

Thermal ecology of small animals*

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One of the most representative cases in which the relation individual-environment is evident is the heat exchange between animals and their physical environment. Based on the physical laws regulating heat exchange and on the geometrical relationships between areas and volumes, I show in this articles some strategies for avoiding heat loss used by small animals. The article is organized in four sections. The introduction deals with the laws of radiation, conduction, convection and evaporation, and how they constraint the strategies for avoiding heat loss. Next, how these strategies are related to the larger area of small animals (with regard to their volume). The remaining sections refer to some aspects of the thermal ecology of both exothermic and endothermic animals, based on Chilean examples. Emphasis is placed on the responses to heat exhibited by bugs (exothermic animals), which may select substrate temperatures and use the thermal key for host attraction, and on the huddling behaviour of rodents (endothermic animals) that shows how geometrical constraints may be important for energy saving.

Key terms: endothermy, exothermy, heat exchange, huddling, thermal ecology

INTRODUCTION

Ecology studies the factors affecting the number and distribution of the organisms on time and space. Most of the time, the biotic and non biotic environmental factors affect firstly the physiology or the structure of an individual and then, its physiological and structural characteristics secondarily impose constraints to the behaviour, number and distribution of the organism. This intermediate level, the individual, is recognised by the ecophysiology which studies these aspects. One of the most representative cases in which the relations environment-

individual and individual-distribution or behaviour are evident is the heat exchange between animals and their physical environment (thermal ecology). In this article, based on the physical laws regulating heat exchange and on the geometrical relationship between area and volume, some of the responses to heat of both exothermic and endothermic animals and some strategies for avoiding heat loss are shown.

Animals exchange heat with their environment by four mechanisms: radiation, conduction, convection and evaporation (Kleiber, 1961; Birkebak, 1966; McNab, 1974).

* Manuscript based on a presentation delivered in a Workshop on Physiology and Environment, held during the 13th Annual Meeting of the Chilean Society of Physiological Sciences, Quinamávica, Chile, 5-8 April 1998.

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Radiation refers to processes which transmit energy by means of electromagnetic waves. When we consider thermal radiation, we deal with waves with wavelengths between 10^{-1} and 10^2 μm . The exchange of heat between an animal and its surrounding environment by means of radiation follows Stefan-Boltzmann's law:

$$dQ/dt = A \cdot \sigma \cdot \epsilon (T_b^4 - T_a^4),$$

where dQ/dt is the rate of heat exchange; A , the exposed surface of the organism; σ , the constant of Stefan-Boltzmann; ϵ , the emittance (emissive power in terms of a black body); and T_b and T_a , the body and environmental temperatures, respectively.

Conduction accounts for the flow of heat in a solid, as a result of the transfer of energy from one molecule to an adjacent one, with the net energy exchange proceeding from the higher temperature to the lower temperature region. It follows the Fourier's law:

$$dQ/dt = -(k \cdot A/d) \cdot (T_b - T_a),$$

where k is the thermal conductivity; and d , the thickness of the exchange surface.

Convection deals with the transfer of heat between a fluid and a solid surface which is in contact with the fluid. When the fluid motion is caused only by temperature differences between the surface and the surrounding fluid, the heat exchange is referred to as free or natural convection, but when the motion of the fluid is caused by some external source it is referred to as forced convection. The heat exchange by both natural and forced convection follows Newton's law:

$$dQ/dt = h \cdot A \cdot (T_b - T_a),$$

where h is the heat transfer coefficient, which unlike the thermal conductivity is not solely a property of the solid or the fluid but is dependent on many parameters of the system: speed of the fluid, thermal conductivity, viscosity, density of the fluid and geometry of the solid.

Evaporation plays an important function in the temperature regulation of

animals and plants. In animals, most of the evaporative heat loss occurs in the respiratory system or the skin. It is the product of the mass evaporated (E) times the latent heat of vaporisation (I):

$$dQ/dt = I \cdot E \text{ (McNab, 1970).}$$

Combining the four mechanisms described above, the following equation results:

$$dQ/dt = [\epsilon \cdot \sigma \cdot A \cdot T_a^3 - k \cdot A/d + h \cdot A] \cdot (T_b - T_a) + I \cdot E.$$

Calling "dry thermal conductance" (C') the first part of the right hand of the above equation, we obtain:

$$dQ/dt = C' \cdot (T_b - T_a) + I \cdot E$$

If temperatures are moderate or low, we can write:

$$dQ/dt = C \cdot (T_b - T_a),$$

where C is the "wet thermal conductance". In this simplest form, we can recognise two factors affecting heat exchange between an organism and its surrounding environment: temperature gradient and thermal conductance. Furthermore, thermal conductance includes several environmental parameters, and geometric and structural characteristics of the organism, of which the body area (A) is the most important.

From the later equation, two **strategies to avoid heat loss** are evident: i) without regulation of T_b , maintaining T_b similar to T_a (**exotherms**); and ii) with regulation of T_b , maintaining $T_b > T_a$ (**endotherms**). In the first strategy, the heat loss is minimised, but the metabolism is temperature dependent following Van't Hoff's law:

$$MR_2 = MR_1 \cdot Q_{10}^{0.1 \cdot (T_2 - T_1)},$$

where MR_1 and MR_2 represent the metabolic rates at temperatures T_1 and T_2 , respectively; and Q_{10} is the change in metabolism when the temperature varies 10°C (Schmidt-Nielsen, 1987). On the other hand, in the second strategy, the heat

loss must be compensated for by a high heat production ($MR = dQ/dt$).

THE BODY AREA PROBLEM

Considering the known dimensional relations among length, area and volume, we can write:

$$\begin{aligned} A &\propto V^{2/3}, \\ \text{or: } A/V &\propto V^{-1/3}, \end{aligned}$$

where A is the body area; and V , the volume of the body (body size or body mass, with a density ≈ 1).

In consequence of the above, small animals have a larger area, related to their volume, than large animals and also, they are labile to heat loss. In the endothermic animals, which compensate the heat loss with heat production, the mass-specific metabolic rate and, in consequence, several other physiological parameters (*e.g.*, respiratory frequency, heart rate, *etc*) increase with a decreasing body size. For example, *Sorex cinereus* (*Insectivora*, *Soricidae*), a small shrew of about 3 g, has a metabolic rate about 100 times the metabolic rate per body mass of an elephant of 3000 kg (Schmidt-Nielsen, 1987). This shrew has a heart rate of over 600 beats per minute, while the elephant has one of 25 beats per minute (Morrison *et al*, 1959).

The area problem in endothermic animals was considered by Rubner (1883) in his known surface law:

$$MR \propto W^{2/3}$$

(Günther & Vargas, 1996), but now we know that for a wide range of body size (from unicellular to pluricellular), including endothermic and exothermic animals, the metabolic rate of organisms scales to an exponent $3/4$ (Schmidt-Nielsen, 1987; West *et al*, 1997). Current hypotheses, such as resistance to elastic buckling in terrestrial organisms (McMahon, 1973) or diffusion of materials across hydrodynamic boundary layers in aquatic organisms, cannot explain why

many biological processes scale to this exponent (Günther *et al*, 1992; Günther & Morgado, 1996; Günther & Vargas, 1996; West *et al*, 1997). Recently, some reports suggest that this exponent is related to the fractal geometry of the anatomical structures responsible for the exchange of oxygen and nutrients (Sernetz *et al*, 1985; West *et al*, 1997). The latter authors propose a quantitative model that explains the origin of quarter-power scaling based on three unifying assumptions: i) a space filling fractal-like branching pattern of the network which supplies the entire volume of an organism, ii) a size invariant unit of the final branch of the network, and iii) a minimum of energy required to distribute the resources.

EXOTHERMIC ANIMALS

The exothermic animals maintain a body temperature (T_b) similar to the environmental temperature (T_a). Also their metabolic rate is a function of T_a . For example, *Phylodrias chamissonis*, a Chilean snake, increases its metabolic rate nearly 500% with an increasing temperature from 15 to 30°C (Bozinovic & Rosenmann, 1988a). However, these animals are able to maintain their body temperature nearly to a constant value. *Phylodrias chamissonis* maintained its body temperature around 29 ± 1.4 °C, when exposed to a thermal gradient of 15 to 75°C (Bozinovic & Rosenmann, 1988). In this sense, exothermic animals are not necessarily poikilotherms. They are able to regulate their body temperatures behaviourally, changing: i) their form, as in some hibernating lizards, which roll themselves, reducing their exposed area to the environment; ii) their posture, as in lizards which extend their legs separating their bodies from the hot stones, avoiding heating by conduction and permitting free convection; and iii) their position, as in lizards which change their positions in a wall, exposing their bodies to the sun in the morning and the evening, permitting the heating, but avoiding the sun rays in the midday. Also, all exothermic animals are

able to find micro-environments of adequate temperature for their physiological requirements (see Porter & Tracy, 1983).

The bugs *Triatoma infestans* and *Mepraia spinolai* (Hemiptera, Reduviidae) are good examples of the relation between exothermic animals and heat. The environmental temperature affects the fecundity and the maturity rate of the individuals (Table I). *Mepraia spinolai* is able to reproduce only when temperature is over 20°C. Also, when the temperature is low, it stops its development in IV- or V-intars nymphs (Ehrenfeld *et al.*, 1998). *Triatoma infestans* shows a similar pattern (Jörg, 1960, 1989).

The dispersion of *T. infestans* is also affected by temperature. When the environmental temperature increases over 25°C, the proportion of individuals which begin to flight also increases (Lehane *et al.*, 1992).

In spite of this vulnerability to the heat, both *T. infestans*, a diurnal species, and *M. spinolai*, a nocturnal one, are able to select substrate temperatures. When they are exposed to a thermal gradient of 16 to 50 °C, both species have cycles of preferred temperatures, showing a preference for higher temperatures between 16 to 20 hours for *M. spinolai* and from 16 to 4 hours for *T. infestans* (Table II) (Canals *et al.*, 1997b). Both species are strictly hematophagous.

Table I

Some demographic parameters of the bugs *Triatoma infestans* and *Mepraia spinolai* under different temperatures.

Species	Temperature	Stage	Reproduction
<i>Mepraia spinolai</i>	28°C	Adults (12.4 mo)	+
		Adults (9.5 mo)	+
	20°C	V instar (8.8 mo)	-
		IV instar (10.5 mo)	-
<i>Triatoma infestans</i>	28°C	Adults (100%)	+
	18.5°C	Adults (60%)	+
	10°C	Adults (30%)	-

Individuals of the species *M. spinolai* were followed during 16 months (Ehrenfeld *et al.*, 1998). Time at which developmental stages was reached is shown within parentheses. Individuals of *T. infestans* were followed during 12 months (Jörg, 1960, 1989). Proportion of adults within parentheses.

Table II

Temperature preferred by *Mepraia spinolai* and *Triatoma infestans* in a thermal gradient of 16 to 50 °C during the photophase (p) and the scotophase (s) (Canals *et al.*, 1997b).

Hour	Phase	<i>M. spinolai</i>	<i>T. infestans</i>
6 - 8	p	23.9	23.1
8 - 10	p	23.5	23.0
10 - 12	p	23.4	22.0
12 - 14	p	25.2	21.2
14 - 16	p	26.0	23.7
16 - 18	p	26.3	23.4
18 - 20	p	27.3	23.9
20 - 22	s	26.7	24.7
22 - 0	s	24.9	25.8
0 - 2	s	24.2	23.8
2 - 4	s	23.3	24.5
4 - 6	s	23.0	23.8

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and they use the thermal key for the orientation and attraction by their potential hosts (Lazzari & Nuñez, 1989; Canals *et al*, 1998b). This is also true for other species of triatomines, as *Rhodnius prolixus* (Nicolle & Mathis, 1941; Friend & Smith, 1971; Fujita & Kloetzel, 1976), which would be able to perceive thermal gradients by convection currents (Wigglesworth & Gillet, 1934a,b). Lazzari and Nuñez (1989) found that *T. infestans* can also perceive radiant heat with intensities of $4.2 \cdot 10^{-6}$ Watt/cm², which represents an increase of 0.004°C of the temperature of the receptor. The thermal receptors would be located in the sensilas coeloconicas distributed along the body, and in two fossae located in the antennae (Lazzari & Nuñez, 1989).

ENDOTHERMIC ANIMALS

When endothermic animals are exposed to cold, they present social and individual strategies to avoid cooling (Table III), associated to structural and physiological changes. The simple change, from a mammalian to an spherical form, decreases the exposed area nearly in 50% (*i.e.*, changes in the Meeh's constant (*k*) from 10 to 4.84 in $A = k \cdot V^{2/3}$). However, below some critical threshold (the lower limit of the thermoneutral zone), they must compensate the heat loss by increasing its metabolic rate.

Some animals which live in extreme cold weather, hibernate reducing their metabolic rate, heart rate, respiration and many other functions (Schmidt-Nielsen, 1987). Some others can fall in daily torpor (Herreid & Schmidt-Nielsen, 1966; Bozinovic & Rosenmann, 1988). It has been proposed that torpor is a reflect of a primitive physiology of the organisms (Kaiser, 1961); however, in the last two decades, torpor was found to be related to the concurrence of a small body size and a low metabolic rate. A limit line of endothermy proportional to $W^{-2/3}$ (W = body mass) has been proposed (McNab, 1982). A good example of torpor is found in bats, which present facultative torpor when exposed to cold (Schmidt-Nielsen, 1987). *Myotis chiloensis*, a small South American bat, presents two possible responses to cold: i) increasing its metabolic rate, maintaining an homeothermic temperature ($36.6 \pm 2.2^\circ\text{C}$); or ii) decreasing its metabolic rate, maintaining the body temperature similar to the environmental one, about 0.5°C over T_a (Bozinovic *et al*, 1985).

Some of the most interesting reactions to cold are the social responses, such as huddling and nesting.

Huddling is one of the most relevant behavioural adaptations that increases winter survival (Sealander, 1952). It consists in the grouping of individuals close together to keep warm. It is effective in decreasing the metabolic rate per body mass; hence, it increases energy savings

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Table III

Strategies for regulating body temperature of endothermic animals exposed to cold (modified from Guyton, 1987).

Cold	Social	↓ Heat Loss	Huddling Nesting
	Individual	↑ Heat Production	Shivering ↑ Hunger ↑ Activity ↑ Adrenaline & Noradrenaline
		↓ Heat Loss	Vasoconstriction Piloerection Form changes Hibernation and Torpor

allowing resources allocation to somatic growth and reproduction (Canals *et al*, 1997a). The reduced energy expenditure is mainly attributed to the reduced area/volume ratio of the group (Contreras, 1984). This author proposed that the ratio between the exposed surface of huddling / non-huddling individuals (R_a) would follow: $R_a = n^{-1/3}$, with n the number of huddled individuals. He based on the assumption that a group of n individuals of the same volume (V_1) was equivalent to one individual of a volume $V = n \cdot V_1$. This is an auto simile, or fractal idea, of the huddling behaviour, but it presents one problem:

if $n \rightarrow \infty$, then $R_a \rightarrow 0$.

Canals *et al* (1989, 1997a) probed analytically and experimentally that the area ratio of grouped/non-grouped prisms, spheres and deformable bodies follows:

$$R_a = \emptyset \cdot (1/n) + (1-\emptyset),$$

with $\emptyset = 2 a/A$, a deformation coefficient which represents twice the average relative area that is lost by grouped bodies, that is two times the area lost (a) divided by the average area of the body (A). Combining the equation:

$$MR = C \cdot (T_b - T_a)$$

with the allometric relationship:

$$C = 3.4 W^{0.49}$$

(Herreid & Kessel, 1967), Canals *et al* (1997a) found that the metabolic ratio of huddled/non-huddled individuals followed:

$$R_m = f(n) \cdot [\emptyset (1/n) + (1-\emptyset)]^{0.735}.$$

The asymptotic value of R_m is obtained when $n \rightarrow \infty$, that is.

$$M_m = (1-\emptyset)^{0.735},$$

then, the maximum energy saving during huddling or "huddling effectiveness" is:

$$H_e = 1 - M_m.$$

One important consideration in the model is that species with high deformation capacity ($\emptyset$) might have high huddling effectiveness too.

The above model fully adjusts to several species (Canals *et al*, 1997a, 1998a) and it is possible to attribute over 85% of the saving energy to the decreasing surface during huddling. The huddling effectiveness of species from several locations ranged from 17.8 to 59.7%. The huddling effectiveness of Chilean species ranged from 36.8 to 51.5%, which is a significative energy saving (Table IV). The same authors found also that the huddling effectiveness increases when the developmental stage decreases (Table IV; Canals *et al*, 1998a). Furthermore, Bozinovic *et al* (1988) found that the use of nest increases the energy saving during huddling as a consequence of 40% reduction of the conductance of the group.

Both, huddling and nesting are important behavioural responses of small animals to cold, which permit the allocation of the saved energy to growth or reproduction, or to colonise zones of cold weather.

Table IV

Huddling effectiveness (%) of some Chilean small mammals, including rodents, the marsupial *Thylamys elegans*, and adults (a), subadults (sa) and juveniles (j) of mice (Canals *et al*, 1997a, 1998a).

Species	Temperature (°C)	Huddling effectiveness (%)
<i>Abrothrix andinus</i>	12.5	36.8
<i>Abrothrix lanosus</i>	15.0	36.8
<i>Eligmodontia typus</i>	15.0	41.7
<i>Phyllotis darwini</i>	5.0	43.9
<i>Thylamys elegans</i>	12.5	51.5
<i>Mus musculus</i> (a)	20.0	42.4
<i>Mus musculus</i> (sa)	20.0	49.8
<i>Mus musculus</i> (j)	20.0	65.0

I thank Dr
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ACKNOWLEDGEMENTS

I thank Drs Claus Behn and Manuel Oyarzún for inviting me to the workshop "Physiology and environment" of the XIIIth Annual Meeting of the Chilean Society of Physiological Sciences. Also I thank Drs M Rosenmann and A Labra for information on relevant literature, and Dr Francisco Bozinovic for critical comments.

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