

Metabolic rates and thermoregulatory characteristics of *Akodon azarae* (Rodentia: Sigmodontinae)

Tasas metabólicas y características termorregulatorias de *Akodon azarae* (Rodentia: Sigmodontinae)

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ABSTRACT

In this work, we evaluated the energetic status, activity daily metabolic rate, thermoregulatory capacity and the existence of torpor in *Akodon azarae* (Fisher 1829). Basal metabolic rate (BMR) was similar to the expected value from Kleiber's, and also according to the BMR of phylogenetically related species. No statistical difference in BMR between sexes was detected. For both males and females, activity daily metabolic rate was 235 % of BMR. Body temperature was not statistically different, neither at different ambient temperatures nor between sexes. In the thermoneutral zone, body temperature was 36.1 ± 1.5 °C. Thermal conductance was lower than the expected for mammals whereas thermoregulatory capacity was 136 % of the expected. *Akodon azarae* did not show evidence of torpor.

Key words: metabolic rates, thermoregulation, energetic, *Akodon azarae*.

RESUMEN

En este trabajo fueron evaluadas, para *Akodon azarae* (Fisher 1829), la tasa metabólica basal (BMR) y de actividad diaria así como la capacidad termorregulatoria y la posible existencia de torpor. La BMR no presentó diferencias estadísticas con la esperada por la ecuación de Kleiber así como con la esperada para especies filogenéticamente relacionadas. Tampoco fueron detectadas diferencias significativas en la BMR entre sexos. La tasa metabólica de actividad diaria para ambos sexos fue el 235 % de la BMR. La temperatura corporal no presentó variaciones entre individuos mantenidos a diferentes temperaturas ambiente ni tampoco entre sexos y en termoneutralidad fue de $36,1 \pm 1,5$ °C. Por otra parte, la conductancia térmica fue menor a la esperada mientras que la capacidad termorregulatoria fue el 136% de la esperada. *Akodon azarae* no presenta sopor.

Palabras clave: tasas metabólicas, termorregulación, energética, *Akodon azarae*.

INTRODUCTION

Endothermy is very expensive (McNab 1974) and endotherms expend most of the energy consumed to produce heat. Endotherms have sufficient fur insulation and thermogenic capacity to survive at low temperatures, but they need a regular food supply to do so. In consequence, endothermy allows mammals to maintain high body temperatures and independence of environmental conditions, but it becomes prohibitive in both unproductive and/or cold habitats (French 1992).

Body size measured as body weight (W), is the physical translator between the environment and the organism. Consequently, it constitutes the

primary factor that determines the basal metabolic rate (BMR) and thermal conductance of individuals (C). Most vertebrates follow the Kleiber (1961) relation down to a "critical" W , below which the scaling of BMR must be changed to ensure the maintenance of endothermy. According to McNab (1983), the minimal W for endothermy in species that have a level of BMR similar to the Kleiber relation, is namely about 20 g. Contreras (1989), reported that, the minimal W to have a level of BMR similar to the Kleiber, is above 50 g. Therefore, a combination of a small body mass and a low BMR would cause animals enter in torpor. Kleiber's equation has been discredited as a reference curve (Hayssen & Lacey 1985).

However, Kleiber's equation has been used countless quantity of times in most of the research on energetics, for which it has a great comparative value. McNab (1988) discussed that Kleiber's recommended curve have an acceptable level. Moreover, Bozinovic & Rosenmann (1988b) confirm the universality of the (-0.25) mass-specific allometric value reported by Kleiber and favor its use as a standard reference. On the other hand, independent of the influence of W, in mammals, food habits exert an important effect on BMR (McNab 1986).

Some endothermic species, when facing low temperatures, reduce substantially their heat production, entering torpor and thus balancing their total energy requirements. Thus, during daily torpor, animals drop their body temperatures between approximately 10°C and 25 °C and torpor bouts of less than 24 h (Hudson 1973). This mechanism, which allows species to inhabit both unproductive and/or cold areas, has been found in five species of South American rodents (Bozinovic & Contreras 1990, Caviedes-Vidal et al. 1990, Bozinovic & Marquet 1991). Bozinovic & Rosenmann (1988b), based on preliminary data set, hypothesized that other South American rodents such as *Akodon azarae* (Fisher 1829), *Calomys ducilla*, *C. musculinus* and *Eligmodontia typus* would show evidence of torpor at low ambient temperatures.

Other energetic studies have been accomplished on South American rodents (Caviedes-Vidal et al. 1987, Bozinovic & Rosenmann 1988a). For *A. azarae*, Dalby & Heath (1976) obtained BMR values on a single observation, not allowing any type of statistical comparison on BMR and thermoregulatory capacity nor between the sexes. In the present study, BMR, activity daily metabolic rate, thermoregulatory characteristics, and the existence of torpor in *Akodon azarae* are evaluated. For small omnivores as *A. azarae* an intermediate BMR (90 to 110% of Kleiber) would be expected. Furthermore, rodents as *A. azarae*, which tolerate low temperatures during winter having both, low BMR and small body mass, should show torpor or low thermal conductance.

MATERIAL AND METHODS

Animals

Animals of both sexes (26 females and 27 males) were collected using Sherman live traps at Necochea, Buenos Aires Province, Argentina (38°29' S, 58°50' W). This region is known as the "Pampeana" biogeographic province (Cabrera &

Willink 1973). *Akodon azarae* is a mouse of 24 g, strongly associated to natural grasslands, particularly to open formations (Bonaventura et al. 1992, Redford & Eisenberg 1992). This species, which is the most numerically representative rodent of the pampas grasslands, is found from southern Brazil to central Argentina (Redford & Eisenberg 1992).

Captured rodents were carried to the laboratory and housed individually in animal cages (0.3 x 0.22 x 0.15 m). Wood shaving and cotton for nesting material were placed on cage floors. All animals were maintained on a natural photoperiod (L:D = 10:14). Ambient temperature (T_a) ranged from 19 to 25 °C, whereas relative ambient humidity ranged from 50 to 70 %. Animals were fed with pellets ad libitum (composition in %: minimum protein: 21, maximum fiber: 4.5, minimum fat: 8, average calcium: 1.8, phosphorous: 1.1, maximum ashes: 8). Tap water was provided ad libitum.

Energetics

The energetics variables were individually estimated by measurements of oxygen consumption (VO_2) in metabolic chambers at different T_a 's using a modified closed automatic system, based on the design of Kalabukhov-Skvortsov (Gorecki 1975). The metabolic chamber was a double wall aluminum cage with polyurethane between walls. Animals were put inside the chamber, which was closed with a 20 mm thick acrylic window-door to observe the animals regularly. A thermocouple was used to measure temperature inside the chamber. Heat was interchanged with the outside chamber automatically by two Pelittier intercoolers (Melcor, model CP-1.4-127-06l) connected to a PC and controlled by software. Ambient temperature inside the chamber was maintained with an accuracy of 0.1 °C. An internal and an external pressure sensor monitored air pressure. Oxygen influx was assessed through two electrovalves. Pressure sensors and electrovalves were connected to a PC and controlled by a software. CO_2 and H_2O were removed by ascarite and drierite. In order to achieve a post-absorptive state, metabolic rates (MR) were measured in 24 h food deprived animals. Animals were weighted before each VO_2 measure. VO_2 was always measured in the morning. Data were discarded when activity was observed. To minimize the effect of stress, VO_2 records during the first 30 min were discarded. Basal metabolic rate was estimated from the minimal metabolic rate when it showed independence of T_a . For measuring activity daily metabolic rates (ADMR),

animals were disposed into the respirometer during 24 h with food at thermoneutrality, provided with a treadmill.

VO₂ is reported as mass-specific metabolic rate (ml/gh). All results are presented as means ± standard deviation (SD). All measures of VO₂ were corrected to standard temperature and pressure of dry air. Nickerson et al. (1989) method, that identifies the best fit for a continuous n-phase regression, was used to represent the relationship between T_a and MR. This method estimates the point at which the relationship between independent and dependent variables change (i.e. threshold point). The best n-phase regression model was selected by comparing from, a three-phase regression models to a simple regression model.

Body temperature and thermal variables

Body (rectal) temperatures (T_b) and ambient temperature (T_a) were measured using a YSI probe (model 93k73545-402) connected to a Cole-Parmer instrument thermistor (model 8402-10). Body temperature, was recorded at the beginning (T_{bb}) and at the end (T_{be}) of each VO₂ measurement by inserting a thermocouple 2 cm into the rectum of the mouse for a period no longer than 30 s. Decrease in T_b after each VO₂ measurement was estimated as $DT_b = T_{be} - T_{bb}$. The slope of the first phase of the best fitted n-phase regression that related MR and T_a was used as an estimate of minimal thermal conductance (C_{min}). Thermoregulatory capacity was estimated by the equation $DT_m = BMR/C$ (McNab 1974). The equations of: Kleiber (1961): $BMR = 3.4 W^{-0.25}$; Morrison & Ryser (1951): $C = 1.0 W^{-0.5}$; McNab (1983) BMR (endothermic limit) = $15.56 W^{-0.67}$; and the minimal thermal differential $DT_m = 15.56 W^{-0.17}$; were taken as standard references for eutherian mammals. The equation of Hayssen & Lacey (1985): $BMR = 5.73 W^{-0.359}$ was taken as standard references for murid rodents.

Daily torpor

Since in the field sampling, during winter, mortality of 80 % was observed when animals were in the traps for more than 4 h at T_a lower than 10 °C, VO₂ was measured in individuals at 15 °C during 4 h.

Statistics

ANOVA was used both to test the null hypothesis of no differences among metabolic rates at

different T_a between sexes and to test the null hypothesis of no differences among DT_b neither at different T_a nor between sexes. A posteriori Tukey's test was used to identify differences among DT_b, both at different T_a and between sexes.

A t- test was used either to evaluate the null hypothesis of no differences between observed BMR and the expected one by Kleiber's equation; to evaluate the null hypothesis of no differences between observed BMR and the expected one by Hayssen & Lacey's equation (1985); to test the null hypothesis of no differences in ADMR between sexes; to test the null hypothesis of no differences between the BMR observed and the expected one by McNab's equation on the eutheric limit; and finally for animals reared in animals room to test the null hypothesis of no differences in T_b between sexes. A t- test for comparisons between two slopes was used to test the null hypothesis of no differences between observed and expected C_{min}. An analysis of sensitivity was used to solve the possible meaningless of SD values of estimated BMR and C_{min}, since these parameters reflect the variance of W between the animals.

RESULTS

Metabolic measurement

No statistical differences among MR of males and females were detected at any T_a (F = 0.71, n = 70, df = 7, P > 0.5). To analyze the relationship between MR and T_a, data from both sexes were pooled. Mean MR was lowest at 35 °C (best fit: was a two-phase lineal regression, break point = 35 °C, Fig. 1, Table 1). Estimated BMR was not statistically different to the expected for a 22.5 g mammal neither by the Kleiber relation nor by the Hayssen & Lacey relation (Table 2). Sensitive analysis of the observed/expected BMR of *A. azarae*, shows that a bias of 347 % from Kleiber (t obs = t crit = 2.57, BMR expected = BMR observed ± 0.57, df = 5, P < 0.001) and a bias of 435 % from Hayssen & Lacey (t obs. = t crit. = 2.57, BMR expected = BMR observed ± 0.57, df = 5, P < 0.05) would be necessary to alter the latest conclusion.

The relation between VO₂ and T_a was (Fig. 1):

$$MR = 6.73 - 0.148 T_a \text{ if } T_a \leq 35$$

$$MR = -57.98 + 1.68 T_a \text{ if } T_a > 35$$

TABLE I

Statistical comparisons between either, one phase; two phases and three phases lineal regression model that related rate of metabolism and ambient temperature in *Akodon azarae*. Arrow indicates increase of the parameters number. Sse: squared sum of error, Fobs: observed F-statistic, Fcrit: critical F-statistic, b1 and b2: slopes of the first phase and second phase of the regression model, respectively

Comparaciones estadísticas entre los niveles de ajuste de modelos de regresión lineal de una, dos y tres fases que relacionan, en *Akodon azarae*, la tasa metabólica y la temperatura ambiente. La flecha indica el incremento en el número de parámetros. Sse: suma del cuadrado de los errores, Fobs: estadístico-F observado, Fcrit: estadístico-F crítico, b1 y b2: pendientes de la primera y segunda fase, respectivamente, del modelo de regresión

one	<	two	<	two	=	Three
phase	P < 0.042	phases	P < 0.001	phases	P = 1	phases
sse = 196	Fobs = 8.78	b1 = 0	Fobs = 92.56	b1 ≠ 0	Fobs = 0	b2 = 0
	Fcrit = 7.71	sse = 163	Fcrit = 7.71	sse = 59	Fcrit = 7.71	sse = 59

→

MR at 40 °C was estimated on only one individual since other mice exhibited thermal shock at this T_a .

Activity daily metabolic rate

No statistical differences between ADMR for males and females was detected ($t = -0.77$, $n_1 = 16$, $n_2 = 7$, $df = 21$, $P > 0.45$). For the pooled data, mean value was 4.04 ± 1.16 ml/gh (Table 2).

Body temperature and thermal variables

No statistical differences were detected between T_b of males and females ($t = -0.70$, $n = 70$, $df = 68$, $P > 0.4$). Body temperature of *A. azarae*, in the thermoneutral zone (TNZ), was 36.1 ± 1.5 °C (Table 2) whilst DT_b was statistically different between sexes only at 5 °C (DT_b females = -6.77 ± 2.18 and DT_b males = 0.42 ± 2.31 ; $F = 9.29$, $n = 67$, $df = 7$, $P < 0.005$). Thus, DT_b of males and females were pooled. No statistical differences

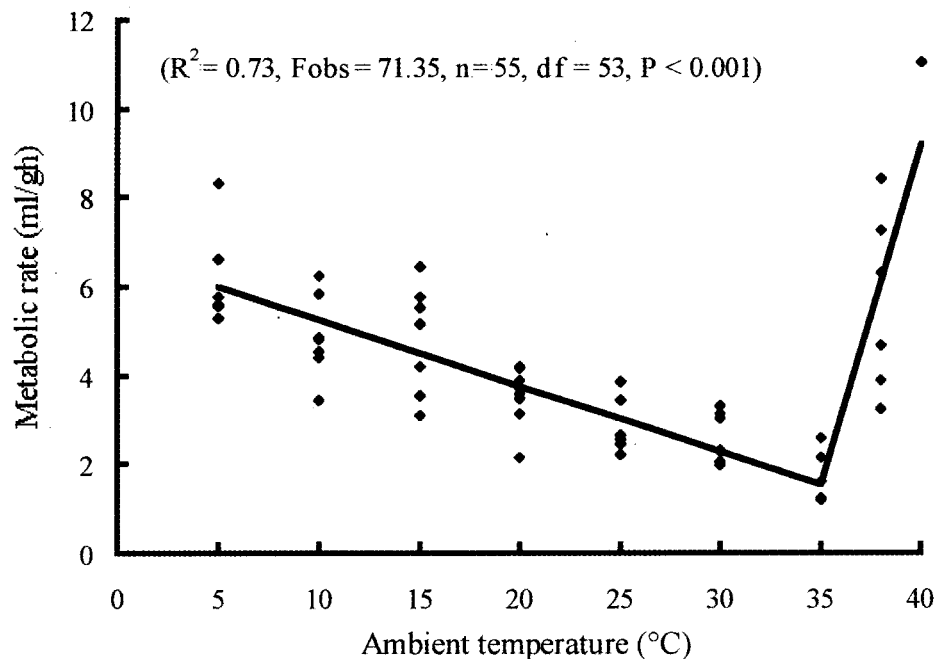


Fig. 1. Relationship between rate of metabolism and ambient temperature in *Akodon azarae*.

Relación entre tasa metabólica y temperatura ambiente en *Akodon azarae*.

between DT_b at different T_a were detected ($F = 1.03$, $n = 68$, $df = 7$, $P > 0.4$). On the other hand, C_{min} below TNZ was lower than expected from McNab's equation (Table 2). Sensitive analysis of the observed/expected C_{min} shows that a bias of 156 % in the estimated C_{min} of *A. azarae* would be necessary to alter the latest conclusion ($t_{obs} = t_{crit} = 2.01$, $BMR_{expected} = BMR_{observed} \pm 0.25$, $df = 48$, $P < 0.001$). In addition, DT_m was 136 % of expected from McNab's equation (Table 2).

Torpor

No statistical differences were detected between BMR and the energetic limit of euthermy expected from McNab (1983) (2.02 ± 0.46 ml/gh; $t = -1.02$, $t_{crit} = 2.23$, $n = 12$, $df = 10$, $P > 0.005$; Fig. 2). The lowest MR measured at 15°C of T_a was 2.66 ± 0.49 ml/gh. Then, *A. azarae* at experimental conditions did not enter in torpor.

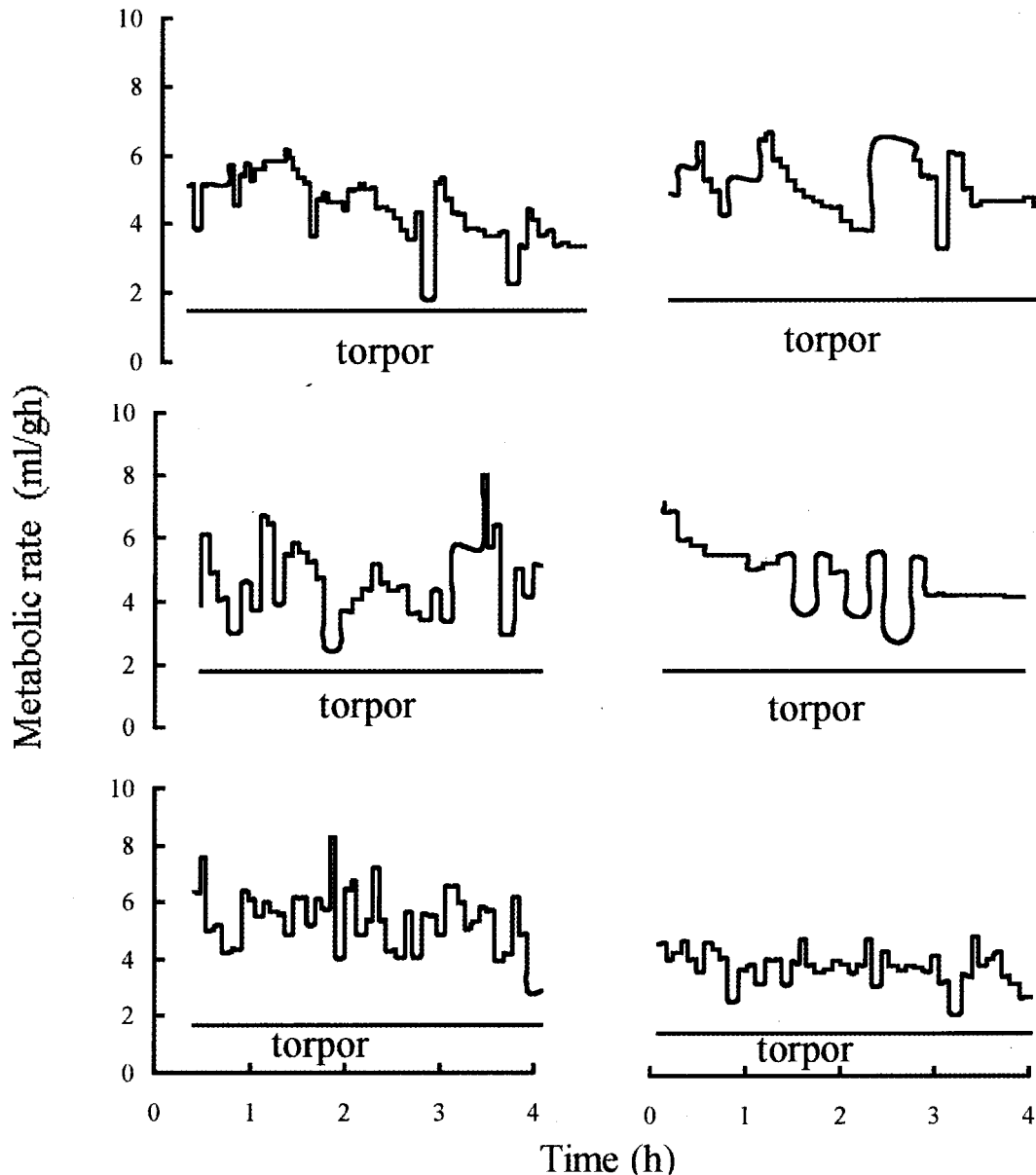


Fig. 2. Relationship between metabolic rate and time at 15°C in *Akodon azarae*. The line shows the limit of euthermy.

Relación entre tasa metabólica y tiempo de exposición a 15°C en *Akodon azarae*. Las líneas trazadas bajo las curvas representan el gasto energético mínimo para mantener la eutermya.

TABLE 2

Energetic parameters in *Akodon azarae*. Data are expressed as mean \pm SD. BMR: basal metabolic rate (ml/gh); ADMR: activity daily metabolic rate (ml/gh); T_b : body temperature ($^{\circ}$ C); C_{min} : minimal thermal conductance (ml/gh $^{\circ}$ C); DTm: thermoregulatory capacity ($^{\circ}$ C). Expected by Kleiber (1961)*. Expected by Hayssen and Lasey (1985)**

Parámetros de la energética de *Akodon azarae*. Los datos son expresados como el promedio \pm DE. BMR: tasa metabólica basal (ml/gh); ADMR: tasa metabólica de actividad diaria (ml/gh); T_b : temperatura corporal ($^{\circ}$ C); C_{min} : conductancia térmica (ml/gh $^{\circ}$ C); DTm: capacidad termorregulatoria ($^{\circ}$ C). Esperado según Kleiber (1961)*. Esperado según Hayssen and Lasey (1985)**

Parameter	Observed	Expected	Statistics t	n	df	P
BMR	1.72 \pm 0.54 (6)	1.58 \pm 0.12 (6)*	0.62	12	6	> 0.5
		1.91 \pm 0.22 (6)**	0.77	12	7	> 0.4
ADMR	4.04 \pm 1.16 (23)	—	—	—	—	—
T_b	36.14 \pm 1.47 (8)	—	—	—	—	—
C_{min}	0.14 \pm 0.09 (48)	0.20 \pm 0.03	5.41	49	47	< 0.001
DTm	12.29	9.01	—	—	—	—

DISCUSSION

The inadequacy of W alone to account for the variation in standard energetic led some biologists to examine the effect of both, environment and food habits on mammalian energy expenditure (McNab 1992). The type of diet is crucial since it places limitations on the net amount of energy that can be assimilated and therefore affects metabolic rate. *Akodon azarae* is an omnivore rodent eating different parts of plants and including insects in its diet (Bilenca 1993). Then, the value of BMR found for *A. azarae* was according either, to the expectation of the Kleiber relation and, to the expectation of the Hayssen & Lacy (1985) relation for murid rodents.

Males and females of *A. azarae*, had the same BMR. According to Heusner (1982) similarity in oxygen consumption between males and females would imply similarity in body composition. This prediction is in agreement with the fact that both, males and females of *A. azarae* have the same body composition (del Valle personal communication).

Furthermore, in the same sense, similarities in ADMR for males and females of *Akodon azarae* in non-reproductive condition could imply similar selection pressures on the amount of energy allocated to behavioral activities. In accordance, Bilenca (1993) has reported that males and females of *A. azarae* do not have differences in habitat use. Activity daily metabolic rate in *A. azarae* was 235 % higher than BMR, suggesting that the cost of locomotion is as expensive as the

reproductive cost of lactation which, as stated by Sikes (1995), could be 66 to more than 200 % over non reproductive requirements.

Akodon azarae is a good thermoregulator. As microtine rodents (Hart 1971), its thermoregulatory capacity was higher than the expected. Moreover, it has a lower than expected minimal thermal conductance and in consequence, its differential in body temperature did not show differences with changes in ambient temperature. As it was found a high mortality in traps at low field temperatures, torpor was evaluated in periods shorter than 24 h. We found that this species did not evidence torpor states, as happen with other Southamerican species such as *Calomys musculinus*, *Eligmodontia typus*, *C. venustus*, and *Phyllotis darwini rupestris* (Bozinovic & Rosenmann 1988a, b, Caviedes-Vidal et al. 1990, Bozinovic & Marquet 1991). In spite of the short time that individuals were exposed to cold temperatures, our results are consistent with both, the high thermal insulation observed and with a BMR not lower than the expected for an euthermic mammal. The high field mortality found in traps, could be due to the impossibility to support in winter, a high cost of termoregulation for long times at low temperatures with limited food resource. Thus, Bozinovic & Rosenman (1988b) predictions, about the possible existence of torpor in *Akodon azarae* are not supported by our data.

Burrow construction (Hodara et al. 1997) and temporal selectivity in habitat use (Antinuchi 1996) in *A. azarae* has been discussed as a

mechanism that allow the avoidance of extreme low ambient temperatures. Although this behaviour would contribute to diminish the quantity of energy assigned to thermoregulation, it may also be important in minimizing the risk of predation. On the other hand observed decreasing field activity of *A. azarae* during warm hours during summer (Bilenca 1993) could be attributed mainly to thermal characteristics of this species. The avoidance of high T_a in the field was in accordance with the fact that, MR responses to ambient temperatures above TNZ was abrupt and reached its highest value at 40 °C. *A. azarae* is the most numerically important species from pampas grassland and the above mentioned adaptations would contribute to the success of this species.

Further studies on energetic of the reproduction, thermoregulatory acquisition, and metabolism in the development of newborn of *A. azarae* will allow a better understanding of the relationship among energetics, life history traits, and behavior in this species.

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LITERATURE CITED

- ANTINUCHI CD (1996) Balance hidrosalino y metabolismo energético de *Akodon azarae*. Tesis doctoral, Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Mar del Plata, Mar del Plata. 118 pp.
- BILENCA DN (1993) Caracterización de los nichos ecológicos y organización de las comunidades de roedores cricétidos en la región pampeana. Tesis doctoral, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Buenos Aires. 183 pp.
- BONAVENTURA SM, FO KRAVETZ & OV SUAREZ (1992) The relationship between food availability, space use and territoriality in *Akodon azarae* (Rodentia, cricetidae). *Mammalia* 56: 407-416.
- BOZINOVIC F & M ROSENMAN (1988a) Daily torpor in *Calomys musculus*, a South American rodent. *Journal of Mammalogy* 69: 150-152.
- BOZINOVIC F & M ROSENMAN (1988b) Comparative energetics of South American cricetid rodents. *Comparative Biochemistry and Physiology A* 91: 195-202.
- BOZINOVIC F & LC CONTRERAS (1990) Basal rate of metabolism and temperature regulation of two desert herbivorous octodontid rodents: *Octomys mimax* and *Tympanoctomys barrerae*. *Oecologia* 84: 567-570.
- BOZINOVIC F & PA MARQUET (1991) Energetics and torpor in the Atacama desert-dwelling rodent *Phyllotis darwini rupestris*. *Journal of Mammalogy* 72: 734-738.
- CABRERA AL & A WILLINK (1973) Biogeografía de América latina. Monografía N°13. OEA, Washington. 122 pp.
- CAVIEDES-VIDAL E, F BOZINOVIC & M ROSENMAN (1987) Thermal freedom of *Graomys griseoflavus* in a seasonal environment. *Comparative Biochemistry and Physiology A* 87: 257-259.
- CAVIEDES-VIDAL E, E CAVIEDES-CODELIA, V ROIG & R DOÑA (1990) Facultative torpor in the South American Rodent *Calomys venustus* (Rodentia: Cricetidae). *Journal of Mammalogy* 71: 72-75.
- CONTRERAS LC (1989) Ecofisiología de mamíferos chilenos. Mimio. Universidad de La Serena, Chile. 20 pp.
- DALBY PL & AG HEATH (1976) Oxygen consumption and body temperature of the Argentine field mouse, *Akodon azarae*, in relation to ambient temperature. *Journal of Thermal Biology* 1: 177-179.
- FRENCH AR (1992) Mammalian Dormancy. In: Tomasi TE & TH Horton (eds) *Mammalian Energetics*: 105-121. Comstock Publishing associates, Ithaca and London.
- GORECKI A (1975) Respirometry. 10. C. Kalabukhov-Skvortsov respirometer and resting metabolic rate measurement. In: Grodzinski W, RZ Klekowski & A Duncan (eds) *Methods for Ecological Bioenergetic*. IBP Handbook 24: 309-313. Blackwell Sci., Oxford.
- HART JS (1971) Rodents. In: Whittow GC (ed) *Comparative physiology*. *Mammals*: Vol II, 1-149. Academic Press, New York.
- HAYSEN V & RC LACY (1985) Basal metabolic rates in mammals: taxonomic differences in the allometry of BMR and body mass. *Comparative Biochemistry and Physiology A* 81: 741-754.
- HEUSNER AA (1982) Energy metabolism and body size. II Dimensional analysis and energetic non-similarity. *Respiration Physiology* 48: 13-25.
- HODARA K, OV SUAREZ & FO KRAVETZ (1997) Nestling and digging behaviour in two rodent species (*Akodon azarae* and *Calomys laucha*) under laboratory and field conditions. *Zeitschrift für Säugetierkunde* 62: 13-19.
- HUDSON JW (1973) Torpidity in mammals. In: Whittow GC (ed) *Comparative physiology of thermoregulation*: 97-165. Academic Press, New York.
- KLEIBER M (1961) *The fire of life*. Wiley, New York. 454 pp.
- MCNAB BK (1974) The energetics of endotherms. *The Ohio Journal of Science* 74: 370-380.
- MCNAB BK (1983) Energetics, body size, and the limits to endothermy. *Journal of Zoology* 199: 1-29.
- MCNAB BK (1986) The influence of food habits on the energetics of mammals. *Ecological Monograph* 56: 1-19.
- MCNAB BK (1988) Complications inherent in scaling the basal rate of metabolism in mammals. *The Quarterly Review of Biology* 63: 25-54.

- MCNAB BK (1992) Energy expenditure: a short history. In: Tomasi TE & TH Horton (eds) Mammalian Energetics: 1-15. Comstock Publishing Associates, Ithaca and London.
- NICKERSON DM, DM FACEY & GD GROSSMAN (1989) Estimating physiological thresholds with continuous two-phase regression. *Physiological Zoology* 62: 866-887.
- MORRISON PR & FA RAYSER (1951) Temperature and metabolism in some Wisconsin mammals. *Federation Proceedings* 10: 93-94.
- REDFORD KH & JF EISENBERG (1992) Mammals of neotropics. The south cone. The University of Chicago Press, Chicago. 430 pp.
- SIKES RS (1995) Costs of lactation and optimal litter size in northern grasshopper mice (*Onychomys leucogaster*). *Journal of Mammalogy* 76: 348-357.