



Effect of ambient temperature on evaporative water loss in the subterranean rodent *Ctenomys talarum*



María Belén Baldo*, C. Daniel Antenucci¹, Facundo Luna

Grupo de Ecología Fisiológica y del Comportamiento, Departamento de Biología, Instituto de Investigaciones Marinas y Costeras (IIMyC), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) – Universidad Nacional de Mar del Plata, Mar del Plata, Argentina

ARTICLE INFO

Article history:

Received 12 May 2015

Received in revised form

14 September 2015

Accepted 15 September 2015

Available online 16 September 2015

Keywords:

Ctenomys talarum

Evaporative water loss

Metabolic rate

Temperature

Heat dissipation

Burrow

ABSTRACT

Subterranean rodents face unique thermoregulatory challenges. Evaporative water loss (EWL) is a crucial mechanism for maintaining heat balance in endotherms subjected to heat stress but also leads to potential dehydration. EWL depends on gradients of temperature and humidity between the surface of the individual and the surrounding environment. Underground burrows generally provide a stable water vapor saturated atmosphere which may impede evaporative heat loss (EHL). This will mainly occur when ambient temperature exceeds the upper limit of individual's thermoneutral zone, or when body temperature rises as result of digging activities. Here we evaluate the effect of ambient temperature on EWL and energy metabolism in the subterranean rodent *Ctenomys talarum* (tuco-tucos), which inhabits sealed burrows, but makes an extensive use of the aboveground environment. We observed that EWL is increased when ambient temperature rises above thermoneutrality; below this point, evaporation remains stable. Though EWL contributes to total heat loss by increasing ~1.3 times at 35 °C, dry thermal conductance is raised four times. In tuco-tucos' burrows both non-evaporative and, to some extent, evaporative and behavioral mechanisms are essential for body temperature regulation, preventing overheating at high ambient temperatures in a water vapor-saturated atmosphere.

© 2015 Elsevier Ltd. All rights reserved.

1. Introduction

Water balance is essential and challenging depending on animal's particular habitat, behavior and/or physiology. In endotherms, a significant route of water loss is through evaporation, including both cutaneous and respiratory routes. Although evaporative water loss (EWL) is inevitable, individuals can regulate and use it for cooling, as produced heat is dissipated by evaporating body water. EWL depends on temperature and humidity gradients between the surface of the individual and the environment (McNab, 2002). Nevertheless, species show strategies that reduce EWL at different levels: morphological, physiological levels, and also through behavior.

Respiratory EWL can be modified by morphology, blood perfusion, and also by the expression of aquaporins and ion transporters at the nasal turbinates (Cortés et al., 1990; Gallardo et al., 2008). The efficiency for conditioning air flux determines how much water is recycled, and hence, EWL value (Schmidt-Nielsen and Schmidt-Nielsen, 1950). There is a wide variation among

species in the ability for recovering this water which is largely related to adaptations to a particular environment (Schmidt-Nielsen et al., 1970; Cortés et al., 1990).

Among several behavioral strategies, habitat selection is another way to control EWL. Inhabiting a relatively stable environment, characterized by low day–night fluctuations in ambient temperature (T_a) and a steady relative humidity (RH) can make it possible, when physiological regulation is inadequate and some sort of compensation is needed. In some cases, living within an underground burrow may diminish both daily and seasonal ambient temperature fluctuations. As observed in ground squirrels (*Spermophilus beecheyi*), the use of burrows protects individuals from high T_a s during the day and low T_a s at nights, and from the high RH variations found aboveground (Baudinette, 1972). In the strictly subterranean *Heterocephalus glaber*, burrows and grouping protect individuals from high rates of heat loss and EWL (Buffenstein and Yahav, 1991). Consequently, behavior may be enough to stabilize EWL and protect animals from negative water balance. However, evaporative water loss is not only important for water budget but it also plays a key role in maintaining thermal balance (McNab, 2002).

Despite EWL is mostly constant at low temperatures (i.e. below thermoneutral zone), it appears to be an important but not exclusive route of heat transfer for mammals at high temperatures

* Corresponding author.

E-mail address: mbbaldo@mdp.edu.ar (M.B. Baldo).

¹ Formerly Antinuchi.

(Withers et al., 2012). In species that live almost permanently in closed tunnels, heat produced during digging activities inside the sealed burrow system, characterized by low convection and high humidity, could cause overheating. In this scenario, McNab (1966, 1979) proposed that physiological characteristics of subterranean rodents, such as the low basal metabolic rate (BMR) and the high wet thermal conductance (C_{wet}) compared to surface-dwelling species of the same body mass, are adaptations to avoid overheating during digging (“thermal stress hypothesis”; see Vleck (1981, 1979), for an alternative hypothesis).

Ctenomys talarum (tuco-tucos) lives inside underground burrows in the coastal grasslands of Buenos Aires Province (Argentina). These burrows are a system of closed galleries composed of a main tunnel connected to several lateral branches (Antinuchi and Busch, 1992). As occurs for other subterranean rodents (Nevo, 1999), the atmosphere of a burrow presents a low concentration of oxygen, high levels of carbon dioxide, and also high water vapor concentration (19.3% O₂, 1.9% CO₂, > 90% RH; Baldo (unpublished data)). This is remarkably different to the African mole rat burrows that show no differences in gas composition compared to the aboveground atmosphere (Burda et al., 2007). As tuco-tucos emerge daily to forage and also for dispersal and reproduction at particular moments of the reproductive cycle (Malizia et al., 1995), they make an extensive use of the aboveground undergoing atmospheric variations in water content and temperature. Moreover, seasonal fluctuations in biomass and water content of coastal grasses consumed (Fanjul et al., 2006) may affect water balance, as this species does not drink and relies solely on food for all water (Zenuto et al., 2001). It has also been observed that tuco-tucos present morpho-physiological characteristics which contribute to low energy requirement and low water exchange ratio that also diminish the necessity of heat dissipation (Buffenstein, 2000). These features are similar to those found in other subterranean species (Luna et al., 2009).

In this context, the aim of this study was to evaluate the effect of T_a on EWL and the energetic metabolism of the subterranean rodent *C. talarum*. In agreement with previous observations in other endotherms, we expected an increment in EWL as T_a increases. However, due to the species extensive use of burrows, characterized by a water-saturated atmosphere, such temperature-induced increases in EWL may be lower than that in a surface-dwelling rodent.

2. Material and methods

2.1. Animals and maintenance

Adult individuals of *C. talarum* were live trapped in Mar de Cobo (37° 46'S, 57° 26'W), Buenos Aires. Animals were transported to the laboratory and housed in individual cages with wood shavings and a place for refuge, consisting in a half terracotta flowerpot. Acclimation period was 12 days. Photoperiod (L:O 12:12), ambient temperature ($T_a=25\text{ }^\circ\text{C}$) and humidity (50–60% RH) were controlled. Animals were fed ad libitum with sweet potato, lettuce, corn and sunflower seeds. Water was not provided, as these rodents do not drink free water. Animal manipulation was carried out in accordance to the guidelines of the American Society of Mammalogists (Sikes and Gannon, 2011) and current laws of Argentina for capture, handling and care of mammals in captivity.

2.2. Measurements

To test the effect of ambient temperature (T_a) on water balance and minimal energy budget, measurements of evaporative water loss (EWL) and metabolic rate (MR) were obtained for each animal

at different temperatures (from 5 °C to 35 °C, at 5 °C increments). We reported minimal metabolic rate as resting metabolic rate (RMR) for MR below or above thermoneutral zone (TNZ), and basal metabolic rate (BMR) for MR within TNZ (25–30 °C in Busch (1989)). A respirometric technique was used to estimate EWL and MR (Lighton, 2008). Resting and basal metabolic rates were obtained from O₂ consumption values, measured by using a computerized positive-pressure open-flow respirometry system (Sable System, Las Vegas, USA). Animals were individually placed in a chamber (1.8 L) that received air at 1.4 L/min from a flowmeter (Cole-Parmer Instrument Company, Vernon Hills, USA). Air passed through a CO₂-absorbent (IQB[®]) and water scrubber (Drierite[®]) before going through the chamber. Excurrent air from the chamber was subsampled at 130 ± 10 mL/min and moved through a CO₂ analyzer (CA-10, Sable Systems) to determine carbon dioxide production. Subsequently, the air was passed through CO₂ and H₂O scrubbers (IQB[®] and Drierite[®]) before reaching an O₂ analyzer (FC-1B, Sable Systems). Voltage-related concentrations of CO₂ and O₂ were recorded every 0.5 s by Expedata-PC program (Sable Systems). Baseline-corrected data of O₂ and of CO₂ were converted into mL of each gas using standard respirometric equations (Withers, 1977). Measurements at each experimental ambient temperature did not start up until 1 h after individuals were placed inside the chamber to ensure they remained still. Oxygen consumption and CO₂ production were continuously monitored until stable readings were attained and held for at least 15 min. Immediately after the CO₂ analyzer, EWL was measured by connecting a small column containing water absorbent (Drierite[®]) for 30 min. The column was weighed before and after sampling and EWL was determined gravimetrically (see Bernstein et al. (1977) for a validation of this technique compared to open flow respirometry). Total experimental period lasted 2–4 h, depending on the time required to reach each specific temperature T_a . Data were discarded when individuals urinated within the chamber. In these cases, the chamber was cleaned and dried, and the collection of data was repeated. Circadian O₂ consumption has not been observed for this species (Meroi et al., 2014), hence data collection was made between 8 and 17 h. Body weight (W) was obtained before each measurement, and body temperature (T_b) was measured by inserting 2 cm of a small probe connected with a thermistor (Cole-Parmer) into the rectum after each O₂ consumption trial. Wet thermal conductance (C_{wet}) was calculated as $C_{wet} = MR / (T_b - T_a)$, owing to the fact that when extrapolating the MR curve to the T_a axis, T_b did not equal T_a (see McNab (1980)). Minimal C_{wet} was obtained as the mean of C_{wet} s for temperatures below the thermoneutral zone (i.e. $5\text{ }^\circ\text{C} \leq T_a < 25\text{ }^\circ\text{C}$; see Busch (1989)). For comparative purposes, C_{wet} was expressed in cal/h °C. Respiratory quotient (RQ) was determined as the ratio between CO₂ production and O₂ consumption to determine potential differences in substrate catabolism (Schmidt-Nielsen, 1997). Additionally, two others parameters were obtained: evaporative heat loss (EHL = EWL * 0.603 cal/mg H₂O; see Stitt, 1976) and heat production (HP = MR * 5.011 cal/ml O₂; see Haim et al. (2008)). Finally, dry thermal conductance (C_{dry}) was calculated as (HP-EHL)/($T_b - T_a$), also expressed in cal/h °C.

2.3. Statistics

All data were expressed as mean \pm SE. Body weight (W) was analyzed for differences among T_a s using a one-way ANOVA test. Since basal metabolic rate of *C. talarum* did not differ among individuals despite differences in W between males and females (Antinuchi et al., 2007), physiological data for males and females were pooled. Segmented regression analysis was performed for total EWL and MR using SegReg software (www.waterlog.info). This analysis consisted in fitting a linear regression to data with no

linear relationship by introducing a breakpoint. Thus, a broken regression was obtained. Confidence intervals for breakpoints were calculated selecting the breakpoint with the smallest interval. Among the different functions obtained, we selected the one that maximized the statistical coefficient of explanation. Variations among T_{aS} in T_b , C_{wet} , RQ and derived calculations were analyzed by a one-way ANOVA test. When the ANOVA test assumptions failed, a Kruskal–Wallis non parametric test was performed.

3. Results

3.1. Body weight

Mean W values were 121.24 ± 8.89 g for females ($n=7$) and 142.46 ± 18.16 g for males ($n=5$). As sexes were pooled for each T_a s, no differences were detected for W between different T_a s (one-way ANOVA, $F_{6,49}=0.27$, $P=0.95$).

3.2. Evaporative water loss

The best fitting model explaining the relationship between EWL and T_a s was a segmented regression with a horizontal segment (slope forced to 0) that breaks and continues with a positive slope. Thus, EWL remained constant at 326 mg H_2O/h when $T_a < 28.7$, and at higher T_a s, EWL increased at a rate of EWL (mg H_2O/h) = $17.4 T_a - 173$ (Fig. 1).

3.3. Body temperature, basal metabolic rate, thermal conductance and respiratory quotient

Body temperature varied among ambient temperatures (one-way ANOVA, $F_{6,49}=7.52$, $P < 0.001$), being higher at $T_a=35$ °C from that observed at 5 °C $< T_a < 30$ °C (Tukey, all, $P=0.05$; Fig. 2). When the relationship between MR and T_a was analyzed, the best fitting model was once more a function with a segment that had zero slope. So, with a breakpoint at $T_a=27.2$ °C, two regression equations were obtained: MR (ml O_2/h) = $-7.36 T_a + 319$ and $MR=119$ ml O_2/h , below and above the breakpoint, respectively (Fig. 2).

Minimal wet thermal conductance below the thermoneutral zone was 0.078 ± 0.01 ml O_2/g h °C. Differences in C_{wet} among T_a s were observed (one-way ANOVA, $F_{6,49}=55.92$, $P < 0.001$). As expected, an increment was detected in C_{wet} above the

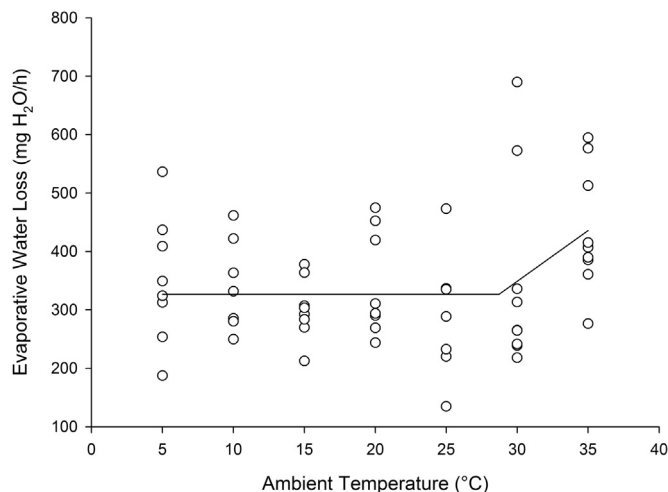


Fig. 1. Segmented regression for evaporative water loss of *Ctenomys talarum* as a function of ambient temperature ($n=12$).

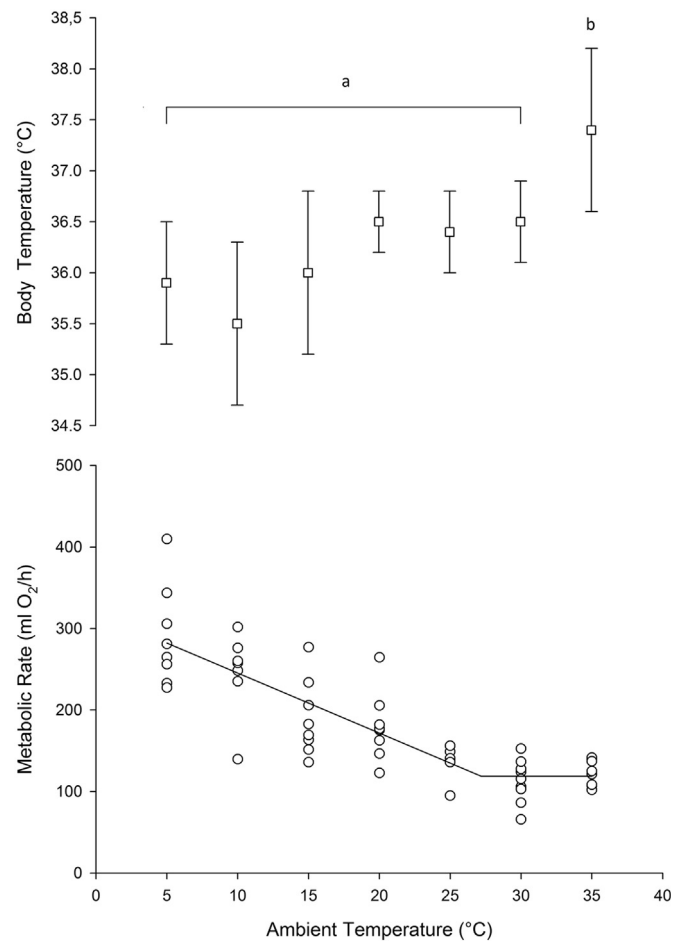


Fig. 2. Segmented regression for metabolic rate and body temperature of *Ctenomys talarum* as a function of ambient temperature ($n=12$).

thermoneutral zone. At $T_a=35$ °C, C_{wet} was higher than the observed between 5 °C and 30 °C (Tukey, all, $P < 0.001$). Also, C_{wet} at $T_a=30$ °C was also higher from that detected below thermoneutrality, except for $T_a=25$ °C (Tukey, all, $P < 0.001$; $25-30$ °C, $P=0.19$; Fig. 2). Likewise, C_{dry} was higher at $T_a=35$ °C compared to our observations below this temperature (one-way ANOVA, $F_{6,49}=20.12$, $P < 0.001$, Tukey, all, $P < 0.001$; Fig. 3). Respiratory quotient did not differ among T_a s (ANOVA, $F_{6,49}=1.21$, $P=0.32$), with a constant at value of 0.88 ± 0.11 .

3.4. Other physiological parameters

By analyzing HP with a segmented regression test, we obtained a similar pattern to that of MR, as this variable decreased until $T_a=27.2$ °C and remained constant at higher T_a s. Evaporative heat loss and EWL showed a similar pattern, remaining constant until $T_a=28.7$ °C, and raising as T_a increased. Segmented equations of HP and EHL are provided in Fig. 4. The ratio EHL/HP is a dimensionless indicator that represents the contribution of EWL to heat dissipation. This ratio differed among T_a s (Kruskal–Wallis, $H=38.36$, $df=6$, $P < 0.001$, Dunn, $P < 0.05$ (Fig. 4)).

4. Discussion

Based on our results, EWL is an effective way of heat loss at high T_a s in the subterranean rodent *C. talarum*. We found that EWL at $T_a=35$ °C, increases 1.33 times compared to that observed between 5 and 30 °C (Fig. 1). A similar pattern was observed in the

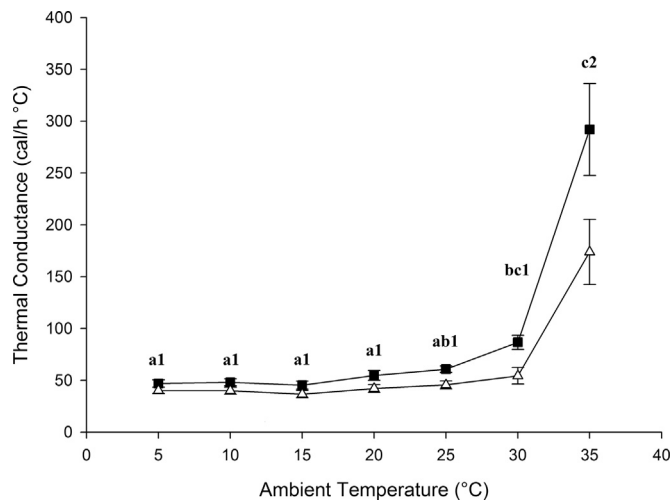


Fig. 3. Wet (C_{wet}) and dry (C_{dry}) thermal conductance of *Ctenomys talarum* as a function of ambient temperature ($n=12$). Squares: C_{wet} . Triangles: C_{dry} . Significant differences in C_{wet} among ambient temperatures are indicated by different letters ($P < 0.05$), and differences in C_{dry} are indicated by different numbers ($P < 0.05$).

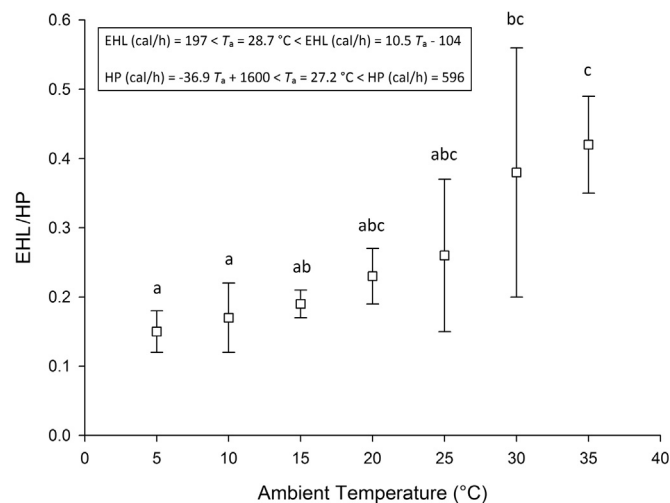


Fig. 4. Ratio of evaporative heat loss to heat production (EHL/HP) of *Ctenomys talarum* as a function of ambient temperature ($n=12$). Significant differences in EHL/HP among ambient temperatures are indicated by different letters ($P < 0.05$). Equations of the segmented regressions for EHL and HP are provided.

closely related *Ctenomys fulvus* (Cortés et al., 2000). Interestingly, even though *C. fulvus* inhabits an extremely arid environment, EWL increases 1.13 times at $T_a=35^\circ\text{C}$ compared to T_a s below TNZ. However, this increment is lower than the one observed in the poikilothermic subterranean *H. glaber* (whose EWL increases almost 25 times at 30–35 °C; Buffenstein and Yahav (1991)). Compared to *Ctenomys* species, EWL in surface dwelling rodents at high T_a s appears to be more variable. The increment of EWL at T_a s above TNZ varied from 1.2 times in *Perognathus longimembris* (Hinds and MacMillen, 1985) to more than 7 times as found in *Dipodomys merriami* measured at $T_a=40^\circ\text{C}$ (Tracy and Walsberg, 2001). Nevertheless, in other three *Perognathus* species EWL is independent from T_a (see Hinds and MacMillen (1985)).

Moreover, body temperature of *C. talarum* ranges from 35.9 °C to 37.4 °C (from $T_a=5^\circ\text{C}$ to $T_a=35^\circ\text{C}$, respectively). Although changes in T_a affect T_b , hyperthermia does not occur up to $T_a=35^\circ\text{C}$ (Fig. 2), as it has been observed in *C. fulvus* (Cortés et al., 2000). Despite EWL increases above thermoneutrality, high RH within burrows may reduce the capacity for heat dissipation; then, produced heat may be stored at high temperatures (Lovegrove

et al., 2013). In tuco-tucos, it has been observed that individuals can no longer maintain T_b at normothermic levels at ambient temperature close to 40 °C (Busch, 1989; Cortés et al., 2000). At this temperature, RMR of *C. talarum* increased by 63%, revealing that heat dissipation is energetically expensive (Busch, 1989). This possibly indicates that *C. talarum* is not adapted to resist a significant T_a increment, which agrees with the fact that this species has a temperate and mesic distribution. In addition, burrows protect individuals from abrupt changes in ambient temperature and RH (Baudinette, 1972; Buffenstein and Yahav, 1991). However, the extensive use of burrows does not preclude that tuco-tucos find occasionally high T_a s on surface, since this species is active throughout the day and forage on the surface (Luna et al., 2000; Cutrera et al., 2006). It may be interesting for future investigations to explore if these animals present regularity in opening burrow entrances to allow air renewal. Variations in the activation of capture traps and activities associated with burrow ventilation were observed along day (Antenucci, unpublished data). Probably, air exchange could cause a reduction in RH of burrows, facilitating EWL if required. Therefore, aboveground activities and behaviors associated with the ventilation of burrows described above could be common strategies displayed for heat dissipation.

It is well known that subterranean rodents show physiological features as a result of their underground habit: low BMR and high wet thermal conductance compared to surface rodents of the same body mass. Such physiological adaptations are associated to the possibility of lowering overheating during digging activities (McNab, 1966, 1979; Luna et al., 2009). Despite this, Luna and Antinuchi (2007) found that *C. talarum* incurs in an additional cost during digging to dissipate the produced heat at high temperature, but these authors could not determine the relative contribution of both, EHL nor conduction. In this study, we detected that C_{wet} and EWL have similar increment patterns in function of T_a , but with different magnitudes. As stated before, EWL increases ~1.3 times at $T_a=35^\circ\text{C}$, but C_{wet} augments almost 5 times at the same temperature. The rise of C_{wet} above TNZ pointed out that the dry component of heat loss is, in fact, more important than evaporative cooling. Indeed, C_{dry} increases ~4 times at $T_a=35^\circ\text{C}$ (see Fig. 3). In addition, the heat balance ratio EHL/HP remains below 1 (even at the highest temperature measured: $T_a=35^\circ\text{C}$, EHL=42% of HP, see Fig. 4) suggesting that non-evaporative ways of heat loss are more significant than EWL even though its contribution increases with T_a . A non-evaporative way to offload heat could be related to changes in posture, as observed in marsupial species (e.g. *Trichosurus vulpecula*, Cooper and Withers (2008); *Dasyurus geoffroyi*, Schmidt et al. (2009)). Tuco-tucos also modify their posture at high T_a s: in the chamber, individuals sprawl out with their fore and hind limbs extended. Similarly, during digging vaults at high temperatures, tuco-tucos rest over the less hairy ventral zone (Cutrera and Antinuchi, 2004) appressing it against the low-temperature substrate (Luna and Antinuchi, 2007). Thus, heat loss by conduction through contact with the soil may be the most relevant non-evaporative way to maintain T_b roughly constant (Baudinette, 1972; Luna and Antinuchi, 2007). Also, individuals of several species spread saliva over their body or snouts and lick their fur or paws to enhance EHL (Larcombe et al., 2006), but none of these behaviors were observed in tuco-tucos at $T_a=35^\circ\text{C}$, albeit in some cases they urinated and lied down over the excretion (Luna, personal communication).

Significant changes in C_{dry} and EWL suggest a strong thermoregulatory response of *C. talarum* to high T_a s. Moreover, conduction through the soil could be considered the main path of heat loss, an expected result considering burrow characteristics in this species: reduced humidity gradient among individuals and surrounding atmosphere, which results in a restricted evaporation potential (Baudinette, 1972; Luna and Antinuchi, 2007). All of

these mechanisms might enhance heat loss, but at the same time, increase the possibility of water loss. However, ventilation of burrows may be a behavioral response to enhance heat dissipation when EWL and conduction are depleted (see above).

On the other hand, though *C. talarum* does not drink free water, individuals require an intake of exogenous water to maintain its balance, especially if T_a increases. As a generalist species, *C. talarum* selects food depending on its availability and composition during each season, especially in periods in which vegetation shows low water content (Fanjul et al., 2006). Food items consumed might provide different proportions of water and biomolecules that also contribute differently to endogen water production when metabolized. In the case of the desert rodent *Dipodomys venustus*, high consumption of seeds, hence lipids, might ensure high production of endogenous water, allowing individuals to survive after several weeks without drinking (Church, 1969). Respiratory quotient is an indicator of the type of substrate mainly being used by an individual (Schmidt-Nielsen, 1997). We detected that RQ of tuco-tucos remains constant ($RQ=0.88 \pm 0.11$), suggesting that a mix of energetic substrates, mainly carbohydrates and lipids, is being used at all analyzed T_a s, (Schmidt-Nielsen, 1997). This supports the idea that balancing water budget in *C. talarum* requires not only the protecting environment of the burrow but also the intake of food items with a relatively high water content.

5. Conclusion

Evaporative water loss remains low and almost invariable below thermoneutrality, preserving body water. However, when T_a exceeds thermoneutral zone, evaporation rate in *C. talarum* augments and also does the C_{wet} , contributing with heat dissipation. Nevertheless, it has been demonstrated that C_{dry} is more relevant for heat loss. Furthermore, as observed during digging at high T_a s (Luna and Antinuchi, 2007), conduction might be an important avenue through which heat is dissipated. Therefore, due to the characteristics of burrows and habits of tuco-tucos, non-evaporative and to some extent evaporative mechanisms, are indispensable for T_b regulation preventing overheating at high T_a s. Further work in behavioral strategies, related with burrows ventilation in response to variations in atmospheric RH and temperature, might contribute to complete the ecophysiological perspective of this study.

Acknowledgments

We would like to thank all members of Laboratorio de Ecología Fisiológica y del Comportamiento, specially to Federico Vera and Julieta Merlo, for their assistance in field and laboratory work. We also are grateful to Federico Vera and Ana Paula Cutrera for the English revision. Finally, we appreciate reviewers' comments on an early draft of this manuscript. This study was supported by Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET, PIP0272), Agencia Nacional de Promoción Científica y Tecnológica (ANPCyT, PICT 0998) and Universidad Nacional de Mar del Plata (EXA649/14). This work is part of the Doctoral Thesis of MB Baldo, supported by a CONICET Doctoral Fellowship.

References

Antinuchi, C.D., Zenuto, R.R., Luna, F., Cutrera, A.P., Perissinotti, P.P., Busch, C. 2007. Energy budget in subterranean rodents: insights from the tuco-tuco *Ctenomys talarum* (Rodentia: Ctenomyidae). The quintessential naturalist: Honoring the

life and legacy of Oliver P. Pearson. University of California Publications in Zoology 134:1-981.

Antinuchi, C.D., Busch, C., 1992. Burrow structure in the subterranean rodent *Ctenomys talarum*. Z. Säugetierkd. 57, 163–168.

Baudinette, R.V., 1972. Energy metabolism and evaporative water loss in the California ground squirrel. J. Comp. Physiol. A 81, 57–72.

Bernstein, M.H., Hudson, D.M., Stearns, J.M., Hoyt, R.W., 1977. Measurement of evaporative water loss in small animals by dew-point hygrometry. J. Appl. Physiol. 43, 382–385.

Buffenstein, R., 2000. Ecophysiological responses of subterranean rodents to underground habitats. In: Lacey, E.A., Patton, J.L., Cameron, G.N. (Eds.), Life Underground: The Biology of Subterranean Rodents. University of Chicago Press, Illinois, pp. 62–110.

Buffenstein, R., Yahav, S., 1991. Is the naked mole-rat *Hererocephalus glaber* an endothermic yet poikilothermic mammal? J. Therm. Biol. 16, 227–232.

Burda, H., Sümbera, R., Begall, S., 2007. Microclimate in burrows of subterranean rodents-revisited. In: Begall, S., Burda, H., Schleich, C.E. (Eds.), Subterranean Rodents: News from Underground. Springer, Heidelberg, pp. 21–33.

Busch, C., 1989. Metabolic rate and thermoregulation in two species of tuco-tuco, *Ctenomys talarum* and *Ctenomys australis* (Caviomorpha, Octodontidae). Comp. Biochem. Physiol. A 93, 345–347.

Church, R.L., 1969. Evaporative water loss and gross effects of water privation in the Kangaroo rat, *Dipodomys venustus*. J. Mammal. 50, 514–523.

Cooper, C.E., Withers, P.C., 2008. Allometry of evaporative water loss in marsupials: implications of the effect of ambient relative humidity on the physiology of brushtail possums (*Trichosurus vulpecula*). J. Exp. Biol. 211, 2759–2766.

Cortés, A., Rosenmann, M., Báez, C., 1990. Función del riñón y del pasaje nasal en la conservación de agua corporal en roedores simpátridos de Chile central. Rev. Chil. Hist. Nat. 63, 279–291.

Cortés, A., Miranda, E., Rosenmann, M., Rau, J.R., 2000. Thermal biology of the fossorial rodent *Ctenomys fulvus* from the Atacama desert, northern Chile. J. Therm. Biol. 25, 425–430.

Cutrera, A.P., Antinuchi, C.D., 2004. Cambios en el pelaje del roedor subterráneo *Ctenomys talarum*: posible mecanismo térmico compensatorio. Rev. Chil. Hist. Nat. 77, 235–242.

Cutrera, A.P., Antinuchi, C.D., Mora, M.S., Vassallo, A.I., 2006. Home-range and activity patterns of the South American subterranean rodent *Ctenomys talarum*. J. Mammal. 87, 1183–1191.

Fanjul, M.S., Zenuto, R.R., Busch, C., 2006. Seasonality of breeding in wild tuco-tucos *Ctenomys talarum* in relation to climate and food availability. Acta Theriol. 51, 283–293.

Gallardo, P., Herrera, S., Saffer, K., Bozinovic, F., 2008. Distribution of aquaporins in the nasal passage of *Octodon degus*, as South-American desert rodent and its implication for water conservation. Rev. Chil. Hist. Nat. 81, 33–40.

Haim, A., Zubidat, A.E., Van Aarde, R.J., 2008. Daily rhythms of body temperature and heat production of sibling *mastomys* species from different ecosystems—The response to photoperiod manipulations. Comp. Biochem. Physiol. A 151, 505–510.

Hinds, D.S., MacMillen, R.E., 1985. Scaling of energy metabolism and evaporative water loss in heteromyid rodents. Physiol. Zool. 58, 282–298.

Larcombe, A.N., Withers, P.C., Nicol, S.C., 2006. Thermoregulatory, metabolic and ventilatory physiology of the eastern barred bandicoot (*Perameles gunnii*). Aust. J. Zool. 54, 9–14.

Lighton, J.R.B., 2008. Measuring Metabolic Rates: A Manual for Scientists. Oxford University Press, New York.

Lovegrove, B.G., Canale, C., Levesque, D., Fluch, G., Řeháková-Petrů, M., Ruf, T., 2013. Are tropical small mammals physiologically vulnerable to Arrhenius effects and climate change? Physiol. Biochem. Zool. 87, 30–45.

Luna, F., Antinuchi, C.D., 2007. Energetics and thermoregulation during digging in the rodent tuco-tuco (*Ctenomys talarum*). Comp. Biochem. Physiol. A 146, 559–564.

Luna, F., Antinuchi, C.D., Busch, C., 2000. Ritmos de actividad locomotora y uso de las cuevas en condiciones seminaturales en *Ctenomys talarum* (Rodentia, Octodontidae). Rev. Chil. Hist. Nat. 73, 39–46.

Luna, F., Antenucci, C.D., Bozinovic, F., 2009. Comparative energetics of the subterranean *Ctenomys* rodents: breaking patterns. Physiol. Biochem. Zool. 82, 226–235.

Malizia, A.I., Zenuto, R.R., Busch, C., 1995. Demographic and reproductive attributes of dispersers in two populations of the subterranean rodent *Ctenomys talarum* (tuco-tuco). Can. J. Zool. 73, 732–738.

McNab, B.K., 1966. The metabolism of fossorial rodents: a study of convergence. Ecology, 712–733.

McNab, B.K., 1979. The influence of body size on the energetics and distribution of fossorial and burrowing mammals. Ecology 60, 1010–1020.

McNab, B.K., 1980. On estimating thermal conductance in endotherms. Physiol. Zool. 53, 145–156.

McNab, B.K., 2002. The Physiological Ecology of Vertebrates: A View from Energetics. Cornell University Press, New York.

Meroi, F.R., Luna, F., Antenucci, C.D., 2014. Variación estacional de la tasa metabólica de reposo en *Ctenomys talarum* (Rodentia, Ctenomyidae): ausencia de efectos ambientales. Mastozool. Neotrop. 21, 241–250.

Nevo, E., 1999. Mosaic Evolution of Subterranean Mammals: Regression, Progression, and Global Convergence. Oxford University Press, New York.

Schmidt, S., Withers, P.C., Cooper, C.E., 2009. Metabolic, ventilatory and hygric physiology of the chuditch (*Dasyurus geoffroi*; Marsupialia, Dasyuridae). Comp. Biochem. Physiol. A 154, 92–97.

- Schmidt-Nielsen, K., 1997. *Animal Physiology: Adaptation and Environment*. Cambridge University Press, New York.
- Schmidt-Nielsen, B., Schmidt-Nielsen, K., 1950. Pulmonary water loss in desert rodents. *Am. J. Physiol.* 162, 31–36.
- Schmidt-Nielsen, K., Hainsworth, F.R., Murrish, D.E., 1970. Counter-current heat exchange in the respiratory passages: effect on water and heat balance. *Respir. Physiol.* 9, 263–276.
- Sikes, R.S., Gannon, W.L., 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *J. Mammal.* 92, 235–253.
- Stitt, J.T., 1976. The regulation of respiratory evaporative heat loss in the rabbit. *J. Physiol.* 258, 157–171.
- Tracy, R.L., Walsberg, G.E., 2001. Intraspecific variation in water loss in a desert rodent, *Dipodomys merriami*. *Ecology* 82, 1130–1137.
- Vleck, D., 1979. The energy cost of burrowing by the pocket gopher *Thomomys bottae*. *Physiol. Zool.* 52, 122–135.
- Vleck, D., 1981. Burrow structure and foraging cost in the fossorial rodent, *Thomomys bottae*. *Oecologia* 49, 391–396.
- Withers, P.C., 1977. Measurements of VO_2 and VCO_2 and evaporative water loss with a flow through a mask. *J. Appl. Physiol.* 42, 120–123.
- Withers, P.C., Cooper, C.E., Nespolo, R.F., 2012. Evaporative water loss, relative water economy and evaporative partitioning of a heterothermic marsupial, the monito del monte (*Dromiciops gliroides*). *J. Exp. Biol.* 215, 2806–2813.
- Zenuto, R.R., Vassallo, A.I., Busch, C., 2001. A method for studying social and reproductive behaviour of subterranean rodents in captivity. *Acta Theriol.* 46, 161–170.