

Modulating factors of the energetic effectiveness of huddling in small mammals

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Huddling is effective in decreasing metabolic rate permitting energy saving. However, this decrease varies among different species depending on physical, physiological and behavioral characteristics of the huddled individuals. Following a general model we analyzed the effects of ambient temperature, thermal conductance and ontogeny on the huddling effectiveness (energy saving level from huddling behaviour) in white mice *Mus musculus*. Also, we studied the effects of thermal conductance by using the Sigmodontine *Abrothrix andinus* as a model organism. To put our results in a general context we analyzed literature data of huddling of several species of rodents at different temperatures. No effects of temperature and thermal conductance was detected. However, based on literature data, we found that at temperatures lower or near thermoneutrality the huddling effectiveness decrease. Also, the huddling effectiveness depends on the stage of development. Temperature probably affects the intensity of huddling, while changes in huddling effectiveness at early stages of development are likely consequences of structural (morphological) changes during the ontogeny. In this sense, it appears that the capacity to change the body form is an individual structural constraint which is extended to the huddling group.

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Introduction

Crowding of small rodents may be a result of predation pressures and temporal changes in availability of food and space (Alexander 1974, Wittemberg 1981). However, these conditions are not sufficient to explain all grouping situations because additional physical aspects of the environment such as temperature and

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humidity within the nest need to be considered (Madison 1984, Hayes *et al.* 1992). For example, huddling is an important response to low ambient temperatures (Sealander 1952, Springer *et al.* 1981, Madison 1984, West and Dublin 1984, Yahav and Buffenstein 1991). It is effective in decreasing the metabolic rate and maintenance cost, hence it increases energy savings allowing resources (= energy) allocation to productive events as somatic growth and reproduction (Trojan and Wojciechowska 1968, Tertilt 1972, Vogt and Lynch 1982, Karasov 1983, Andrews and Belknap 1986, Bozinovic *et al.* 1988).

Recently, we proposed a general model to explain the decrease of metabolic rate during huddling, as a function of the number of grouped animals (Canals *et al.* 1989, Canals *et al.* 1997). This decrease was represented by the expression:

$$R_m = f(n) [(\phi/n + (1 - \phi))^{0.735}] \quad [1]$$

where R_m is the relationship between the mass-specific metabolic rate of grouped and separated individuals and n the number of individuals, being ϕ a parameter obtained from the exposed surface lost during huddling, which regulates the decrease slope of R_m (high values of ϕ indicate a high slope). This parameter was called deformation coefficient because it represents twice the average surface lost by the huddled individuals and determines the effectiveness of animals in reducing the metabolic rate of the group from huddling (H_E – huddling effectiveness) (Canals *et al.* 1997). The $f(n)$ parameter is affected by the number of grouped individuals (n) and by the temperature gradient between body (T_b) and ambient (T_a), that is $(T_b - T_a)$. In this parameter we include the positive and negative effects on the metabolic rate caused by crowding of n individuals, and possible T_b modifications when n individuals are grouped. Thus, in our model $f(n)$ represents the behavioral and physiological changes during huddling, whilst $[(\phi/n + (1 - \phi))^{0.735}]$ represents the physical and structural changes during the same behaviour.

Based on model 1 it is possible to calculate the theoretical minimum value of R_m . That is, when $n \rightarrow \infty$ then $R_m = M_m = (1 - \phi)^{0.735}$. Empirically we found that a practical approach to M_m is obtained when $n = 5$ in equation 1. It follows that it is possible to compute the maximum energy saving by huddling behavior or huddling effectiveness (H_E), being theoretical ($n \rightarrow \infty$) or empirical ($n = 5$) with the following relationship (Canals *et al.* 1997):

$$H_E = 1 - M_m \quad [2]$$

If the deformation coefficient (ϕ) is related to organismic traits such as the intensity by which the individuals huddle, and to the individual capacity to change form and shape (Webb *et al.* 1990), then the ontogeny (developmental stage) and other factors as ambient temperature and thermal conductance of individuals may also affect directly or indirectly this parameter and in consequence the huddling effectiveness. Thus, the study of the effects of each of these factors in reducing heat loss by the huddling group is the main purpose of the present communication.

It has been shown that the energetic benefits of huddling decrease at high temperatures (Górecki 1968, Gębczyńska and Gębczyński 1971, Contreras 1984).

These effects may be reflected by changes in huddling effectiveness. Regarding ontogeny, many young mammals huddle together or cuddle close to their parents (Hull 1973). This fact may affect the area lost when the individuals are huddled, and in consequence the huddling effectiveness. It is well known that thermal conductance in small individuals is higher than in larger ones (Morrison and Ryser 1951, Bozinovic and Rosenmann 1988), but the effects of thermal conductance changes on the metabolic decrease during huddling are unknown. Animals with low thermal conductance (higher isolation) could huddle together weakly, putting a small surface in contact with other individuals.

Assuming that the huddling behavior is an important adaptive feature, we expected that the effectiveness of huddling may be inversely related to the stage of development, to the animal's thermal conductance and also to the ambient temperature.

Methods

Metabolic rate in two rodents was estimated by measuring oxygen consumption. Each measurement was conducted during 2–8 h at different temperatures (T_a) and in several specific groups, formed with different number of grouped individuals. First, the metabolic rate of single individuals was measured separately, and later in groups of 2 to 7 individuals. The groups were performed with subsets of the sample of each species in a way that the individuals of different groups of the same number, were different. Ambient temperature was the same for a given group during all the period. To avoid hypothermia, we recorded oxygen consumption during two hours for the experiments of thermal conductance and ontogeny in early stages of development. The metabolic rate was measured using a modified closed circuit automatic system, based on the manometric design of Morrison (1951), considering a minimum steady state value.

The effect of varying thermal conductance (C) was studied in the Sigmodontine *Abrothrix andinus* (Philippi, 1858), ($m_b = 34.6 \pm 3.5$ g, $n = 11$) and in white (albino) mice, strain CF1 (*Mus musculus* Linné, 1758), ($m_b = 24.7 \pm 5.0$ g, $n = 29$) at 12.5 and 15°C respectively, by measuring MR_h (metabolic rate of the huddled group) under normal conditions and by changing their thermal insulation using two different methods: (a) application of sunflowerseed oil on the fur of *A. andinus* and, (b) exposing white mice to an He–O₂ (80–20%) atmosphere, which is four times more conductive than normal air (Rosenmann and Morrison 1974). The effect of developmental stage was analyzed in white mice by measuring metabolic rates at 20°C in adults (59 weeks, $m_b = 24.7 \pm 5.0$ g, $n = 29$), subadults (7 weeks, $m_b = 22.5 \pm 3.0$ g, $n = 12$) and juveniles (21 days, $m_b = 11.34 \pm 0.6$ g, $n = 12$). The adults were the same individuals used in thermal conductance experiments, but the metabolic measures were performed formerly. The individuals of the groups juveniles and subadults were the same, followed from the weaning.

The effect of ambient temperature was studied indirectly in two ways: (1) comparing our results of *M. musculus* at 15 and 20°C, both temperatures at least 5°C below the thermoneutral zone (Hull 1973); and (2) analyzing, at the light of our model, reported data for several species of small mammals at different temperatures.

The relationship of the metabolic rate between huddling and nonhuddling individuals (metabolic ratio – R_m) was estimated with $R_m = MR_h/MR_1$, where MR_h is the mass-specific metabolic rate of the group and MR_1 is the average mass-specific metabolic rate of the individuals measured separately (thus, R_m is equivalent to the coefficient of metabolic decrease, *sensu* Grodziński *et al.* 1977). We note

that if the huddling behavior is ineffective in energy saving then $R_m = 1$. Also, given that R_1 is an average metabolic rate, some of the single animals (groups of one) are below, equal or above the unity.

In all situations the statistical treatments was regression analyses between R_m and the number of grouped individuals following the model of equation [1], considering $f(n) = 1$ and replacing $(1 - \phi)$ by a free parameter k , that is:

$$R_m = [(\phi/n + k)]^{0.735} \quad [3]$$

In this statistical treatment it is necessary to note three facts: (a) If we consider $Y = R_m^{(1/0.735)}$ and $X = 1/n$, the analysis becomes a simple linear regression; (b) when adjusting the model with equation [3] ($f(n) = 1$), it represents the decrease of R_m with an increasing number of huddled individuals gave by physical and morpho-structural changes of individuals, and its R^2 represents the variability explained by these factors. The non explained variability (around the model) is given by factors that affect $f(n)$ (physiological and behavioral factors) and to stochastic factors; and (c) since k is calculated as a free parameter $k = Y - \phi X$, there is no statistical reason so that k must be similar to $(1 - \phi)$, as predicts our model (equation 1). Then, a good approach of this parameter (k) to the value of $(1 - \phi)$ appears as a test of a right running of the model.

To test the homogeneity of ϕ (slope in the linear model Y vs X) in the different experimental conditions, a Student t -test for comparisons of slopes were performed. If the treatments were more than two, covariance analysis (ANCOVA) and Tukey's multiple comparisons were used (Zar 1996). When untreated data were not available (literature information), the Friedman test for two way classification was used (Siegel and Castellan 1988). By using Friedman test we analyzed the homogeneity of the response variable (R_m) to several treatments (T_a) and blocks (n).

Results

Thermal conductance

The decrease in R_m of *A. andinus* at 12.5°C with and without vegetable oil on the fur is shown in Tables 1 and 2. No significant differences were found between the ϕ values ($t = 1.05$, $p > 0.05$). The application of oil on the fur of the animals produced a mean increase of 47.3% in metabolic rate, which is equivalent to an increase of similar magnitude in thermal conductance, at constant body temperature. In *M. musculus* at 15°C exposed to normal conditions and also to a He-O₂ atmosphere, ϕ values were not statistically different ($t = 0.18$, $p > 0.05$), in spite of a mean increase of 36.8% in thermal conductance caused by the atmospheric change in conductivity (Tables 1 and 2).

Ontogeny

The effects of the developmental stage on the decrease of R_m are shown in Fig. 1. The ANCOVA (Table 3) revealed statistical differences among ϕ values of the different developmental stages ($F = 4.70$, $p < 0.05$). Multiple comparisons showed that these differences are sustained primarily by the difference between adults and juveniles ($p < 0.05$) and secondarily by the difference between subadults and juveniles ($p = 0.06$). Adults and subadults did not show statistical differences in ϕ . It is interesting to note that in spite of the juveniles and subadults were the same individuals followed from weaning, the later showed a deformation coefficient similar to the adults.

Table 1. Decrease of the mass-specific metabolic rate (MR: mlO₂/gh) and metabolic ratio (Rm) with an increasing number of grouped individuals (*n*) with different thermal conductances elicited by oil in *Abrothrix andinus* and He-O₂ in *Mus musculus* (see text). SD is the standard deviation of Rm, the number in brackets are the number of independent replicates of each group, and Rme is the expected value of Rm from the fitted model (equation 3).

<i>n</i>	MR	Rm	SD	Rme	<i>n</i>	MR	Rm	SD	Rme
<i>Abrothrix andinus</i> (12.5°C)									
Normal fur					Oiled fur				
1(3)	3.68	1.00	0.19	1.00	1(4)	4.84	1.00	0.04	1.00
2(1)	2.76	0.75	–	0.78	2(2)	4.30	0.89	0.01	0.84
3(3)	2.55	0.68	0.19	0.70	3(3)	3.58	0.74	0.03	0.79
4(1)	2.32	0.63	–	0.66	4(2)	3.49	0.73	0.01	0.76
5(2)	2.40	0.66	0.05	0.63	5(2)	3.90	0.81	0.01	0.74
<i>Mus musculus</i> (15.0°C)									
Air					He-O ₂				
1(5)	5.83	1.00	0.14	1.01	1(5)	8.40	1.00	0.20	1.02
2(2)	5.10	0.87	0.02	0.79	2(2)	6.80	0.81	0.05	0.77
3(1)	4.41	0.77	–	0.72	3(1)	5.32	0.63	–	0.68
5(2)	3.80	0.65	0.18	0.65	5(1)	5.22	0.62	–	0.61
7(2)	3.20	0.55	0.03	0.62	7(1)	4.76	0.57	–	0.58

Table 2. Parameters and regression analysis of the curve: $Rm = [\phi/n + k]^{0.735}$ in huddling *Abrothrix andinus* and *Mus musculus* with changes in fur properties. T_a – ambient temperature (°C), ϕ – deformation coefficient, SE – standard error of the estimate, k – intercept, and R² – determination coefficient.

	T _a	ϕ	SE	k	SE	R ² (%)	F	p
<i>Abrothrix andinus</i>								
Oiled fur	12.5	0.58	0.12	0.42	0.07	59	25.1	< 0.01
Normal fur	12.5	0.42	0.06	0.58	0.03	85	56.8	< 0.01
<i>Mus musculus</i>								
Air	15.0	0.58	0.12	0.44	0.08	72	25.4	< 0.01
He-O ₂	15.0	0.62	0.18	0.39	0.13	61	12.0	< 0.01

Temperature

The metabolic ratio (Rm) decreased during huddling with an increasing number of individuals huddled ($R^2 = 0.98$ at 15°C and $R^2 = 0.71$ at 20°C). The deformation coefficient and, in consequence, the huddling effectiveness at 15°C were not different to those obtained at 20°C ($t = 0.34$, $p > 0.05$). The analyses of previous reported data showed only little decreases in huddling effectiveness at temperatures above 20°C (Table 4).

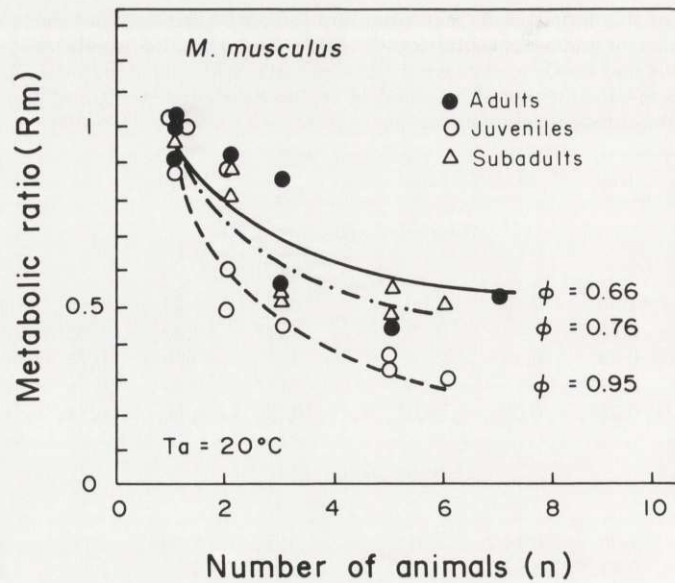


Fig. 1. Decrease of the metabolic ratio (R_m) with an increasing number of grouped individuals (n) in *Mus musculus* at different stages of development. The solid line represents the fitted regression. The deformation coefficient (ϕ) at each age is indicated.

Table 3. Effects of developmental stage on the deformation coefficient (ϕ) and huddling effectiveness (H_E) in *Mus musculus*. M_m is the minimum value of R_m (when $n = 5$, see text) and $H_E = (1 - M_m) \times 100$ - huddling effectiveness (%). SE is the standard error of ϕ and R^2 is the determination coefficient (%). Also the Tukey multiple comparison test is included (equal letters indicates equal groups). * ? when $p = 0.06$.

Group	ϕ	SE	R^2	M_m	H_E	Tukey test
Adults	0.66	0.17	72	0.58	42.4	a
Subadults	0.76	0.11	87	0.50	49.8	a b? *
Juveniles	0.95	0.09	94	0.35	65.0	b

Discussion

Mice did not show differences in their deformation coefficient and huddling effectiveness exposed to changes in ambient temperature. Though the lack of statistical differences in the efficiencies of white mice could be ascribed to statistical β -type error, because this species showed a small change in ϕ , this change occurred in a manner which is contrary to the expected (we would expect an increased effectiveness at lower temperatures). Thus, this small difference is

Table 4. Effect of varying ambient temperature (T_a) in °C on the deformation coefficients (ϕ) and huddling effectiveness (H_E) reported for some rodent species. M_m is the minimum value of R_m (when $n = 5$, see text) and $H_E = (1 - M_m) 100$ - huddling effectiveness. R^2 - determination coefficient in %. ¹ Fedyk (1971), ² Gębczyński (1969), ³ McManus and Singer (1975), ⁴ Whithers and Jarvis (1980), ⁵ This study, ⁶ Canals *et al.* (1989).

T_a	ϕ	R^2	M_m	H_E
<i>Apodemus flavicollis</i> ¹				
5	0.61	85	0.61	38.9
10	0.63	92	0.59	40.6
15	0.64	90	0.59	41.1
20	0.67	96	0.58	43.3
25	0.43	71	0.73	26.6
<i>Clethrionomys glareolus</i> ²				
5	0.57	98	0.65	35.1
10	0.49	98	0.70	30.4
15	0.29	96	0.82	17.7
20	0.47	86	0.71	29.1
30	0.35	41	0.79	21.4
<i>Meriones unguiculatus</i> ³				
5	0.82	90	0.45	54.7
10	0.80	90	0.47	52.9
15	0.79	92	0.48	51.7
20	0.63	98	0.60	40.4
25	0.69	96	0.55	44.7
<i>Heterocephalus glaber</i> ⁴				
15	1.06	79	0.32	68.0
20	0.88	96	0.41	59.1
25	0.72	98	0.53	43.7
30	0.77	94	0.50	50.5
<i>Mus musculus</i> ⁵				
15	0.58	98	0.63	36.7
20	0.66	71	0.58	42.4
<i>Octodon degus</i> ⁶				
0	0.67	99	0.57	43.1
5	0.68	99	0.56	43.9
10	0.66	99	0.58	42.4

probably within the range of variability of the metabolic response to cold. When we considered previous data in the Octodontid rodent *Octodon degus* ($m_b = 198.7 \pm 17.5$ g) at 0, 5 and 10°C (Table 4, Canals *et al.* 1989) we found similar results in deformation coefficient and huddling effectiveness at different T_a 's. In this species ϕ values were 0.67 ($R^2 = 0.99$), 0.68 ($R^2 = 0.99$) and 0.66 ($R^2 = 0.99$) at 0, 5 and 10°C respectively.

Literature data of other four different species show that the huddling effectiveness at several temperatures (fitted to our model) decreases only at high

Table 5. Variability in deformation coefficient (ϕ) and huddling effectiveness (H_E) in several species of rodents. Ambient temperature (T_a) in °C, determination coefficient (R^2) in %, body mass (m_b) in grams, and conductance (C) in $\text{mlO}_2/\text{g h } ^\circ\text{C}$. Values of conductance from: ¹ Bozinovic and Rosenmann (1988), ² C. Veloso (pers. comm), ³ Bradley and Deavers (1980), ⁴ Rosenmann and Morrison (1974), ⁵ Andrews *et al.* (1987). References: a – This study, b – Canals *et al.* (1989), c – Górecki (1968), d – Fedyk (1971), e – Gębczyński (1969), f – Whithers and Jarvis (1980), g – McManus and Singer (1975), h – Grodziński *et al.* (1977), i – Gębczyńska (1970), j – Andrews *et al.* (1987), k – Mark (1975).

Species	T_a	m_b	C	ϕ	R^2	M_m	H_E
<i>Abrothrix andinus</i>	12.5	34.6	0.145 ¹	0.58	58	0.633	36.7a
<i>Abrothrix lanosus</i>	15.0	23.5	0.152 ²	0.58	77	0.636	36.4b
<i>Apodemus agrarius</i>	20.0	21.9	0.240 ³	0.71	98	0.540	46.0c
<i>Apodemus flavicollis</i>	20.0	43.9	0.128 ³	0.68	96	0.561	43.9d
<i>Clethrionomys glareolus</i>	20.0	19.5	0.210 ³	0.47	86	0.708	29.2e
<i>Heterocephalus glaber</i>	20.0	40.2	0.390 ³	0.88	96	0.410	59.0f
<i>Meriones unguiculatus</i>	20.0	45.7	0.150 ³	0.63	98	0.596	40.4g
<i>Microtus arvalis</i>	20.0	20.0	0.190 ³	0.47	81	0.766	23.4h
<i>Microtus oeconomus</i>	20.0	33.0	0.178 ⁴	0.29	98	0.821	17.8i
<i>Microtus townsendii</i>	18.5	–	0.125 ⁵	0.35	96	0.786	21.4j
<i>Mus musculus</i>	20.0	24.7	0.190 ³	0.66	85	0.577	42.3a
<i>Peromyscus leucopus</i>	15.0	22.1	0.199 ³	0.89	98	0.403	59.7k

temperatures (Table 4). Furthermore, we found no statistical differences in the efficiencies of *Apodemus flavicollis*, *Heterocephalus glaber* and *Meriones unguiculatus* when huddling at different temperatures (Friedman test: 3.4, 5.6 and 5.4 respectively, $p > 0.05$). However, comparing ϕ values at extreme T_a 's, a decreasing trend of huddling effectiveness can be seen with increasing temperatures. *Clethrionomys glareolus* presented statistical differences in H_E (Friedman test = 13.84, $p < 0.05$). Nonparametric multiple comparisons indicate that this variation is supported by the different ϕ values between 30 and 5°C and between 30 and 10°C ($p < 0.05$).

These analyses concurrent with our results, lead us to propose that the huddling effectiveness may be independent of temperature if huddling events occur at least 5°C below the lower limit of the thermoneutral zone. This lower critical temperature is 30°C in *C. glareolus*, *A. flavicollis* and *M. unguiculatus* (Robinson 1959, Gębczyński 1969, Fedyk 1971) and 31°C in *H. glaber* (Jarvis 1978). Above this boundary T_a (5°C below the critical temperature), the huddling effectiveness decrease (see also Gębczyński 1969, Gębczyńska and Gębczyński 1971, Contreras 1984).

Probably, near the lower critical temperature, the effectiveness of huddling might be related to the huddling intensity (how closely the individuals huddle themselves). It appears that there is a temperature threshold below which the huddling behavior exhibit its highest intensity. The small variability of the deformation coefficient below this boundary temperature, may be a consequence of a structural constraint such as the capacity of grouped individuals to change form or shape, reflected in the deformation coefficients. The area lost by the

individuals in an effective huddling could be around 35% (the average of $\phi/2$ in Table 4, excluding the values at 30°C).

Reported data of several species (Table 5) show a decrease in metabolic rate that fully adjust to our model. It is particularly demonstrative the case of *Microtus arvalis* from data of Grodziński *et al.* (1977), who worked with groups as large as fifteen individuals. In this species the huddling effectiveness is 23.4% and the expected M_m is 0.766, similar to the asymptotic value 0.71 found empirically by these authors. Furthermore, the huddling effectiveness in the same species, but estimated from an independent set of data (Trojan and Wojciechowska 1968) is consistent with these values: $M_m = 0.827$, $H_E = 17.3\%$. The species of Table 5, including *Cricetidae*, *Muridae* (or *Cricetinae* and *Murinae*, *sensu* Nowak, 1991) and the Bathiergidae *Heterocephalus glaber*, show different huddling effectiveness, ranging between 17.8 to 59.7%. But also they show different thermal conductances and body masses.

In *A. andinus* and *M. musculus*, the huddling effectiveness was constant in spite of changes of up to 47.3% in thermal conductance. When H_E values of the species of Table 5 was confronted with their thermal conductance, we did not find correlation among these variables ($r_S = 0.437$, $p > 0.05$), which is consistent with our results. The reported values of conductance were obtained with different methods and at different temperatures, then the probability of detecting significant correlation between conductance and huddling effectiveness is low, but it is demonstrative to note that *Peromyscus leucopus*, with a thermal conductance of 0.199 ml O₂/g h °C, has a H_E similar to the one of *H. glaber*, which shows a twice as large conductance (0.39 ml O₂/g h °C).

From Table 5 it is also evident a phylogenetic component in the variability of the huddling effectiveness. At inter-generic level, H_E varies from 17.8 to 59.7%, which represents a range $R = 41.7\%$ of variation. In contrast, at intra-generic level, this range is $R = 0.3\%$ in *Abrothrix* (36.4 to 36.7%), $R = 2.1\%$ in *Apodemus* (43.9 to 46.0 %) and $R = 5.6\%$ in *Microtus* (17.8 to 23.4%). Also, this fact reinforces the lack of correlation between the huddling effectiveness and thermal conductance, because the subtraction of the variability of H_E introduced by the phylogenetic component would decrease the correlation coefficient (Felsenstein 1985).

Mus musculus changed their huddling effectiveness in relation to the developmental stage. The juveniles had the greatest effectiveness, followed by the subadults and finally, by the adults. The maximal energetic saving came up to 65% in juveniles white mice, compared with 42% in adults (Table 3).

Analyzing previous data in juveniles (12 days) and adults of the Sigmodontine *Phyllotis darwini* at 5°C (Canals *et al.* 1989), there were not differences in ϕ values of adults of 53 g ($\phi = 0.68$) and those juveniles of 15 g ($\phi = 0.74$), although ϕ was 8% larger in younger animals ($T = 0.593$, $p > 0.05$). Although results obtained in this species did not reach significant levels, they showed a similar pattern. In *M. musculus* the greatest effectiveness were reached at weaning, which takes place at 21 days (Smith and McManus 1975), but in *P. darwini* weaning takes place

earlier. In this regard, 11 g individuals (approximately 10 days old), have been observed weaned. So that 12 days old *P. darwini* used in our experiments, represent a comparatively advanced stage of development that may explain the lack of significant differences in effectiveness with respect to huddling adults.

The differences in huddling effectiveness in white mice during different developmental stages could be ascribed to dissimilar body masses. However, a correlation analysis between body mass and H_E (Table 5) indicates a $r_S = 0.246$, $p > 0.05$. Likewise, according to our results, these variations cannot be attributed to differences in masses. Furthermore, this is other, but indirect evidence that conductance, metabolic rate or mass-specific metabolic rate did not affect ϕ , because these are allometric functions of body mass (Kleiber 1961, Herreid and Kessel 1967).

An alternative explanation may be based on a probable greater intensity of huddling during early stages of development (Webb *et al.* 1990). However, this factor appears to be important only at temperatures near the thermoneutral zone. In our case, specially in the experiments on early stages of development, the ambient temperature fell far to the left of this boundary. Moreover, *M. musculus* presents a narrow thermoneutral zone and displaced toward high temperatures (Hull 1973). In consequence, we propose that differences in huddling effectiveness mainly results from variations in the capacity to change form or shape when huddling at different times along the ontogeny.

In our theoretical model, the variability around the adjusted model is represented by $f(n)$ (see equation 1). Martin *et al.* (1980) suggested that energy saving by huddling may be completely independent of physical contact and rather depend on chemically mediated effects between individuals in sufficiently close proximity that they share an air supply (see Contreras 1984 for an alternative explanation). Hayes *et al.* (1992) suggested that two dominant physical effects interact to produce the observed energy savings: first, the reduced surface area and, second, the effect of the grouped animals on the local microclimate. The latter study concluded that only 50% of observed huddling may be attributed to reduced surface effects.

Given by physical and structural changes, in average, our results explain a $86.05 \pm 17.27\%$ (R^2 of the fitted model) of the variability. From the total of the fitted models, including our results and data from the literature, only in four cases R^2 was lower than 66.67% (see Tables). Previous studies reported a percentage of observed energy saving attributed to the reduced surface effect ranged from 58 to 94% (Canals *et al.* 1997).

In conclusion, only temperatures near the thermoneutral zone and early stages of development, affect the huddling effectiveness of species. Each of the two factors acts in a different way. Temperature probably affects the intensity of huddling, while changes in the effectiveness at early stages of development are likely consequences of structural (morphological) changes during the ontogeny. Finally, when huddling behaviour is presented at its highest intensity, the capacity to alter form or shape is an individual structural constraint which is extended to the huddling group.

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