{\cdot}01$). In contrast, EWL remains a good predictor of torpor duration over the entire range of T_a ($r^2 = 0{\cdot}46$, $P < 0{\cdot}001$). A multiple regression including T_b and V_{O_2} explains approximately the same amount of variation in torpor bout duration ($r^2 = 0{\cdot}49$) as EWL alone. However, a stepwise multiple regression including torpor duration as the dependent variable and T_b, V_{O_2} and EWL as independent variables, selects EWL as the only significant variable over T_a of −2° to 8 °C ($\alpha_{\mathrm{enter}} = 0{\cdot}15$, $\alpha_{\mathrm{remove}} = 0{\cdot}15$, $P < 0{\cdot}001$).

Using the regression equations generated for $T_a \geq 2$ °C to predict torpor duration at −2 °C shows that T_b, V_{O_2} and EWL do not perform equally well (Table 3; Fig. 1). The regression based on T_b alone predicts a torpor duration of 15·2 days which is 6·7 days (79%) longer than the 8·5 days observed at −2 °C. The regression based on V_{O_2} alone predicts a torpor duration of −40·4 days, suggesting that animals should not be able to sustain torpor at −2 °C. In contrast, the regression based on EWL alone predicts a torpor duration of 8·4 days at −2 °C, a value only 0·1 days (1%) less than that observed at this temperature.

Total EWL is a robust predictor of torpor duration in that it is resistant to error in the estimation of cutaneous EWL. Varying cutaneous EWL from 150% to 33% of the value predicted by equation 1 has no effect on the correlation between torpor duration and total EWL ($r^2 = 0{\cdot}50$) and only a minor effect on torpor duration predicted at $T_a = -2$ °C (Table 3).

Discussion

To our knowledge, all studies of mammals hibernating under steady-state conditions show that $T_b > T_a$ (e.g. Hammel *et al.* 1968; McNab 1974; Geiser & Kenagy 1988) and that WVP may be at or below saturation (Fisher & Manery 1967; Davis 1970). This creates the gradient in WVP between the body surfaces and the surrounding atmosphere that will necessarily drive evaporation. Thus, all hibernators should face finite EWL even when T_b is depressed to approach T_a during bouts of torpor and when relative humidity approaches 100%.

As our modelling shows, EWL is at its lowest when T_a approaches T_{set}, thereby reducing both ΔWVP and the rate of pulmonary ventilation. Animals hibernating at $T_a > T_{\mathrm{set}}$ have increased EWL, primarily because of the exponential increase in saturation WVP with increasing temperature (Weast 1979). For *S. saturatus*, although ΔT remains relatively constant at + 1·3 °C, ΔWVP (and hence EWL) increases as T_a rises. Animals hibernating at $T_a < T_{\mathrm{set}}$ face increased EWL for two reasons. As T_a declines below T_{set}, both

ΔT and ΔWVP rise, thus increasing both cutaneous and pulmonary EWLs. These water losses are compounded by the increased ventilation rate required to sustain the high metabolic rate observed for *S. saturatus* at –2 °C. On the basis of this pattern, one would predict that the duration of torpor bouts would decrease as T_a deviates in either direction from T_{set} if water loss is implicated in arousals. This is indeed the case.

Our analysis shows that the duration of torpor bouts in *S. saturatus* are more closely correlated with total EWL than with either T_b or V_{O_2}. For T_a of 8 to –2 °C, a stepwise regression model selects EWL as the only significant variable. Furthermore, the relation between torpor duration and EWL above T_{set} (i.e. $T_a \geq 2$ °C) accurately predicts the duration of torpor bouts below T_{set} (i.e. $T_a < 2$ °C). This is particularly interesting because the reasons for high EWL above and below T_{set} differ, yet the relation between torpor duration and water loss persists. In contrast, neither T_b nor V_{O_2} accurately predict torpor duration below T_{set}.

Water loss could also explain why the degree of saturation of dietary lipids affects torpor duration (Geiser & Kenagy 1987). Polyunsaturated lipids depress T_{set} which in turn reduces both cutaneous and pulmonary EWL. If water balance is implicated in the arousal process, then animals that receive polyunsaturated lipid diets and exhibit a depression in T_{set} should show an increase in the duration of torpor bouts.

The scaling of area-specific cutaneous EWL from an animal the size of a bat (*c.* 6·4 g) to one the size of a ground squirrel (250 g) is prone to error. Inaccurate values for surface areas and humidity, minor differences between skin and core temperatures, and taxon-related differences in fur thickness may act to reduce cutaneous EWL for *S. saturatus* below that predicted by our model. However, the sensitivity analysis shows that EWL remains a robust predictor of torpor duration despite major variations in cutaneous EWL.

In our analysis, we did not account for metabolic water production because it is far from clear to what degree it is available to compensate for EWL. In torpor, protein catabolism continues, albeit at a much reduced rate (Reidesel & Steffen 1980). Glomular filtration may either be arrested (Moy 1971; Tempel & Musacchia 1975) or it may continue at a greatly reduced rate (Zatzman & South 1972, 1975; Ondrich, Albert & Panuska 1974). During arousal, however, normal renal function resumes and ground squirrels produce a hypertonic urine containing urea (Moy, Lesser & Pfeiffer 1972). Whether urine production and urea excretion occur during torpor or the succeeding arousal, water is required for excretion. We conclude that some and possibly all of metabolic water production is required for excretion and thus is not available to offset EWL.

Although this study cannot establish a causal relationship between EWL and torpor duration, it does suggest that water loss (or some process closely linked with water loss) is implicated in the arousal process. It may be that the correlation between torpor bout duration and EWL is an artefact resulting from a close correlation between EWL and other biological processes. EWL is largely determined by V_{O_2} which controls pulmonary water loss and by T_b which affects cutaneous losses. Thus, it is possible that the close correlation between torpor bout duration and EWL may reflect the interaction between T_b and V_{O_2} as suggested by Geiser & Kenagy (1988). However, it remains that a stepwise multiple regression identifies EWL as the key factor affecting torpor bout duration. A study where EWL is varied independently of T_b and V_{O_2}, by controlling atmospheric WVP, will allow us to determine whether EWL acting alone or T_b and V_{O_2}acting in concert determine torpor bout duration.

If water loss is involved in triggering arousals, then it follows that animals may be forced to find water upon arousal. Most bats hibernate in humid caves or mines where there is access to drinking water and they have been observed drinking or licking condensed water when aroused (Davis 1970). Certain bats and other hibernators may show intermittent feeding activity through the hibernation period, permitting them to obtain water (Speakman & Racey 1989; Fowler & Racey 1990). Ground squirrels and other rodents, however, hibernate in subterranean burrows with no obvious access to free water. Although we do not know whether burrowing rodents obtain water during the hibernation period, here we propose a physical mechanism that could provide it.

Burrowing rodents typically hibernate in a tunnel system having at least one chamber located a depth of ≥ 60 cm (Young 1990). The hibernaculum frequently has an earth plug that seals the entrance, to some degree reducing gas exchange. As winter progresses, soil temperatures decline with the deeper layers remaining warmer than surface layers. At high latitudes and altitudes, surface soil temperatures are commonly < 0 °C, but the degree and depth of freezing is dependent on the snow cover and local winter temperatures.

Because the soil is moist, it is often assumed that the hibernaculum atmosphere is saturated with respect to water vapour (Fisher & Manery 1967) and that there is no net evaporation. However, the temperature gradient between the warm lower and cold higher levels will make the burrow system the biological equivalent of a condensation tower. Air will cool in the upper sections and flow down to pool in the deeper sections. As the air warms to the T_a of the lower sections, the saturation deficit will increase and water will evaporate from the soil surface (and the hibernating animal). Decreased air density, associated with the increase in saturation and temperature (Weast 1979), will force air to rise to the coldest levels and cool. Water will subsequently condense onto the tunnel surfaces either as ice crystals ($T_a < 0$ °C) or as water droplets ($T_a > 0$ °C). This process, driven by a temperature gradient, will continue to pump water vapour from the deeper sections and condense it in the higher levels of the hibernaculum throughout the winter.

Although we know of no studies that have looked specifically at the movements and activity of hibernating rodents during the more or less prolonged arousal periods (French 1982), we suggest that animals may move to the upper levels of their hibernacula and glean ice crystals or water droplets from the plug or the tunnel walls before re-entering torpor. Young (1990) noted that radio-collared *S. columbianus* could be found up to 2 m from the main hibernaculum chamber during arousals, confirming that squirrels do at least move within the tunnel system as we suggest.

Our proposition that EWL is implicated in over-winter arousals is based solely on a correlation analysis and thus remains unproven. However, the physical and microclimatic conditions prevailing in a burrow system suggest that hibernators should face finite EWL, and EWL does have a good capacity to predict torpor duration across the entire range of T_a tested in the laboratory. We argue that EWL warrants further study in the context of hibernation, arousals and winter energy budgets.

Acknowledgements

This study was funded through the Alexander von Humboldt Foundation and grants from the US National Science Foundation, Natural Sciences and Engineering Council of Canada and Fonds pour la Formation de Chercheurs et à l'Aide à la Recherche (Quebec). We thank M. Festa-Bianchet, W. King, P. Young and G. J. Kenagy for constructive comments on various drafts. This is contribution no. 104 of the Groupe de Recherche en Écologie, Nutrition et Énergétique.

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Received 22 August 1996; revised 25 November 1996; accepted 5 December 1996