Model of Thermal Regulation of Animals Based on Entropy Production Principle

Michael Zakharov[*]

PetPace LTD,

Kibbutz Shefayim, Israel

Michael G. Sadovsky[†]

Institute of Computational Modelling SB RAS,

Akademgorodok, 50/44, Krasnoyarsk, 660036 Russia

A novel model of thermal regulation of homoeothermic animals is implemented.

Keywords: thermoregulation, heat production, skin temperature, entropy production, homoeothermic animals.

Introduction

Physically, any living being is a heat engine consuming fuel (a food) and an oxidizer (oxygen, at most) and producing some mechanical work accompanied with (obvious) production of a heat. In such capacity, we skip plants, mushrooms, etc. so called autotrophic organisms from further consideration.

Keeping the analysis within the animals, we also should discrete them into two basic classes: haematocryal (or poikilothermal) creatures, and homoiothermal creatures. The difference is crucial, from the point of view of excessive, or "junk" heat production. Obviously, the animals from both classes have to produce some heat, as a by-product of the mechanical work to be done. The point is that poikilothermal animals (those from the first class) are considered to be in a thermal equilibrium with the environment, while the homoiothermal ones exhibit good maintenance of the body temperature.

Evidently, any creature producing mechanical work from a fuel oxygenation may not be in absolute temperature equilibrium with the environment; meanwhile, the ratio of V_p to V_h has a figure proximal to $10^{-5} \div 10^{-3}$, where V_p (V_h, respectively) is a "junk" heat production by a poikilothermal animal (by a homoiothermal animal, respectively).

A diversity of living conditions observed worldwide falls beyond any imagination. It seems to be surprising, but it isn't so: there is the most general biological law which forces to inhabit any possible space. In spite of the great biological significance of that law, we shall not discuss it here. Nonetheless, such dense inhabitation poses another problem in modelling of thermal regulation of both poikilothermal and homoiothermal animals: the problem of overheating. Indeed, any living being lives within the clearly determined (for a given specie, of course) range of environmental

[*]trapman.hunt@gmail.com

[†]msad@icm.krasn.ru

conditions, where temperature is one of the most important parameters. Thus, a model of thermal regulation must take into account this problem from both "ends" of the viable temperature range.

From thermodynamic point of view metabolism is a chain of non-equilibrium chemical reactions in which energy is produced and consumed by the body. These reactions generally form a *steady state process* (the process which is not in thermodynamic equilibrium, but has no dependency on time). Steady state is more general than *dynamic equilibrium* because it accepts that some of the processes may be irreversible. If system is in a steady state then some flows and entropy production may be non zero, while certain properties of the system are unchanging in time [20].

This article describes any details of neither metabolism in general, nor particular mechanisms of energy generation by certain chemical reactions or mechanical work of the muscles. These details can be found elsewhere (a good starting point can be [18], or [31]).

The major point is the well known fact that significant part of the generated energy is released in form of *heat* and part of the heat is not used for any purposes inside of the body. Rate (power) of this heat generation is further noted as *excessive heat rate*, or H_{exc}. Density (volumetric) of this heat source is mentioned below as h_{exc}.

This excessive heat should be transferred out of any endothermic animal's body core. The transfer itself should involve minimal extra activity to be at the maximum of efficiency. In other words, excessive heat should be dissipated as passively as possible. The best candidate mechanics is heat convection and diffusion into the ambience through the shell (skin) of the animal.

One of the major flaws of the present models is that they use Newton's cooling to estimate energy balance and/or temperature of an animal. This seems to be incorrect because the system (animal) is not cooling, but actively works against it. Newton's cooling may be proper description of some processes that establish thermal equilibrium, while living system struggles against thermal equilibrium because it is just euphemism of "death" from the life's point of view.

1.   The model

The animal model follows well known "core and shell" description of animal's body [3,29,37]. The model describes heat transfer through the shell (skin) of an animal. The importance of this heat dissipation mechanics is founded by the heat dissipation limit theory introduced in [32]. Other modes of heat dissipation (e.g. dog's panting) are not in the model scope. In other words, the model describes heat dissipation of an animal that performs on near to rest metabolism, and is situated in environment with a temperature that is within thermo neutral zone of the animal.

Major theoretical foundations of heat dissipation by animals can be found in [1,14,41]. The model is not related to the animal as a whole, but rather describes local behaviour of heat transfer and possible mechanisms of heat transfer regulation. Animals body is schematically drawn by Fig. 1.

1.1. Core

Core is the animal's body central compartment, where the heat is generated in metabolic processes. From the proposed model point of view the metabolism is a chain of irreversible, non-equilibrium chemical reactions producing energy that is utilized in the body. These reactions generally form a *steady state process* (the non-equilibrium thermodynamic process having no dependency on time). Steady state is more general than *dynamic equilibrium* since it accepts
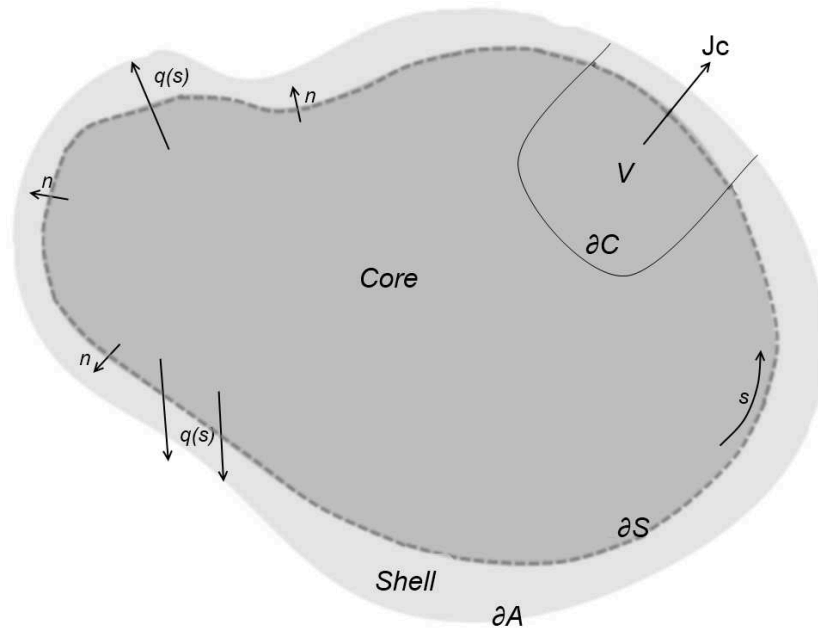
Fig. 1. Core and Shell Model

that some of the processes may be irreversible. If system is in a steady state then some flows and internal entropy production may be non zero, while certain properties of the system do not change in time [18, 20].

This model describe no details of either a metabolism in general, or particular mechanisms of energy generation by certain chemical reactions or mechanical work of the muscles. These details can be found elsewhere (a good starting point can be [18], or [31]).

The major point of the core functionality model is the well known fact that significant part of the generated energy is released in form of *heat* and part of the heat is not used for any purposes inside of the body. Rate (power) of this heat generation is further noted as *excessive heat rate*, or H_{exc}. Density (volumetric) of this heat source is mentioned below as h_{exc}. It is important that H_{exc} is produced by *irreversible process*, i. e. in metabolism.

1.1.1. Assumptions

The model does not concern about internal functionality of the core, but is focused on a heat flow from the core to the ambience instead.

The first assumption is that the *core is big, homogeneous closed system and does not have effective spatial structure*. This assumption allows us to consider the core as a system that is entirely in a steady state, ignore local (internal to the core) flows, mass transfer, and use semi-classical approach for core temperature calculation. This "big system" assumption follows the idea that the core has permanent volume, and does not produce any work: $dU_c = dQ_c - pdV_c = dQ_c$, where dU_c is the differential of internal energy of the core.

Another assumption is that the *core should always* (on the model's time scale) *be in a steady state*. It means that total entropy production of the core $dS_c = dS_c^{\mathrm{ext}} + dS_c^{\mathrm{int}} = 0$, where $dS_c^{\mathrm{int}} \geqslant 0$ due to the Second Law of thermodynamics. Since internal entropy is generated in irreversible

process (metabolism), all excessive heat should be transferred to the core externals (see details in [18]):

$$dS_c = dS_c^{\text{ext}} + dS_c^{\text{int}} = 0 \quad \Rightarrow \quad dS_c^{\text{ext}} = -dS_c^{\text{int}}$$

$$dS_c^{\text{int}} = \frac{dQ_{\text{exc}}}{T_c} \quad \Rightarrow \quad dS_c^{\text{ext}} = -\frac{dQ_{\text{exc}}}{T_c}, \quad \text{or}$$

$$\frac{dS_c^{\text{ext}}}{dt} = -\frac{1}{T_c}\frac{dQ_{\text{exc}}}{dt} = -\frac{1}{T_c}H_{\text{exc}}\,; \tag{1}$$

it means that core internal energy is constant:

$$dU_c = dQ_c - pdV_c = dQ_c = T_c dS_c = 0\,, \tag{2}$$

and the core temperature $T_c = Q_c/C_v$ does not depend on time:

$$\frac{\partial T_c}{\partial t} = \frac{\partial Q_c}{\partial t} = 0\,. \tag{3}$$

Note that full differential dQ is implemented instead of classical "imperfect differential" δQ because the model describes steady states of non-equilibrium processes, as opposite to classical description of thermodynamic equilibrium, see [18, 20] for detailed explanation.

A specific core temperature T_c is one of the properties of a steady state, and may have different figure in another steady state. In the same time, metabolism depends on some enzymes which performance depends (among other things) on temperature, so keeping T_c inside a preferred temperature range, or even constant, is an advantage. These considerations lead us to the following assumptions of the core model:

 – core heat production H_{exc} is constant (h_{exc} is stationary function of coordinates);

 – core temperature T_c is stationary function of coordinates regardless of external parameters.

Basically, these assumptions (or constraints if we speak about thermoregulation) describe simplified thermodynamic of an endothermic animal.

1.1.2. Formalization

Entropy balance equation (1), constant internal energy equation (2), core heat production rate h_{exc}, and stationary distribution of temperature inside of the core (3) can be combined into *continuity equation* that is just another form of the First Law of thermodynamics:

$$\int_{\partial S} \vec{\mathbf{q}}(s) \cdot \vec{\mathbf{n}}(s)\,\mathrm{d}S = \int_{V_{\text{core}}} h_{\text{exc}}(\vec{\mathbf{r}})\,\mathrm{d}\vec{\mathbf{r}}, \tag{4}$$

where ∂S is the core surface, $\vec{\mathbf{q}}(s)$ is heat flow, $\vec{\mathbf{n}}(s)$ is the outward-pointing unit normal to ∂S, s is a parameter that defines coordinate on the surface, V_{core} denotes entire space of the core, h_{exc} is the density of heat generated in core (see above), and $\vec{\mathbf{r}}$ is coordinate inside of the core; Fig. 1 illustrates this scheme.

Equation (4) simply means that *total outgoing heat flow is equal to the total heat generation rate of the core*. One can apply Gauss theorem (divergence theorem) to re-write (4) as

$$\int_{V_{\text{core}}} \nabla \cdot \vec{\mathbf{q}}(\vec{\mathbf{r}})\,\mathrm{d}\vec{\mathbf{r}} = \int_{V_{\text{core}}} h_{\text{exc}}(\vec{\mathbf{r}})\,\mathrm{d}\vec{\mathbf{r}}, \tag{5}$$

and write differential form of continuity equation for stationary distribution of heat in the core:

$$\nabla \cdot \vec{\mathbf{q}} = h_{\text{exc}}(\vec{\mathbf{r}})\,. \tag{6}$$

Equation (6) is written for unit volume (in volumetric quantities). This equation is valid for any sub-volume of the core. Because of this we continue model built-up for an arbitrary volume V that is adjacent to the shell and is separated (conventionally) from the core by surface ∂C as illustrated in Fig. 1.

To have well-defined problem in V, one must define boundary conditions for the equation (6). Since we assume a constancy of the heat generation density rate in core $\left(\dfrac{\partial h_{\mathrm{exc}}}{\partial t} = 0 \right)$, the equation (4) can be written as

$$\int_{\partial S} \vec{\mathbf{q}}(s) \cdot \vec{\mathbf{n}}(s)\, \mathrm{d}S = \mathrm{const}. \tag{7}$$

Note that $\vec{\mathbf{q}}(s)$ may be a function of time on any given part of the surface ∂S, while the whole integral (7) can not. Consider the following example: divide the surface by even number of tiles N, and "assign" heat flow J_{odd} to each odd numbered tile and heat flow $J_{\mathrm{even}} \neq J_{\mathrm{odd}}$ to each even numbered tile. Equation (7) is fully satisfied and looks like

$$\sum_{n=1}^{N/2} (J_{2n-1} + J_{2n}) = \sum_{n=1}^{N/2} J_{\mathrm{odd}} + \sum_{n=1}^{N/2} J_{\mathrm{even}} = J\,; \tag{8}$$

swap J_{odd} and J_{even} on all tiles: set flow J_{odd} to even numbered tiles, and flow J_{even} for odd ones. Total flow as it is defined by (7) becomes

$$\sum_{n=1}^{N/2} (J_{2n-1} + J_{2n}) = \sum_{n=1}^{N/2} J_{\mathrm{even}} + \sum_{n=1}^{N/2} J_{\mathrm{odd}} = J\,. \tag{9}$$

Obviously, it is exactly equal to (8). If we run a recurrent process then every J_n depends on time eventually, while both (8) and (9) are still equal and constant.

We assume that any time dependency in $\vec{\mathbf{q}}(s,t)$ is a very slow function:

$$\vec{\mathbf{q}}(s,dt) = \vec{\mathbf{q}}(s,0) + \sum_{n=1}^{\infty} \frac{dt^n}{n!} \left. \frac{\partial^n}{\partial t^n} \right|_{t=0} \vec{\mathbf{q}}(s,t) = \vec{\mathbf{q}}(s,0) + o(dt) \sim \vec{\mathbf{q}}(s)\,. \tag{10}$$

It means, for example, that local heat flows may significantly change on circadian time scale, or even slower.

With this assumption we can finally formulate the local heat balance equation for the core:

$$\begin{aligned} \nabla \cdot \vec{\mathbf{q}} &= h_{\mathrm{exc}}, \\ \vec{\mathbf{q}} \cdot \vec{\mathbf{n}}\big|_{\partial S} &= J_c\,, \end{aligned} \tag{11}$$

where all quantities are volumetric, $h_{\mathrm{exc}} > 0$, and $J_c \geqslant 0$ by definition and the coordinate system choice.

Note that we have not discussed any properties of the flux $\vec{\mathbf{q}}$ yet, and the problem (11) is a very general form of heat balance representation.

1.1.3. Convection-diffusion equation

The model provides the description of this flux by the means of convection-diffusion equation, or advection-diffusion equation. The different names for the same equation are used depending on nature of the subject: "convection" is correctly used for vector quantities like magnetic field $\vec{\mathbf{B}}$,

and "advection" is correctly used for scalar quantities like heat Q, and the difference can be very important under certain circumstances. Nevertheless, it is not important in our case and we continue to use "convection-diffusion equation" as more familiar term.

The convection-diffusion equation is very well known in many fields of physics and mathematics:

- drift-diffusion equation or the Smoluchowski equation (describes the flow of ions dissolved in a liquid in presence of an electric field, or drift current in semiconductors);
- Fokker-Plank equation (describes the time evolution of the probability density function of the velocity of a particle);
- various applications that describe random motion with diffusivity and velocity (or any bias) field, including financial mathematics (e. g. Black-Scholes equation).

The model stipulates that $\vec{\mathbf{q}}$ is a combination of two types of fluxes: *diffusive flux* due to thermal diffusion, and *advective flux* which is the flux associated with advection of heat by flow of fluid:

$$\vec{\mathbf{q}} = \vec{\mathbf{q}}_{dif} + \vec{\mathbf{q}}_{adv}\,. \tag{12}$$

Diffusion here is a thermal diffusivity process due to temperature gradient between core and shell, and convection exists due to the blood flow inside of the core and from the core to shell.

Blood can work well in advection of heat because the viscosity of blood is $4-5$ times higher than the water (and salt water) viscosity, so the velocity boundary layer exceeds the diffusive boundary layer in greater proportion than of water (i. e. Prandtl number $Pr_{\text{blood}} \sim 30$, while $Pr_{\text{water}} \sim 6$ at the typical core temperature $T_c \sim 38°C$). Prandtl number is defined as:

$$Pr = \frac{c_p \mu}{k}\,, \tag{13}$$

where c_p is specific heat, μ is dynamic viscosity, and k is the thermal conductivity of the fluid. A discussion of exact properties of the blood and blood flow falls beyond the scope of this article and can be found in other researches; see, for example, $[8, 16, 26, 36]$.

Advective flux is proportional to the velocity:

$$\vec{\mathbf{q}}_{adv} = \vec{\mathbf{v}}\,Q\,, \tag{14}$$

where Q is heat, and $\vec{\mathbf{v}}$ is the velocity of the fluid bearing the thermal energy (e. g. blood $[41, 42]$).

Diffusive flux can be approximated by Fourier's law (i. e. the flux is proportional to the local temperature gradient), which is analogous to the Flick's first law $[12]$ well known in biology, where it is used to describe gas flow through the cell membrane, for example):

$$\vec{\mathbf{q}}_{dif} = -D\nabla Q\,, \tag{15}$$

where D is diffusivity and is defined as *thermal diffusivity* $D = \dfrac{k}{\rho c_v}$ for the heat transfer applications $[38]$.

In this definition, k is the *thermal conductivity* (SI unit of $W/(m \cdot K)$), ρ is density, and c_v is *specific heat capacity*. Thermal diffusivity has SI unit of m^2/sec and is the material property. Under these approximations the total flux from the core surface can be presented as:

$$\vec{\mathbf{q}} = -D\nabla Q + \vec{\mathbf{v}}\,Q\,, \tag{16}$$

and the heat balance equation (11) for the flux converts to the equation for the heat Q:

$$
\begin{aligned}
\nabla \cdot (-D\nabla Q + \vec{\mathbf{v}}\, Q) &= h_{\text{exc}}, \\
(-D\nabla Q + \vec{\mathbf{v}}\, Q) \cdot \vec{\mathbf{n}}\,\big|_{\partial S} &= J_c, \\
Q\,\big|_{\partial C} = f(\vec{\mathbf{r}}) &= \text{const},
\end{aligned}
\tag{17}
$$

where the additional boundary condition on the (virtual) surface ∂C has been added to make the problem (now the second order PDE) well-defined.

The boundary condition on ∂C is Dirichlet (or the first type) boundary condition. This type of boundary conditions are necessary here to make the solution unique (see [34]). The surface ∂C can be an arbitrary one with known temperature distribution, or an isothermal surface, as suitable and as conforming the core internal structure (e. g. tissues morphology).

The boundary condition on ∂S is Robin (or the third type) boundary condition. This type of boundary condition for the convection-diffusion equation is a general form of the *impedance boundary condition* (insulating in case of $J_c = 0$). That latter is quite common in thermodynamic problems, especially for the convective heat exchange applications, see [35] for comprehensive introduction.

It should be noticed that the boundary condition on ∂S is natural and has meaning of Neumann (or the second-type) boundary condition, in this model, because it simply defines a heat flow across the boundary. The flow has a convective part demonstrating that ∂S is not rigid and has some permeability.

This boundary position can be estimated using Péclet number Pe. This number is defined as

$$
Pe = \frac{|\vec{\mathbf{v}} \cdot \nabla T|}{|k\nabla^2 T|} = \frac{Lv}{D} = Re \cdot Pr
\tag{18}
$$

for heat transfer applications, where L is a characteristic length, v is a characteristic velocity, D is a thermal diffusivity (as defined above), Re is Reynolds number, Pr is Prandtl number. Péclet number has the meaning of:

$$
Pe = \frac{rate\ of\ advection}{rate\ of\ diffusion}\,.
\tag{19}
$$

According to this definition, we can say that ∂S lays in a region where Péclet number $Pe \sim 1$, or Reynolds number of the blood flow becomes equal to reciprocal of the blood Prandtl number, $Re \sim 1/Pr$. In that region, the diffusive heat flow becomes more important than the advective heat transfer.

Using known blood flow characteristics (numbers are taken from [8] and it's citations) and values of thermal properties of animal tissues from [5], we can roughly classify the model regions according to Péclet number of the blood flow (see Tab. 1, where Prandtl number of the blood $Pr = 30$ is used, see (13)).

Region	Reynolds number Re (by order of magnitude)	Péclet number Pe
Core vascular	$100 - 1000$	$3000 - 30000$
Subcutaneous vascular	$1 - 10$	$30 - 300$
Microvascular	0.001	0.03

Table 1. Péclet numbers

The boundary ∂S lays inside the subcutaneous vascular system, close to the internal boundary of the capillary network, as Fig. 2 shows. In a simple environment where the diffusion coefficient

is constant and the flow is incompressible the equation (17) can be simplified to:

$$
\begin{aligned}
&- D\nabla^2 Q + \vec{\mathbf{v}} \cdot \nabla Q = h_{\text{exc}}, \\
&(-D\nabla Q + \vec{\mathbf{v}} Q) \cdot \vec{\mathbf{n}} \big|_{\partial S} = J_c, \\
&Q \big|_{\partial C} = f(\vec{\mathbf{r}}) = \text{const},
\end{aligned}
\tag{20}
$$

or, using core temperature T_c defined from $Q = \rho c_v T_c$ and assuming that c_v and ρ are both constant:

$$
\begin{aligned}
&- k\nabla^2 T_c + \rho\vec{\mathbf{v}} \cdot c_v \nabla T_c = h_{\text{exc}}, \\
&(-k\nabla T_c + \rho\vec{\mathbf{v}} c_v T_c) \cdot \vec{\mathbf{n}} \big|_{\partial S} = J_c, \\
&T_c \big|_{\partial C} = g(\vec{\mathbf{r}}) = \text{const},
\end{aligned}
\tag{21}
$$

where all the quantities are volumetric, T_c is the core temperature, k $[J/(sec \cdot m \cdot K)]$ is the thermal conductivity, ρ $[kg/m^3]$ is the density, c_v $[J/(kg \cdot K)]$ is the specific heat capacity, and $\vec{\mathbf{v}}$ $[m/sec]$ is the blood flow velocity. All these properties may be determined either by a tissues, or by the blood, because the core tissues are well perfused and it is possible to consider the tissue and vasculature as a whole for the heat transfer models [1, 2].
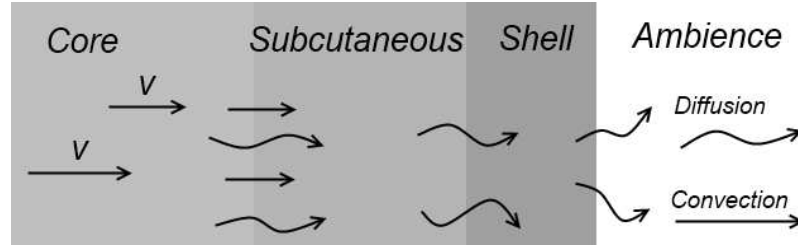

Fig. 2. Illustration of ∂S position

Both J_c and h_{exc} are locally defined and depend on the type and size of the animal (Klieber's law [17, 27]), current activity level of the animal, animal's fit level, etc. Problem (21) can be interpreted as a formalization of the homeostasis property of endothermic animals.

The heat flow J_c to the ambience, metabolic heat production rate h_{exc}, and core temperature T_c define a steady state of the core through equation (21). In this equation h_{exc} is "inhomogeneous right side" of convection equation, and J_c along with T_c are members of boundary conditions.

1.1.4. Core entropy balance estimation

If the core (which can be assumed to be a big system in equilibrium for the illustration purposes) were connected to an ambience (another big system in equilibrium), we could estimate the entropy production in a core and ambience in the following way: the core and ambience heat exchange can be presented as a heat conduction in an isolated system consisting of two parts, where each part is in equilibrium and has well-defined temperature T_c and T_a (assuming $T_c > T_a$, and constant volume). Mass exchange can be neglected since the core is supposed to be a closed system.

This system will maintain a heat flow J_Q that transfers dQ per time dt per unit area from hotter part to the cooler one. Since the volume is constant, the energy changes due to heat flow

only and we can write $dU = dQ$ for each part of the system. The First Law yields $-dQ_c = dQ_a = dQ$, so that the total change of entropy in this system is

$$dS = -\frac{dQ}{T_c} + \frac{dQ}{T_a} = \left(\frac{1}{T_a} - \frac{1}{T_c}\right) dQ\,. \tag{22}$$

Since $T_c > T_a$, one can see that $dS > 0$. This equation can be expressed as $dS = F dX$, where F is *thermodynamic force*, and dX is a *thermodynamic flow* [25]. Finally, we can write expression for the *rate of entropy production* as

$$\dot{S} = \left(\frac{1}{T_a} - \frac{1}{T_c}\right)\frac{dQ}{dt} = \left(\frac{1}{T_a} - \frac{1}{T_c}\right) J_c\,, \tag{23}$$

where $J_c \equiv \dfrac{dQ}{dt}$ is heat flow per unit area from boundary condition of problem (17). Unfortunately, the core is connected to shell and this approach does not work as appropriate. The reason of fault is erroneous assumption of thermodynamic equilibrium in the shell.

1.2. Shell

The model describes a shell as a system confined between two "big" systems: a core and an ambience where both of them have certain temperature (T_c and $T_a < T_c$). There is a heat flow $\vec{\mathbf{J}}_Q(\vec{r}, t)$ through the shell transferring heat from the core to an ambience. The shell is in a steady state most of the time, but sometimes it can pass through some transitive states.

1.2.1. Assumptions

We propose the following assumptions, most of which are basic assumptions of non-equilibrium thermodynamics:
   – all flows are small;
   – variations of flows are small (i. e. gradients and higher order derivatives can be neglected);
   – all thermodynamic forces variations are small;
   – all of the above is true in any part of the shell and is true for the entire shell (i. e. the shell is homogeneous and has "small" thickness).
These assumptions can be combined into just one: the shell conforms to local equilibrium requirements (see details in [18, 20, 25]). We also assume that shell is "passive" and it's metabolism can be neglected (i. e. a shell does not have internal heat sources).

All of the assumptions proposed above seem to be valid and reasonable for the temperature and energy ranges that a living creature may normally meet. The shell is in permanent contact with ambience. The ambience properties may change at any moment in any way that is completely out of one's control. By this reason we *do not assume that shell is in a steady state permanently*. Transient processes are allowed and will be (briefly) evaluated.

The shell moves into transitive state immediately after ambience temperature or some other thermal parameters of the ambience have changed. Life time of transitive state depends on the shell geometry and thermal properties and can be estimated (by order of magnitude) as $\tau_D \sim O(L^2 \frac{\rho c_p}{k})$, where L is the shell thickness and $\frac{\rho c_v}{k}$ is inverse of the shell thermal diffusivity coefficient.

1.2.2. Formalization

We start from a derivation of equation for the temperature distribution in the shell when it is in a steady state. As we have learnt already from equations (1) and (2), steady state means a stationary distribution of temperature as it is formalized by equation (3).

It yields the following equation that is equivalent to the equation (6) while written for $\vec{\mathbf{J}}_Q$:

$$\nabla \cdot \vec{\mathbf{J}}_Q = 0 \,, \tag{24}$$

where $\vec{\mathbf{J}}_Q$ is the heat flow that traverses shell, and $\vec{\mathbf{r}}$ are the coordinates in the shell. The equation is homogeneous because we assume that shell does not contain any heat sources.

The blood flow inside of the shell goes in capillaries and it has velocity that is lower by orders of magnitude than the blood flow velocity in the core, and according to figures from the Tab. 1 the Péclet number for the blood flow in capillaries is $Pe \sim 0.03$.

Thus, we believe that $\vec{\mathbf{J}}_Q$ is diffusive and can be approximated in the same way as in equation (15):

$$\vec{\mathbf{J}}_Q = -D_s \nabla Q \,, \tag{25}$$

where $D_s = \dfrac{k_s}{\rho_s c_s}$ is the thermal diffusivity coefficient for the shell. Since we assume a homogeneity for the shell, then D_s is neither a function of time, nor of coordinates, thus (24) can be transformed into:

$$-D_s \nabla^2 Q = 0 \,, \tag{26}$$

or, taking temperature from $Q = \rho_s c_s T_s$, one can write:

$$\nabla^2 T_s = 0 \,, \tag{27}$$

where T_s is the shell temperature, and k_s is the thermal conductivity of the shell.

We need, further, some boundary conditions to complete the problem definition. The model proposes Dirichlet (or the first type) boundary condition on outer surface ∂A, and Neumann (or the second type) boundary condition on inner surface ∂S. Final equation along with its boundary conditions looks similar to (21), but does not include convection:

$$\begin{aligned}
&\nabla^2 T_s = 0 \,, \\
&k_s \nabla T_s \cdot \vec{\mathbf{n}}|_{\partial S} = -J_Q \,, \\
&T_s|_{\partial A} = T_{\text{outer}} \,.
\end{aligned} \tag{28}$$

Boundary condition on the inner surface ∂S simply means a heat flow continuity. The boundary condition on the outer surface ∂A introduces a new temperature T_{outer}. We may use a common convective heat transfer approximation (Newton's law of cooling) and stipulate that T_{outer} is defined by the equation $J_c = \varkappa(T_{\text{outer}} - T_a)$ (per unit area), where $\varkappa \left[\dfrac{J}{\sec m^2 \, K} \right]$ is the heat transfer coefficient. But, we calculate it from the entropy production rate of the system instead, and demonstrate that convective approximation is just a special case of the more general dependency.

1.2.3. Shell entropy production

Equation for entropy production rate can be written using the same method as is illustrated during evaluation of (23), but the equation should be generalized as equation for production

rate of *entropy density*, $\sigma(\vec{\mathbf{r}}, t)$ in every elementary volume $d\vec{\mathbf{r}}$, because we can assume the local equilibrium only. Taking note that $\left(\dfrac{1}{T_a} - \dfrac{1}{T_c} \right)$ becomes ∇T^{-1}, one can write:

$$\sigma(\vec{\mathbf{r}}, t)\, d\vec{\mathbf{r}} = \nabla \frac{1}{T(\vec{\mathbf{r}})} \cdot \vec{\mathbf{J}}_Q(\vec{\mathbf{r}}, t)\, d\vec{\mathbf{r}}, \tag{29}$$

where $\sigma(\vec{\mathbf{r}}, t)$ is production rate of entropy density, $T(\vec{\mathbf{r}})$ is temperature of the shell, $\vec{\mathbf{J}}_Q(\vec{\mathbf{r}}, t)$ is a heat flow that "traverses" the shell, $\vec{\mathbf{r}}$ is coordinate in the shell.

One can integrate (29) over the shell and obtain the total entropy production rate in the shell as

$$\dot{S}_{\text{shell}}(t) = \int_V \sigma(\vec{\mathbf{r}}, t)\, d\vec{\mathbf{r}} = \int_V \vec{\mathbf{J}}_Q(\vec{\mathbf{r}}, t) \cdot \nabla \frac{1}{T(\vec{\mathbf{r}})}\, d\vec{\mathbf{r}}, \tag{30}$$

where $\int_V d\vec{\mathbf{r}}$ means an integration over the entire shell volume.

For the sake of clear demonstration of the major properties of the system, we consider unit area cross section of the shell and assume that the shell boundaries are perpendicular to the heat flux $\vec{\mathbf{J}}_Q$. Illustration of this model is presented in Fig. 3.
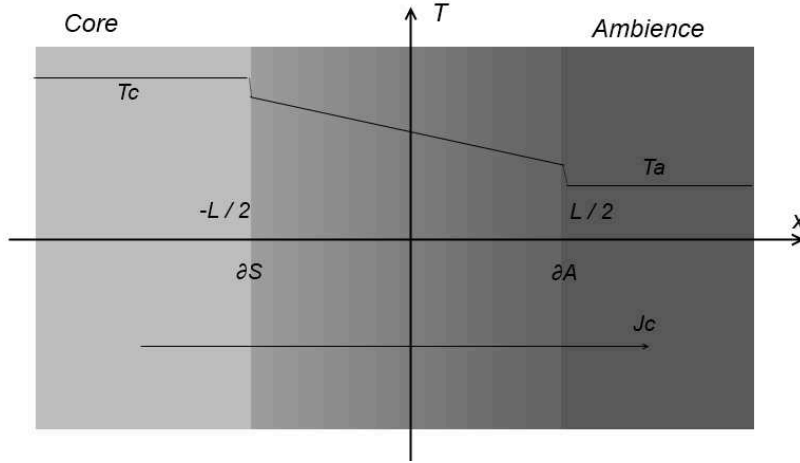

Fig. 3. Shell Temperature Model

This simplification removes routine vector calculus transformations of the volume integral in (30) and reduces 3D equation space to one dimension.

Let's re-write (30) as one-dimensional linear integral. Shell cross section area is omitted because we use per unit area values (and volumetric units as usual):

$$\dot{S}_{shell}(t) = \int\limits_{-L/2}^{L/2} J_Q(x, t) \frac{d(1/T(x))}{dx}\, dx, \tag{31}$$

where L is the shell thickness, and x is the coordinate across the shell. The coordinate system origin is set at the shell median plane and positive direction points to the ambience. In these coordinates the core surface ∂S is at $x = -L/2$ and the ambience surface ∂A is at $x = L/2$, see Fig. 3 for illustration.

Integral (31) can be integrated by parts and evaluates to:

$$\dot{S}_{\text{shell}}(t) = \frac{1}{T(x)} J_Q(x,t) \Big|_{-L/2}^{L/2} - \int_{-L/2}^{L/2} \frac{1}{T(x)} \frac{dJ_Q(x,t)}{dx} \, \mathrm{d}x = \dot{S}_{\text{steady}}(t) + \dot{S}_{\text{transient}}(t) \,,$$

$$\dot{S}_{\text{steady}}(t) = \frac{J_a(t)}{T_a} - \frac{J_c(t)}{T_c} \,, \tag{32}$$

$$\dot{S}_{\text{transient}}(t) = - \int_{-L/2}^{L/2} \frac{1}{T(x)} \frac{dJ_Q(x,t)}{dx} \, \mathrm{d}x \,,$$

where $J_a(t) = J_Q(L/2, t)$ is the heat flux to the ambience, $J_c(t) = J_Q(-L/2, t)$ is the heat flux from the core, $\dot{S}_{\text{steady}}(t)$ is the steady state contribution, and $\dot{S}_{transient}(t)$ is the *transient process contribution*. Equations (32) immediately lead to the steady state entropy production rate formula:

$$\dot{S}_{\text{steady}} = \frac{J_a(t)}{T_a} - \frac{J_c(t)}{T_c} = \left(\frac{1}{T_a} - \frac{1}{T_c} \right) J_c \,, \tag{33}$$

under the local equilibrium assumption $\frac{d}{dx} J_Q(x,t) = 0$ in any steady state, and we have $J_a(t) = J_c(t) = J_c$ (strictly speaking, on average), and J_c is not a function of time. It is clear that $\dot{S}_{\text{steady}} > 0$ if $T_c > T_a$.

This demonstrates an important model limitation: inequality $T_c \geqslant T_a$ must be valid at any time. A transient process contribution $\dot{S}_{\text{transient}}$ can be estimated due to the local equilibrium assumptions. First, expand integrand into Taylor series around $x = 0$:

$$\dot{S}_{\text{transient}}(t) = - \int_{-L/2}^{L/2} \sum_{n=0}^{\infty} \frac{x^n}{n!} \frac{\mathrm{d}^n}{\mathrm{d}x^n} \left(\frac{1}{T(x)} \frac{dJ_Q(x,t)}{dx} \right) \Big|_{x=0} \, \mathrm{d}x \,, \tag{34}$$

where $\frac{\mathrm{d}^0}{\mathrm{d}x^0} f(x) \equiv f(x)$, and then change order of summation and integration:

$$\dot{S}_{\text{transient}}(t) = - \sum_{n=0}^{\infty} \frac{\mathrm{d}^n}{\mathrm{d}x^n} \left(\frac{1}{T(x)} \frac{dJ_Q(x,t)}{dx} \right) \Big|_{x=0} \int_{-L/2}^{L/2} \frac{x^n}{n!} \, \mathrm{d}x \,. \tag{35}$$

Next, taking note that all odd numbered members of the series are zero because of the integration limits symmetry, and any high (i. e. $\geqslant 2$) order derivatives can be neglected by the accepted assumptions, equation (35) can be transformed to:

$$\dot{S}_{\text{transient}}(t) = -L \left(\frac{1}{T(x)} \frac{dJ_Q(x,t)}{dx} \right) \Big|_{x=0} = -L \frac{1}{T_s(t)} \frac{d}{dx} J_Q(t) \,, \tag{36}$$

where the shell temperature is introduced as $T_s(t) \equiv T(0, t)$. Finally, the equation (36) can be expressed as

$$\dot{S}_{\text{transient}}(t) = - \frac{J_a(t) - J_c(t)}{T_s(t)} \,, \tag{37}$$

where $\frac{d}{dx} J_Q(t)$ has been estimated as $\frac{J_a - J_c}{L}$, ignoring high order derivatives.

It is important that one should not use stationary flows in (37), because this equation describes non-steady state, where both J_a and J_c may be functions of time. Same is true for the shell temperature T_s. Complete estimation of total entropy production rate in the shell is then:

$$\dot{S}_{\text{shell}}(t) = \frac{J_a(t)}{T_a} - \frac{J_c(t)}{T_c} - \frac{J_a(t) - J_c(t)}{T_s(t)} \,, \tag{38}$$

where both T_a and T_c are assumed to be weakly dependent on time (at most) in the same sense as explained by (10).

The equation for the steady state entropy production (33) defines the entropy of a steady state as a function of independent variables T_a, T_c, and J_c. Note that T_s is not a part of the formula, and equations (33) and (23) are identical. It means that a shell can be in a steady state for any combination of T_a, T_c, and J_c, but may have arbitrary T_s (until $T_a < T_s < T_c$ and model validity assumptions are held).

On the other hand, T_s presents in entropy production when the system is in a transient state, see equation (37). This means that in spite of the fact that T_s has certain figure in any steady state, it has been set up during the system relaxation from a transient to the steady state and it may depend on the transient state details.

1.2.4. Shell temperature estimation

Since the shell temperature T_s presents only in equation for a transient process (37), we will derive it's value from the transient process properties. The shell can be set into a transient state by the ambient temperature variation.

If ambient temperature T_a changes then the shell should move to another steady state according to the steady state entropy production equation (33). New state depends on a new ambient temperature, $\tilde{T}_a = T_a + \delta T_a$. Because temperatures of both core and ambience, and heat flow J_c are all independent parameters of the steady state, we can choose $J_c = const$. The choice is quite logical since J_c takes its origin in the core, but nothing can force that latter to change J_c at the beginning of the transient process in the shell.

A transition process takes some time τ. During this time the shell entropy production rate is different and "excessive" rate is equal to a value set by equation (37). Explanations of the reasons why the shell should move to a transient state, why it will find another steady state, as well as good estimation of τ are far beyond of this article scope.

A total excessive entropy that the transient process generates during its life time τ is equal to integral of the entropy production rate over time:

$$\delta S_{\text{transient}} = -\int_0^\tau \frac{J_a(t) - J_c}{T_s(t)} \, \mathrm{d}t \,. \tag{39}$$

Using the linear approximations for $T_s(t)$ and $J_a(t)$ as usual, one can write:

$$\begin{aligned} T_s(t) &= T_s(0) + t \left. \frac{\mathrm{d}T_s}{\mathrm{d}t} \right|_0 \\ J_a(t) &= J_a(0) + t \left. \frac{\mathrm{d}J_a}{\mathrm{d}t} \right|_0 , \end{aligned} \tag{40}$$

and equation (39) transforms to:

$$\delta S_{\text{transient}} = -\int_0^\tau \frac{J_a(0) + t \left. \dfrac{\mathrm{d}J_a}{\mathrm{d}t} \right|_0 - J_c}{T_s(0) + t \left. \dfrac{\mathrm{d}T_s}{\mathrm{d}t} \right|_0} \, \mathrm{d}t \,, \tag{41}$$

that after some transformations borrowed from the calculus hand-book has became

$$\delta S_{\text{transient}} = \left(\left.\frac{\mathrm{d}T_s}{\mathrm{d}t}\right|_0\right)^{-1} \left(J_c - J_a(0) + T_s(0)\frac{\left.\frac{\mathrm{d}J_a}{\mathrm{d}t}\right|_0}{\left.\frac{\mathrm{d}T_s}{\mathrm{d}t}\right|_0}\right) \times$$

$$\times \ln\left(T_s(0) + t\left.\frac{\mathrm{d}T_s}{\mathrm{d}t}\right|_0\right)\Bigg|_0^\tau - \left(\frac{\left.\frac{\mathrm{d}J_a}{\mathrm{d}t}\right|_0}{\left.\frac{\mathrm{d}T_s}{\mathrm{d}t}\right|_0}t\right)\Bigg|_0^\tau,$$

(42)

which in turn evaluates to

$$\delta S_{\text{transient}} = \left(\left.\frac{\mathrm{d}T_s}{\mathrm{d}t}\right|_0\right)^{-1} \left(J_c - J_a(0) + T_s(0)\frac{\left.\frac{\mathrm{d}J_a}{\mathrm{d}t}\right|_0}{\left.\frac{\mathrm{d}T_s}{\mathrm{d}t}\right|_0}\right) \ln\left(1 + \frac{\left.\frac{\mathrm{d}T_s}{\mathrm{d}t}\right|_0}{T_s(0)}\tau\right) - \left(\frac{\left.\frac{\mathrm{d}J_a}{\mathrm{d}t}\right|_0}{\left.\frac{\mathrm{d}T_s}{\mathrm{d}t}\right|_0}\tau\right), \quad (43)$$

and, after familiar assumption $T_s^{-1}(0)\left.\frac{\mathrm{d}T_s}{\mathrm{d}t}\right|_0 \tau \ll 1$ finally converts to

$$\delta S_{\text{transient}} \approx \frac{J_c - J_a(0)}{T_s(0)}\tau = -\frac{\delta J_a}{T_s(0)}\tau, \quad (44)$$

because $J_a(0)$ is the heat flow to ambience at the beginning of transient process and can be expressed as $J_a(0) = J_c + \delta J_a$ (in steady state $J_a = J_c$, or $J_a(-0) = J_c$).

An excessive entropy given by equation (44) makes the shell to gain (or loose) amount of heat approximately equal to

$$\delta Q_{\text{shell}} = -\tau\delta J_a. \quad (45)$$

Finally, variance of the shell temperature is equal to

$$\delta T_s = -\frac{\tau}{\rho_s c_s}\delta J_a, \quad (46)$$

where the equation is conveniently written in per unit volume, per unit square units, and ρ_s is the shell density, c_s is specific heat capacity of the shell.

Equation (46) connects shell temperature variance to variance in heat flow to the ambience. Notable property of this equation is the opposite direction of these variances: if the flow increases at the beginning of transient process ($\delta J_a > 0$) then shell temperature decreases by the end of the transition ($\delta T_s < 0$), and *vice versa*. This is true for any type of flow and is not related to the flow dependencies on T_a and T_s (until the model assumptions are valid).

We can estimate the transient process time τ in simple situation, where the heat flow to ambience J_a can be presented as a linear combination of conduction, convection, and radiation flows, and heat transfer from shell to ambience conforms to Newton's law of cooling. Newton's law of cooling application assumes that object (shell) has high heat capacity and high temperature conductivity. Such assumption is more or less valid for large enough animals.

$$J_a = J_{\text{conduction}} + J_{\text{convection}} + J_{\text{radiation}}. \quad (47)$$

It is possible to use linearisation by temperature and express all of them collectively as

$$J_a = \varkappa(T_s - T_a), \quad (48)$$

where $\varkappa$ is the heat transfer coefficient (more correctly, a combination of heat transfer coefficients of different heat transfer modes). A proof of validity and conditions of acceptance of this approach for biological applications can be found in [3].

The heat transfer coefficient is a well-known property of heat exchange. Inverse of $\varkappa$ is often used as "thermal insulance" in heat engineering applications, like lumped system analysis, see [4]. Correct calculation of $\varkappa$ is rather complicated task that involves the estimation or modelling of many details of environment and is out of this article scope. Excellent introduction to this matter from the point of view of biology can be found in [10].

With such representation of J_a it is clear that temperature variances are connected as

$$\delta T_s = \tau \frac{\varkappa}{\rho_s c_s} \delta T_a \,. \tag{49}$$

Due to a steady state definition ($J_a = J_c$) and a constant value of J_c, it is clear that, by the end of transient process, $\delta T_s = \delta T_a$. Of course, this is correct only if equation (48) is feasible and it is better to say that δT_s is a linear function of δT_a.

It gives us the following estimation of τ:

$$
\begin{aligned}
\tau &= \frac{\rho_s c_s}{\varkappa} \quad \text{in per unit volume per unit area units, or} \\
\tau &= \frac{C_s}{\varkappa A_s} \quad \text{in metric units, or} \\
\tau &\sim \frac{\rho_s c_s}{\varkappa} L_s \quad \text{as order of magnitude estimation}\,,
\end{aligned}
\tag{50}
$$

where ρ_s is a shell density, c_s is a specific heat capacity of the shell, κ is a heat transfer coefficient of the environment, C_s is a heat capacity (bulk) of the shell, A_s is a surface area of the shell, L_s is a "characteristic size" of the shell. Estimation (50) is far from numerical precision and just demonstrates dependency of transient process life time from material properties of the shell and environment. Nevertheless, the estimation of τ in (50) is equal to "characteristic time" in solution of Newton's cooling equation, while it has been calculated in completely different way.

1.2.5. Formalization completion

Having results presented by equations (46) and (49), one can return to the steady state shell temperature distribution problem (28) and re-define it in more details:

$$
\begin{aligned}
&\nabla^2 T_s = 0\,, \\
&k_s \nabla T_s \cdot \vec{\mathbf{n}}|_{\partial S} = -J_c\,, \\
&T_s|_{\partial A} = f(J_a) = T_{\text{outer}}(J_c, T_a) = const\,,
\end{aligned}
\tag{51}
$$

where temperature $T_{\text{outer}}(J_c, T_a)$ is a linear function of J_a and T_a as it follows from equation (46). In the simple case of Newton's cooling (analogy) defined by equation (48), this function can be expressed as $T_s|_{\partial A} = T_a + \frac{1}{\varkappa} J_c$.

The problem (51) can be solved for the same one-dimensional model of the shell as has been used for entropy production rate calculation; see commentaries to equation (31) for the coordinate

system definition details.

$$T_s(x) = C_1 x + C_2 \,,$$
$$C_1 = -\frac{1}{k_s} J_c \,,$$
$$C_2 = T_{\text{outer}}\left(J_c, T_a\right) - C_1 \frac{L}{2} \,,$$
(52)

where C_1 and C_2 are integration constants derived from the boundary conditions. Complete one-dimensional solution of steady state temperature distribution in the shell can be presented in the following form:

$$T_s(x) = T_{\text{outer}}\left(J_c, T_a\right) + \frac{1}{k_s} J_c \left(-x + \frac{L}{2}\right) \,,$$
(53)

and temperature at inner surface ∂S is

$$T_s\left(-\frac{L}{2}\right) = T_{\text{outer}}\left(J_c, T_a\right) + \frac{J_c}{k_s} L \,.$$
(54)

For the simple case of Newton's cooling analogy this equation can be written as

$$T_s\left(-\frac{L}{2}\right) = T_a + \left(\frac{1}{\varkappa} + \frac{L}{k_s}\right) J_c \,.$$
(55)

Since L, k_s and $\varkappa$ are all positive, and J_c is non-negative, one can see that $T_s \geqslant T_a$ where the equality is reached if $J_c = 0$. Illustration of this solution is presented in Fig. 3.

The temperature of shell should not exceed the temperature of core $(T_c \geqslant T_a)$, and we can write condition of "maximal heat flow throughput" of the shell:

$$J_c \leqslant \frac{k_s}{L}\left(T_c - T_{\text{outer}}\right) \quad \text{or, for Newton's cooling}$$
$$J_c \leqslant \left(\frac{1}{k_s} L + \frac{1}{\varkappa}\right)^{-1}\left(T_c - T_a\right) \,,$$
(56)

and equivalent "maximal tolerable ambient temperature":

$$T_{\text{outer}} \leqslant T_c - \frac{L}{k_s} J_c \quad \text{or, for Newton's cooling}$$
$$T_a \leqslant T_c - \left(\frac{1}{k_s} L + \frac{1}{\varkappa}\right) J_c \,.$$
(57)

2.   Temperature regulation

All values and functions below are locally defined in volumetric units.

2.1. Regulation goals

The goals of regulation are straightforward:
– temperature distribution $T_c\left(\vec{r}\right)$ in core should be stationary;
– outgoing heat flux J_c should transfer all excessive heat away from the (local volume of) core:

$$\frac{\partial T_c}{\partial t} = 0\,, \quad T_c = g\left(\vec{\mathbf{r}}\right)\,, \tag{58}$$

$$\frac{\partial J_c}{\partial t} = 0\,, \quad J_c - f\left(h_{\text{exc}}\left(\vec{\mathbf{r}}\right)\right) = 0\,. \tag{59}$$

These requirements are not independent actually, and the second one is put here to emphasize that J_c depends on the metabolism heat production rate h_{exc}.

2.2. Regulation inputs

The core should activate temperature regulation because of two major reasons:
– metabolism rate change (e. g. change in activity level)
– changes in environment (e. g. change in temperature, or change in heat transfer coefficient during diving)

$$h_{\text{exc}}\left(\vec{\mathbf{r}}\right) \quad \text{set by metabolism as required}\,, \tag{60}$$

$$T_s\big|_{\partial S} = T_{outer}\left(J_c, T_a\right) + \frac{J_c}{k_s}L \quad \text{set by environment}\,. \tag{61}$$

The first input, h_{exc} is current metabolism rate function and is set according to the core needs and circumstances (e. g. depends on activity level, or daytime, or season — the reasons are not in this article scope). The core sets J_c according to this value.

Second input is a "projection" of the heat exchange with ambience to the core. It modifies $\nabla T_c\big|_{\partial S}$. As one can see from equations (46) (or (49)) and (54), the higher is the heat flow to the ambience, the lower is the shell temperature at its inner border $T_s\big|_{\partial S}$ (and *vice versa*) eventually. Corresponding gradient $\nabla T_c\big|_{\partial S}$ increases when $T_s\big|_{\partial S}$ decreases and decreases when $T_s\big|_{\partial S}$ increases.

Note that $\nabla T_c\big|_{\partial S}$ is always non-positive, because $T_c \geqslant T_s$, but coordinate $\vec{\mathbf{r}}$ increases in opposite direction — from the core to the ambience. Since gradient vector points to higher value (by definition), then $\nabla T_c\big|_{\partial S} \leqslant 0$ in this model.

2.3. Regulation controls

The core regulates a temperature using blood flow variation. It sets flow velocity $\vec{\mathbf{v}}$ according to the current values of J_c and $\nabla T_c\big|_{\partial S}$ as formalized by the following equation:

$$\left(-k_c \nabla T_c + \rho \vec{\mathbf{v}} c_v T_c\right) \cdot \vec{\mathbf{n}}\,\big|_{\partial S} = J_c\,. \tag{62}$$

Note that this equation (62) is one of the boundary conditions of the heat distribution problem (21).

Since both ∇T_c and $\vec{\mathbf{v}}$ are the vectors, it is possible to change value and/or direction of $\vec{\mathbf{v}}$.

2.4. System response

Finally, the figures of $(h_{\text{exc}}, J_c, \vec{\mathbf{v}})$ have been set up to fit the current conditions, and the core temperature changes to be an appropriate solution of the following equation:

$$-k_c \nabla^2 T_c + \rho \vec{\mathbf{v}} \cdot c_v \nabla T_c = h_{\text{exc}}\left(\vec{\mathbf{r}}\right)\,. \tag{63}$$

Speaking precisely, $T_c\left(\vec{\mathbf{r}}\right)$ becomes equal to solution of the problem (21).

2.5. Regulation implementation

The mathematical model seems to be quite heavy and hard to implement in a "controller", but it is not true, and this regulation scheme may be implemented as a very simple fuzzy logic controller, without any noticeable needs in computational power: measure T_c change and then change $|\vec{\mathbf{v}}|$ in the same direction until T_c falls into acceptable range.

Of course, if some extra resources are available, this basic rule can be refined for faster and more precious response.

3.   Results discussion

3.1. Shell surface temperature

The model described above does not imply any global dependencies, works locally and independently in every part of the system (animal's body). It means that shell surface temperature may be very inhomogeneous, because of differences in local heat transfer conditions and, possible, different local core temperature and heat balance requirements.

The model describes heat transfer across the shell surface only, but heat transfer works along the shell surface too, thus any local temperature excess initiates some lateral heat flows.

It concludes that a shell as a whole should not be described by stationary equation, like (28), and one should use full form of the heat transfer equation, including time derivative, spatial dependency of thermal properties, and time-depending boundary conditions:

$$
\begin{aligned}
&\frac{\partial T_s}{\partial t} - \nabla \cdot (k_s(\vec{\mathbf{r}}) \nabla T_s) = 0\,, \\
&k_s(\vec{\mathbf{r}}) \nabla T_s \cdot \vec{\mathbf{n}}|_{\partial S} = -J_c(\vec{\mathbf{r}}, t)\,, \\
&T_s|_{\partial A} = T_{\text{outer}}(J_c(\vec{\mathbf{r}}, t), T_a(\vec{\mathbf{r}}, t))\,,
\end{aligned}
\tag{64}
$$

where function T_{outer} is defined by equations (46) or (48), and is not always known exactly. A solution of equation (51) can be used as initial conditions.

The process of analytical (or numerical) solution of this equation is incredibly laborious.

For practical temperature measurement, it means that the shell surface temperature has no obvious connection to the core temperature. For example, attempts to correlate the skin temperature and rectal temperature will mostly fail.

In addition, equation (64) demonstrates that the average surface temperature is weakly defined on large scale (Laplacian ΔT can be far from zero).

Nevertheless, it is possible to say that in non-extreme conditions an animal maintains more or less constant difference between its skin temperature and temperature of the environment. The value of this difference depends on activity level of the animal, besides some other factors such as health conditions and stress level (i. e. depends on the current level of metabolism rate). The higher activity level causes the bigger difference.

Evidences of linear dependency between ambient and skin surface temperatures were observed in [21], where strong linear correlation was directly measured. Another example of the linear dependence and high inhomogeneity of the skin temperature distribution can be found in [40].

Authors of [15] found that sheared alpacas had lower surface temperature than non-sheared. Such effect can be explained by equation (46) that predicts surface temperature decrease with increase of heat flow into the ambience. The heat flow from alpacas' skin was increased because

shearing significantly decreases thermo-insulation of the skin (in terms of Newton's cooling, it makes the $\varkappa$ figure bigger).

3.2. Newton's law of cooling

Newton's law of cooling is a common method to describe a convection-cooling [4, 37, 38]. It says that "the rate of heat loss of a body is proportional to the temperature difference between the body and its environment". Formal expression of the law is presented by equation (48). It is important to understand that the law is an approximation, and even rather empirical relationship. It is not applicable always, and it's feasibility have some implicit assumptions:

– temperature difference between the body and environment does not depend on which part of body is selected for the temperature measurement,

– body has a large heat capacity and high thermal conductivity comparing to its environment. Thus, heat transfer rate inside of the body is significantly higher than across of the boundary. Sometimes the body can be described as "an onion" of region of interest, or "lumps", but this should be true inside of any region,

– the heat transfer coefficient depends neither on temperature, nor on time.

If some of these assumptions are not valid, the law may break, as it is often observed in presence of the free convection (where the coefficient depends on temperature), or during transition of flow mode (e. g. from laminar to a turbulent one).

Newton's law application in biology is a well-established and rather successful practice [3, 29]. Nevertheless, it should be applied with care, see [37]. Known values of thermal properties of animal tissues can be found in [5] and in [19, Appendix A]. They can be "averaged" and the results are presented in the following table (the values are approximate!), where the core is supposed to be composed from blood, muscles and bones, and the shell is built from fat and skin.

Table 2. Thermal properties of tissues

Media	Specific heat capacity $\left[\frac{J}{kg\cdot K}\right]$	Thermal conductivity $\left[\frac{J}{sec\cdot m\cdot K}\right]$
Core	3700	0.50
Shell	3000	0.20
Air	1000	0.03
Water	4200	0.60

For terrestrial animals an assumption of high body conductivity seems to be valid due to very low heat capacity and thermal conductivity of the air, but for aquatic animals it's validity can be arguable. The model proposed in this article does not require such assumptions regarding thermal properties of the animal's body. It uses different assumptions (see above), where one of the most important constraints slow changes in environment for the shell could be in a steady state.

If this assumption is valid, the model comprises Newton's cooling as a special case (see equations (48–50)). In the model's framework, the Newton's cooling law can be interpreted as an empirical description of transient process between different steady states of the shell. For example, if the temperature of environment is lowers then a skin surface temperature follows it according Newton's law of cooling with apparent characteristic time given by equation (50). The same is true if a transition process has been initiated by the core (change in heat flow because of

metabolism rate variation). For example, if the animal ceases an activity (i.e. breaks down the metabolism rate), the skin surface cools down according to Newton's law.

When the shell is in a steady state, the Newton's law of cooling may not always be an adequate mechanism if one wants to correlate core temperature, skin temperature, and temperature of the ambience using measured or estimated thermal properties of the body and media.

3.3. Regulation limitations

The major claim of the model is the hypothesis about the role of blood flow in thermoregulation of animals. It is absolutely clear that thermoregulation in not a primary purpose of the blood, and temperature regulation is not a top priority task of the blood flow control system.

The blood flow velocity lays inside a specific range, and this range fits the primary purposes of the blood system. From the point of view of thermoregulation, this is a limitation:

$$v_{\min} \leqslant |\vec{\mathbf{v}}| \leqslant v_{\max} \, . \tag{65}$$

Indeed, if $v = v_{\min}$ already, but $\nabla T_c|_{\partial S}$ continues to increase (permanent cooling of ambience) then it can not be compensated any more. Similar problem rises at the high limit of flow velocity range $v = v_{\max}$, see regulation equation (62).

Control mechanics may not be perfect, and if the flow velocity is set up too low (at low ambience temperature) then shell may suffer from chilblain. A high temperature of the ambience and corresponding high flow velocity may cause the abnormal pressure in vessels exceeding breaking point of that later, thus haemorrhages may begin to appear in the shell. There are researches which demonstrated that vasculature could be build in a sophisticated way to relax this limitation. See [9, 23, 29].

Another limitation of the regulation is connected to maximum shell throughput (see (56) and (57)):

$$J_c \leqslant J_{\max} = \frac{k_s}{L} \left(T_c - T_{\text{outer}} \right) \, . \tag{66}$$

This relation demonstrates that the heat flow from the core can not be set arbitrary high, and that the upper limit depends on difference between core temperature and temperature of the environment: the lower is the difference then the lower is the maximum acceptable value of the heat flow $J_{\max}$, see equation (51) for more details about T_{outer}. Some signs of this bottleneck can be found in [40] in the data related to the areas with highest measured heat flow.

This limitation is important if an ambient temperature is high. At high temperature and high metabolism rate (when high J_c is required), the shell may "choke" the heat flow, and the core will be forced to use additional mechanisms of the thermoregulation where possible, and/or lower down the metabolism rate. For example, cease chasing the pray. This "heat sink bottleneck" problem may give additional explanation to some effects that can be observed during work or exercises in hot environment, see [6, 7, 11, 32, 39].

Equation (57) means that for every J_c, and, equivalently for every metabolism rate, there is a maximum of tolerable (operational) temperature of environment. Note that it is better to speak about the heat flows, instead of the temperatures, because this limitation depends on thermal properties of both the body and the media, and upper limit of the temperature in air may not be equal to the limit in water [10].

3.4. Adaptation to climate

Most, if not all, of the regulation mechanics and corresponding limitations depend on thermal properties of body tissues, and some depend on dimensions of the body. The thermal properties (ρ, C, k) form "hard" limitations. One can hardly expect significant change in heat capacity, thermal conductivity, or density of the body in reasonable time, required for the successful thermoregulation.

Another properties are more flexible: for instance, $\varkappa$, which defines "insulation" of the body surface can be cleverly engineered using fur, feathers, behavioural patterns (i. e. staying in shade to reduce radiation heating, walking to the wind during hot day to increase forced convection), etc; see, for example, [13, 22, 33].

Comprehensive investigation of animal's adaptation to cold and hot environment in regard of metabolism rate, body temperature, and temperature of the ambience can be found in [28, 30]. From the proposed model's point of view, the adaptation can be done in some additional ways explained below.

As the regulation equation (62) says, the "initial" value of the temperature gradient $\nabla T_c|_{\partial S}$ can be chosen as appropriate for the expected temperature range of the environment. Thus, in cold climate, where low T_a is quite probable, lower value of the gradient allows the blood flow velocity to be set at higher level, preventing skin chilblain. It can be achieved by increasing subcutaneous thickness (e. g. using thicker layer of fat) for less steepness of the temperature change, and/or by skin thickness increase, which, according to the equation (54), results in a growth of the inner temperature of the skin. In cold climate, thick skin and subcutaneous tissues allow to keep high level of metabolism rate and high blood circulation rate without unnecessary heat loss. Evidence of vascular control role in body temperature regulation in cold climate can be found in [24, 29].

In a hot climate with a high probability of high ambience temperature, this approach should be reversed: higher $\nabla T_c|_{\partial S}$ leaves more freedom in blood flow regulation. Thinner skin also allows to avoid the "heat flow choking", as it can be seen from the equation (66). In hot climate the thin skin and subcutaneous tissues are beneficial if high level of metabolism rate is required.

These adaptation and regulation mechanisms do not include mechanisms related to the core temperature choice, metabolism rate regulation, or mechanisms that are important when ambient temperature is far outside of the thermo neutral zone of the animal, which are neither in this article, nor in the proposed model scope.

4. The model and beyond

Homoeothermal animals differ from any other creatures (either animals, or plants, or fungi) with their ability to maintain the inner temperature of an organism. This ability is absolutely crucial from the point of view of an implementation of a feasible model of thermoregulation of a being. Endothermic animal has a core that permanently generates heat energy because of metabolism. Thus, a model of thermoregulation must include a heat production, heat discharge, and the ways of that latter must be optimal; this item forces a researcher to consider an entropy production and entropy discharge, besides the heat production modelling.

The model described above implies a kind of homogeneity of a core; that latter is supposed to remain in a (quasi)equilibrium: there are no inner heat flows, or entropy flows. From biological

point of view, such species are the *homoeotherms*[‡]. Oppositely, some species are known for a significant variation of the temperature of the compartments of a body; such animals are called *heterothermic* ones. Since most of animals are homoeotherms their core temperature (T_c) should be constant for optimal performance of enzymes that regulate core biochemistry. It holds true for heterotherms also with slight modification to *mostly constant.*

According the the First Law of Thermodynamics this requirement leads to necessity of a heat flow (J_c) that dissipates excessive power to the external environment. The power that should be dissipated is proportional to current metabolism rate value. Constant T_c requirement means constant J_c that is appropriate for a given metabolism rate.

If the core were directly exposed to the environment it would be strongly driven by ambience temperature (as well as other thermal parameters) fluctuations but would not have enough regulation options. That is why the shell is always exists, both in a model and in reality. Thermodynamic parameters regulation means variable material properties (heat capacity, thermal conductivity, density, etc). It leads to obvious difficulties if an immediate response to significant ambience variation is required.

Under the First Law, some work may be involved to control heat gain or loose ($\mathrm{d}U = \mathrm{d}Q + p\,\mathrm{d}V$), but this way fail to meet other constraints that are not related to the thermal balance. For example, variable volume may involve use of some thin elastic constructions that may not provide serious mechanical protection.

Simultaneously, a notable mass exchange ($\mathrm{d}U = \mathrm{d}Q + p\,\mathrm{d}V + \mu\,\mathrm{d}N$) may not provide a solution of the problem: both mass and composition of the core are usually permanent, for any creature. This conservation of course is not absolute: food/water consumption, growth, etc. make some slight variations of those figures. Yet, the variations are too small to be effective in a (rather quick) responding on a temperature change.

These two issues result in a shell implementation, with no ambiguity. The shell acts as a heat buffer that reduces variations of thermal parameters of the environment as they are seen by the core. When ambience warms up, the shell collects an excessive head coming from the body (shell entropy increases). Reciprocally, when the ambience cools down the shell releases some heat (shell entropy decreases) removing the burden from the core.

The shell is just another part of the same body, so the implementation of the mechanisms for heat exchange between the shell and the core seems to be rather simple. Because the shell temperature (T_s) is set up "automagically" by the Second Law of Thermodynamics and is not controlled by the core, it is much easier to achieve another "design goals" (e. g. mechanical protection), because the constraints for the thermal parameters of the skin may be broken through (comparing to the constraints in the case of directly connected core). All mechanics described in this article can work locally. It means, that it is possible to set T_c and J_c as it is optimal locally, and shell will find a steady state as it is appropriate for the given T_a (more strictly, for a given local J_a). This means that shell temperature is not required to be homogeneous over entire surface of the animal.

The model presented here is basically aimed to describe the processes of a temperature regulation for homoeothermic animals: it implies a linear approximation of some processes, a significant difference between an organism and an ambience. Thus, it hardly could be extended for the poikilothermic species, or plants, immediately. Nonetheless, there could be developed the versions of the model for this type of organisms, while the discussion of these issues falls beyond

---

[‡]And man is among them: this fact stands behind the body temperature measurement as a diagnostically valuable medical procedure.

the scope of this paper.

References

[1] J.W.Baish, Heat transport by countercurrent blood vessels in the presence of an arbitrary temperature gradient, *Journal of biomechanical engineering*, **112(2)**(1990), no. 5, 207–211.

[2] J.W.Baish, P.S.Ayyaswamy, K.R.Foster, Heat transport mechanisms in vascular tissues: a model comparison, *Journal of biomechanical engineering*, **108(4)**(1986), no. 11, 324–231.

[3] G.S.Bakken, A Heat Transfer Analysis of Animals : Unifying Concepts ad the Application of Metabolism Chamber Data to Field Ecology, *Journal of theoretical Biology*, **60**(1976), 337–384.

[4] T.L.Bergman, A.S.Lavine, F.P.Incropera, D.P. DeWitt, Fundamentals of Heat and Mass Transfer, Wiley, 2011.

[5] F.H.Bowman, E.G.Cravalho, M.Woods, Theory, Measurement, and Application of Thermal Properties of Biomaterials, *Annual Review Biophysics and Bioengeneering*, **4**(1975), 43–80.

[6] D.J.Brake, The Deep Body Core Temperatures, Physical Fatigue and Fluid Status of Thermally Stressed Workers and the Development of Thermal Work Limit as an Index of Heat Stress Derrick John Brake, PhD thesis, Curtin University of Technology, 2002.

[7] D.J.Casa, Exercise in the heat. I. Fundamentals of thermal physiology, performance implications, and dehydration, *Journal of athletic training*, **34(3)**(1999), no. 7, 246–252.

[8] Y.I.Cho, D.J. Cho, Hemorheology and microvascular disorders, *Korean circulation journal*, **41(6)**(2011), no. 6, 287–295.

[9] J.D.Coffman, Peripheral collateral blood flow and vascular reactivity in the dog, *The Journal of clinical investigation*, **45(6)**(1966), no. 6, 923–931.

[10] M.W.Denny, Air and Water: The Biology and Physics of Life's Media, Princeton University Press, 1995.

[11] Y.Epstein, D.S. Moran, Thermal comfort and the heat stress indices, *Industrial health*, **44 (3)**(2006), no. 7, 388–398.

[12] A.Fick, Ueber Diffusion. *Annalen der Physik und Chemie*, **170(1)**(1855), 59–86.

[13] M.A.Fratto, A.K.Davis, Do black-furred animals compensate for high solar absorption with smaller hairs? A test with a polymorphic squirrel species, *Current Zoology*, **57**(2011), no. 6, 731–736.

[14] H.T.Hammel, Regulation of internal body temperature, *Annual review of physiology*, **30**(1968), no. 1, 641–710.

[15] A.M.Heath, C.B.Navarre, A.Simpkins, R.C.Purohit, D.G.Pugh, A comparison of surface and rectal temperatures between sheared and non-sheared alpacas (Lama pacos), *Small Ruminant Research: the Journal of the International Goat Association*, **39**(2001), no. 1, 19–23.

[16] M.Hussain, S.Kar, R.Puniyani, Relationship between power law coefficients and major blood constituents affecting the whole blood viscosity, *Journal of Biosciences*, **24**(1999), no. 3, 329–337.

[17] M.Kleiber, Body Size and Metabolism, *Hilgardia: A journal of agricultural science. California Agricultural Experiment Station*, **6**(1932), no. 11, 315–349.

[18] D.Kondepudi, Introduction to Modern Thermodynamics, Wiley, 2008.

[19] F.Kreith, CRC Handbook of Thermal Engineering (Handbook Series for Mechanical Engineering), CRC Press, 1999.

[20] G.Lebon D.Jou, Understanding Non-equilibrium Thermodynamics: Foundations, Applications, Frontiers, Springer, 2007.

[21] J.A.Loughmiller, M.F.Spire, S.S.Dritz, B.W.Fenwick, M.H.Hosni, S.B.Hogge, Relationship between mean body surface temperature measured by use of infrared thermography and ambient temperature in clinically normal pigs and pigs inoculated with Actinobacillus pleuropneumoniae, *American journal of veterinary research*, **62**(2001), no. 5, 676–681.

[22] C.L.Myhrvold, H.A.Stone, Elie Bou-Zeid, What is the use of elephant hair? *PLoS ONE*, **7**(2012), no. 10, e47018.

[23] H.Ninomiya, E.Akiyama, K.Simazaki, A.guri, M.Jitsumoto, T.Fukuyama, Functional anatomy of the footpad vasculature of dogs: scanning electron microscopy of vascular corrosion casts, *Veterinary dermatology*, **22(6)**(2011), no. 12, 475–481.

[24] R.P.Olnianskaya, A.D.Slonim, On the adaptability of animal organisms to very low temperatures of the environment, *Bull. Acad. Sci. URSS, ser. Biol*, **2**(1947), 245.

[25] L.Onsager, Reciprocal Relations in Irreversible Processes. I, *Physical Review*, **37(4)**(1931), no. 2, 405–426.

[26] E.Ponder, The coefficient of thermal conductivity of blood and of various tissues, *The Journal of general physiology*, **45**(1962), no. 1, 545–551.

[27] V.M.Savage, J.F.Gillooly, W.H.Woodruff, G.B.West, A.P.Allen, B.J.Enquist, J.H.Brown, The predominance of quarter-power scaling in biology, *Functional Ecology*, **18(2)**(2004), no. 4, 257–282.

[28] P.F.Scholander, R.Hock, V.Walters, L.Irving, Adaptation to cold in arctic and tropical mammals and birds in relation to body temperature, insulation, and basal metabolic rate. *Biol. Bull.*, **99(2)**(1950), 259–271.

[29] P.F.Scholander, R.Hock, V.Walters, F.Johnson, L.Irving, Heat regulation in some arctic and tropical mammals and birds. *Biol. Bull.*, **99(2)**(1950), 237–258.

[30] P.F.Scholander, V.Walters, R.Hock, L.Irving, Body insulation of some arctic and tropical mammals and birds. *Biol. Bull.*, **99(2)**(1950), 225–236.

[31] T.Sousa, T.Domingos, S.A.L.M.Kooijman, From empirical patterns to theory: a formal metabolic theory of life, *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, **363(1502)**(2008), no. 7, 2453–2464.

[32] J.R.Speakman, E.Król, Maximal heat dissipation capacity and hyperthermia risk: neglected key factors in the ecology of endotherms, *The Journal of animal ecology*, **79(4)**(2010), no. 7, 726–746.

[33] C.Stockman, The Physiological and Behavioural Responses of Sheep Exposed to Heat Load within Intensive Sheep Industries, PhD thesis, Murdoch University, 2006.

[34] L.M.Surhone, M.T.Tennoe, S.F.Henssonow,   Dirichlet Boundary Condition, Betascript Publishing, November 2010.

[35] L.M.Surhone, M.T.Tennoe, S.F.Henssonow, Robin Boundary Condition, Betascript Publishing, September 2010.

[36] G.B.Thurston, Viscoelasticity of human blood, *Biophysical journal*, **12**(1972), no. 9, 1205–1217.

[37] C.R.Tracy,   Newton's Law: Its Application for Expressing Heat Losses from Homotherms, *BioScience*, **22**(1972), no. 11, 656–659.

[38] B.K.Venkanna, Fundamentals of Heat and Mass Transfer, Prentice-Hall of India Pvt.Ltd, 2010.

[39] T.J.Walters, K.L.Ryan, L.M.Tate, P.A.Mason, Exercise in the heat is limited by a critical internal temperature. *Journal of applied physiology*, **89**(2000), 799–806.

[40] S.Ward, J.M.Rayner, U.MOLler, D.M.Jackson, W.Nachtigall, J.R.Speakman, Heat transfer from starlings sturnus vulgaris during flight. *J. Exp. Biol.*, **202(12)**(1999), no. 6, 1589–1602.

[41] E.H.Wissler, Steady-state temperature distribution in man, *J. Appl. Physiol.*, **16(4)**(1961), no. 7, 734–740.

[42] E.H.Wissler, Pennes вЪ™ 1948 paper revisited, *J. Appl. Physiol.*, **85**(1998), 35–41.

Модель терморегуляции у животных, основанная на принципе производства энтропии

Михаил Ю. Захаров
Михаил Г. Садовский

Рассмотрена модель терморегуляции теплокровных животных, основанная на принципе производства энтропии.

Ключевые слова: терморегуляция, тепловыделение, температура кожи, производство энтропии, теплокровные животные.