RESEARCH ARTICLE

Huddling Behavior as Critical Phase Transition Triggered by Low Temperatures

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Huddling is a grouping behavior where animals maintain close bodily contact and save energy. We tested the hypothesis that this thermoregulatory behavior behaves as a system with continuous (second-order phase) transition called critical when the environmental temperature (driving parameter) is near a critical value. To do so, we followed theoretical and experimental approaches, examining data from geometrical models, metabolic rate during huddling in small mammals, and also conducting an experiment on thermoregulatory huddling behavior with white mice. Our results support all predictions for systems under continuous-phase transition triggered by low temperatures, a phenomenon reported for first time in a biological system. We suggest that huddling behavior in social animals, a recognized adaptive behavior, may be considered a self-organized system coupled with an external driving parameter. © 2011 Wiley Periodicals, Inc. Complexity 17: 35–43, 2011

Key Words: huddling; self-organization; energy

INTRODUCTION

B elf-organization is central to the description of physical and biological systems and is likely to operate at all levels of integration, including social organization [1, 2]. Among social animals, for example, there are behavioral interactions producing group cohesion. These interactions are viewed as a network of nonlinear connections among the multiple components of the system [3–7]. The rules guiding group organization depend on

Corresponding author: Mauricio Canals, Departamento de Ciencias Ecológicas, Universidad de Chile, Casilla 653, Santiago, Chile. E-mail: mcanals@uchile.cl several key factors: (i) the presence of leaders, (ii) group pattern building directed by a representation of the spatial or temporal relationships of the parts of a pattern (blueprints), (iii) recipes that each individual of the group possesses to build the whole pattern, and (iv) full-size mold that specifies the final pattern (templates) [8]. According to Camazine et al. [8], in terms of genetic coding all these alternatives are energetically costly. In contrast, a system in which a structure or pattern appears from the local interactions of the elements that make up the system, without central authorities or external elements imposing this pattern (i.e., a self-organized biological systems), be quite economical in both physiological and behavioral machinery; therefore, they are more likely to evolve through natural selection [8]. Also, self-organization may be an important mechanism allowing individuals to achieve group-level behavior in the first place, i.e., a process that may generate evolutionary novelties. Thus, it is expected that selective processes will favor mechanisms based on self-organization whenever the alternative mechanisms are costly or not viable. Self-organization in some behavioral patterns is triggered by environmental and/or internal cues, implying a state change from a nonorganized to an organized system. In others, criticality apparently self-organizes as energy and matter flow through the system (self-organized critical system) [2]. These state changes do not follow a discontinuous water-ice model (first-order transition phase) in which near the transition point both phases can coexist, but usually with a continuous variation in the intensity of the organization (second-order transition phase). Secondorder phase transition occurs when a new state of reduced symmetry (a pattern) develops from the disordered (at high temperature) phase. In addition, each phase has different thermodynamics properties. When a self-organized continuous transition is triggered by an external cue, the system follows the paradigmatic model of ferromagnetic materials [9]. During this dynamic change, the system is close to a breakpoint and also to a critical state [8, 9]. The system near a phase transition becomes critical and is characterized by: (i) a phase transition, (ii) a behavior without any characteristic length scale obeying a series of power laws with exponents called "critical exponents," and (iii) a spontaneous fractal organization [9].

Several aggregations have been suggested as self-organized pattern formations, such as the clustering of whirling beetles [10, 11], firebug overwintering aggregations, sow bug aggregations, aggregation of bees, larval aggregation [8], and thermoregulatory huddling behavior [12], among others. Thermoregulatory huddling has developed in several taxonomic groups, including small mammals, birds, reptiles, and insects. Convergence of huddling behavior among animals is a fascinating evolutionary event, emperor penguins being a notable case [13, 14]. In small mammals, huddling appears as an efficient response to low temperature with important consequences in energy saving and allocation of energy, which in turn affect the survival, rates of food ingestion, and individual fitness [15–28].

Thermoregulatory huddling behavior allows animals to survive during harsh environmental conditions, increasing individual fitness [14, 29, 30]. Among small rodents, huddling occurs within the nest and among pups and mothers. In this case, group sizes are comparatively low, between 5 and 10 individuals, which seem to be associated with a decrease in the proportion of energy saved when the group is greater than five individuals [26]. Nevertheless, among bats and birds, huddling groups size are larger [14].

Huddling induces metabolic depression without hypothermia [28] and is mainly attributed to the reduced surface area/volume ratio of the huddling group (but see Ref. 31). Indeed, on the basis of geometrical approaches, previously, we [26] proposed a general model to account for the reduction of the relative exposed area of grouped animals and for the decrease in metabolic energy expenditure during huddling behavior in small rodents. Here, we propose that huddling in our animal model (white mice = Mus musculus; CF-1), a small rodent that usually show this behavior, exhibits characteristics of a critical state system and may emerge as an outstanding example of selforganization with continuous-phase transition in natural systems. If this is accurate, near the phase transition the system could be not sensitive to the constituents or the interactions operating between them, falling into one of a limited set of universal classes that are defined by the exponents in the power laws describing the phase transition. Consequently, to test if huddling behavior near a phase transition becomes critical, we studied social thermoregulation (huddling) in white mice through both theoretical and experimental approaches.

In the theoretical approach, we explored different geometrical arrangements of huddling behavior through changes in the number of grouped individuals (*n*) and their consequences on mass-specific metabolic decrease. We considered a Euclidean array if during huddling there is a tendency to a spherical form, and autosimilar if during huddling there is a tendency to conserve the individual form, that is, if a group can be viewed as composed of parts that are similar to the whole group. Thus, the metabolic response allows us to infer indirectly the geometric assemble used by the grouped animals. Second, we empirically studied huddling behavior in white mice and compared our results against our theoretical proposals by testing if they follow the self-organized system under the critical conditions [9].

ANIMALS AND METHODS

We studied thermoregulatory huddling in 15 female laboratory white-mice CF-1 [body mass = 35.1 ± 3.6 g (average \pm standard deviation)] at eight environmental temperatures (T_a): 35, 32, 28, 24, 20, 16, 12, and 5°C. Each temperature was maintained 2 days. Previously, animals were maintained all together at room temperature and light:dark cycle = 12:12 with rat food pellet and water ad libitum.

Animals were exposed to experimental conditions and videotaped (JVC GR-D35OU) for 60 min from the top of the setup. All experiments started at 18:00 h. We used a circular black-painted open field (0.85 m^2) , which was





maintained inside a thermoregulated climatic chamber. Recordings were made every 2 days. To avoid the analysis of early exploratory behavior, only the last 30 min of each tape record was analyzed through random selection of five frames per test. An 8×8 grid was superposed on each picture, and the number of grouped and nongrouped individuals was counted (Figure 1). Groups were all aggregations where individuals exhibited physical contact. Thus, group size varied between 2 and 15. We measured the size of each group and counted the number of individuals within each grid cell. The variance-mean coefficient (CVM) of the number of individuals in each grid cell was defined as an index of huddling, an index that detected a

random location versus an aggregation pattern. As a direct measurement, we determined the distance (in cm) between each individual (d) by the following four rules: (i) d between two individuals was the minimum distance without the tail, (ii) d of one individual to a group was the minimum distance of the individual to the entire group, (iii) d between individuals of the same group was 0, and (iv) d between one individual within the group and an external one was considered as case ii. In each picture, we measured the distance between pairs of individuals and calculated the mean distance (D), allowing us to obtain five values for each temperature. Also, we estimated the fractal dimension of the edge (=surrounding area) of the

white-black silhouettes of each group (f_d) by the boxcounting method (five per test), implemented with the software BENOIT^(II) 1.2. A fractal is characterized by a fractional f_d , where the more convoluted geometry, the greater their f_d . For example, a convoluted line could have $f_d =$ 1.93, approaching the dimension of a surface ($f_d = 2$). Thus, f_d allows us to estimate directly the convolution of the geometry of the huddling group.

Because we followed a repeated measurement design, CVM of the number of individuals as well as f_d parameters among temperatures were compared with a Friedman test (five measurements per temperature). As an attempt to search for the critical temperature (T_c) and independent of the fundamental measurement (D), we conducted a piecewise linear regression between CVM of the number of individuals and T_{a} . CVM = $(b_0 + b_1T_a) \{T_a \le T_c\} + (b_2 + b_2) \}$ b_3T_a) { $T_a > T_c$ } with the Levenberg–Marquardt algorithm implemented in the STATISTICA[®] software, determining the $T_{\rm c}$ value at which the coefficient of determination (R^2) was maximum. Based on the power law $D = k \left[(T_a - T_c) \right]$ $T_{\rm c}$]^{α} = $k\tau^{\alpha}$, which was proposed for temperature-dependent physical-state transitions [9, 32], we performed a linear regression of log (D) on log (τ) and obtained the critical exponent α . We performed a sensibility analysis through changes in T_c and the number of points in the regression from five to three points nearly $T_{\rm c}$.

RESULTS

Theoretical Test

Metabolic rate (MR) is related to the surface area of an animal (A) and is represented by a power law MR = mA^{v} ; this equation also represents the MR of grouped individuals (MR_h): $MR_h = m_h A_h^{\nu}$, where A_h is the exposed area during huddling; m and $m_{\rm h}$ are arbitrary constants for grouped and nongrouped individuals [26]. Thus, the ratio $MR_h/MR = R_m$, where $R_{\rm m} = (m_{\rm h} / m) R_{\rm a}^{\rm v}$, $R_{\rm a}$ being the area ratio of grouped versus nongrouped animals. The exponent v may be derived from the empirical relationships between body mass (mb) and the thermal conductance [25-27]. As (i) MR at low temperatures follows the relationship MR = $C (T_{\rm b} - T_{\rm a})$, with C =thermal conductance, $T_{\rm b}$ = body temperature, and $T_{\rm a}$ = ambient temperature, (ii) C follows an allometric relation with body mass of 3.4 mb^{0.5} [33, 34], and (iii) assuming that body density is 1, then mb is related to area following mb = $K_{\rm m}A^{3/2}$, with $K_{\rm m}$ the Meh constant, a parameter that depends on the animal form [35]. Combining (i-iii), Canals et al. [26] proposed that MR = $C (T_{\rm b} - T_{\rm a}) = 3.4 \text{ mb}^{0.5} (T_{\rm b} - T_{\rm a}) = b_{\rm o}$ ${
m mb}^{0.5}$ = $b_{\rm o}~(A^{3/2})^{0.5}$ = $b_{\rm o}~A^{0.75}$, where $b_{\rm o}$ is a constant. Thus, the exponent v is 0.75, and $R_{\rm m} = (m_{\rm k}/m)R_{\rm a}^{0.75}$.

Autosimilar (Fractal) Solution

As the area of one individual (A_1) is $A_1 = K_m V_1^{2/3}$, where V_1 is the volume of one individual, the area of *n* non-

grouped similar individuals is $A_n = n \cdot K_{\rm m} V_1^{2/3} [K_{\rm m}$ is the mammalian Meh constant (≈ 10)]. Assuming our autosimilar argument (and also see Ref. [36]), *n* grouped individuals may be considered as one large individual made up of *n* similar individuals; thus, the area of *n* grouped individuals ($A_{\rm h}$) is $A_{\rm h} = K_{\rm m} \cdot (nV_1)^{2/3}$, and the area ratio ($R_{\rm a}$) is as follows:

$$R_{
m a} = rac{K_{
m m} \cdot n^{2/3} \cdot V_1^{2/3}}{n \cdot K_{
m m} \cdot V_1^{2/3}} = n^{-1/3}.$$

Finally, $R_{\rm m} = (m_{\rm h}/m)({\rm n}^{-1/3})^{0.75} = c \cdot n^{-1/4}$, with the initial condition n = 1, then $R_{\rm m} = 1$, and consequently c = 1. Thus, in an autosimilar arrangement of huddling behavior, we expect that $R_{\rm m} = n^{-1/4}$.

Euclidean Solution

However, the problem with an autosimilar solution is that it predicts a large surface with a limited volume, whereas animals in cold environments attempt to minimize their surface. As animals are unable to change their volume, we suggest that $A_{\rm h} = K_{\rm e} \cdot (nV_{\rm l})^{2/3}$, where $K_{\rm e} = 4.83597$ is the sphere-Meh constant. Then,

$$\begin{aligned} R_{\rm a} &= \frac{K_{\rm e} n^{2/3} \cdot V_1^{2/3}}{n \cdot K_{\rm m} \cdot V_1^{2/3}} = (K_{\rm e}/K_{\rm m}) \cdot n^{-1/3} \\ &= 0.483597 \cdot n^{-1/3} \approx 1/2 \cdot n^{-1/3}, \end{aligned}$$

and the Euclidean solution is:

$$R_{\rm m} = (m_{\rm k}/m) \ (1/2n^{-1/3})^{0.75} = 0.58 \cdot c \cdot n^{-1/4} = 0.58 \cdot n^{-1/4}.$$

In this case, we note that when n = 1, $R_{\rm m} = 0.58$, which means that a geometric change to a sphere-like geometry could lead to a 42% individual metabolic energy saving. That could be, for example, the case of isolated small rodents and birds that exposed to cold tend to a sphere morphology, respectively, bristling fur and feathers.

Small Mammal Solution

We previously proved [25, 26] that R_a in grouped deformable spheres and rigid prisms follows $R_a = (\phi/n + (1 - \phi))$, where ϕ is a deformation factor $\phi = 2a/A_1$, twice the ratio between the area *a* lost during grouping behavior and the area of one individual (A_1) [26]. Also, empirically we showed that this is true in deformable cylinders and that the area ratio, when included to explain the behavior of R_m , fully adjusts to the observed decrease of R_m in several small mammals [26, 27]. These relationships allow arriving at the "small mammal solution":

 $R_{\rm m} = (m_{\rm k}/m) \cdot (\phi \cdot n^{-1} + (1-\phi))^{3/4} = c \cdot (\phi \cdot n^{-1} + (1-\phi))^{3/4},$



Squares, rhomboids, and triangles represent the small mammal solution for different usual ϕ values.

Rearranging, this yields:

$$\begin{split} R_{\rm m} &= c \cdot n^{-1/4} \cdot n^{1/4} (\phi \cdot n^{-1} + (1 - \phi))^{3/4} \\ &= c \cdot n^{-1/4} \Big[n(\phi/n + (1 - \phi))^3 \Big]^{1/4}. \end{split}$$

Thus, the function $F(n) = [n(\phi/n + (1 - \phi))^3]^{1/4}$ represents deviations of the fractal as well as the Euclidean solution. If F(n) is close to 0.59, it will be more Euclidean, and if close to 1 it will be more autosimilar. This is a cubic-type function which for values of ϕ ranging from 0.5 to 0.8 decreases to a minimum of 0.68, but does not converge to the Euclidean solution. The minimum values are always obtained at low values of n, between 2 and 8. The function intersects with the fractal solution at $n^* = 5$, 10, and 30 for ϕ values of 0.5, 0.6, and 0.7, respectively (Figure 2). The relative reduction in MR during huddling of small mammals is within the range described by the autosimilar and the Euclidean solutions, but closer to the autosimilar solution because during huddling small mammals are unable to break their own geometrical constraints, and depending on the value of ϕ , the intercept between the small mammal solution and the autosimilar solution varies (Figure 2). Nevertheless, close to these intercept points the decrease of R_m during huddling is similar to the value expected for an autosimilar arrangement. As an example, for $\phi = 0.6$, a value closed to that of mice, $R_{\rm m}$ was 96.2, 97.7, 99.3, 100.8, 102.3, 103.6, and 105.0% of the expected value in the autosimilar solution for group sizes of 8, 9, 10, 11, 12, 13, and 14 individuals, respectively. This suggests that at these group sizes the geometrical assemble of the group approaches fractal geometry.

Experimental Test

Our empirical test of a self-organized huddling behavior in white mice showed that when T_a decreased, both the number of individuals grouped as well as the median size of the group increased to sizes in which the difference between autosimilar and small-mammal solutions was small (Table 1 and curve $\phi = 0.6$ in Figure 2). CVM of the number of individuals in each cell was different among $T_{\rm a}$ s (Friedman- χ^2_7 = 19.87, P = 0.0058) decreasing as a sigmoid (Figure 3).

The fractal dimension of the white-black silhouettes increased from 1.2 \pm 0.10 to 1.52 \pm 0.05 with a decrease of temperature from 35 to 5°C (Friedman- χ^2_7 = 26.20, P = 0.0005). Multiple comparisons showed that differences in f_d at different temperatures were mainly due to the high fractal dimension at temperatures of 16°C or less (Table 1).

The piecewise determination coefficient (R^2) was maximum, $R^2 = 0.947$ (P < 0.05) for a breakpoint $T_c = 16^{\circ}$ C, but was also high at 20°C: $R^2 = 0.859$ (P < 0.05) and at 12° C: $R^2 = 0.878$, but in this last case it was not statistically significant. Considering $T_c = 16^{\circ}C$ and the five points close to the breakpoint, the regression equation between log (D) and log (τ) was as follows: log (D) = 1.672 + (0.272) \pm 0.038) log (τ); $F_{1,2}$ = 50.43; P = 0.006; R^2 = 0.925 (Figure 4). The sensitivity analysis (Table 2) showed that at $T_{\rm c} = 16^{\circ}$ C, the variability in the exponent was small: $\alpha =$ 0.302 ± 0.044 , but considering all significant regressions the exponent " α " ranged from 0.153 \pm 0.011 at 15°C (five

TABLE 1

Characteristics of Huddling at Different Environmental Temperatures (T_a)

<i>T</i> _a (°C)	P (%)	S	f _d
35	32	2.6	1.25 ± 0.09^{c}
32	51	2.6	1.29 ± 0.07^{c}
28	48	3.0	$1.37\pm0.03^{ m b,c}$
24	48	5.8	$1.34 \pm 0.03^{\circ}$
20	45	3.5	1.34 ± 0.07^{c}
16	67	9.3	$1.41 \pm 0.06^{a,b}$
12	76	8.0	1.46 ± 0.03^{a}
5	91	14.5	1.52 ± 0.05^{a}

Proportions (P) of individuals recorded during huddling, values of the median size of each group (S), and fractal dimensions (f_d) of white-black silhouettes of groups (mean \pm 1 standard deviation). Similar letters indicate similar values after nonparametric multiple comparisons



Viduals in each grid cell (CVM) at different environmental temperatures (T_a) in white mice during huddling behavior. At higher T_as , CVM has a tendency to 1, which is expected for a random association. On the contrary, at lower T_as , values of CVM were higher, indicating that individuals became organized and huddled together. Error bars are standard deviations.

points) to 0.303 \pm 0.039 at 16°C (four points) with a mean value $\alpha = 0.240 \pm 0.066$. This suggests that independently of the critical temperature and of the number of points considered, the exponent that characterizes the phase transition exhibited low variability.

DISCUSSION

In the theoretical approach, we followed previous studies which considered that the reduction in surface volume is the principal factor accounting for the reduction in energy expenditure during huddling. Nevertheless, there are alternative explanations for this reduction. In fact, the increase in ambient temperature caused by huddling itself [14, 31], and adjustments in body temperature during huddling and psychophysiological effects [37, 38] have been proposed as mechanistic explanations for MR reductions during huddling. Although Hayes et al. [31] found that the increase in local temperature accounted for 55% of the energetic benefit during huddling in the vole Microtus agrestis, Gilbert et al. [14] reported that in the emperor penguin Aptenodytes forsteri at least two-thirds of energy saving was attributable to the reduction in cold-exposed body surfaces and one-third to the mild microclimate created within the groups. Adjustments in body temperatures and psychophysiological effects appear to have minor effects [36]. Thus, temperature-induced microenvironmental changes by individuals inside a group may effectively



Linear regression between the logarithm of the average distance between individuals (*D*) and the logarithm of the relative deviation of temperature from the critical temperature (τ), which is based on the power law proposed for temperature-dependent physical-state transitions [9, 29]. Error bars are standard deviations.

affect energy saving during huddling; however, these thermal changes seem to affect locally exposed surface areas of the neighbors, which finally decreases the area exposed to environmental temperature. In other words, temperature-induced microenvironmental changes during huddling seem to act through a reduction of the area exposed to cold, which is extremely relevant among large groups of endotherms such as penguins [13, 14], or during huddling in nests or inside burrows [21].

Although we did not conduct a dynamic analysis of the emergence of huddling, there is evidence that this behavior is a self-organized process. Indeed, Schank and Alberts [12] showed that huddling—as an aggregative behavior can emerge as a self-organizing process from autonomous individuals following simple sensorimotor rules. Among

TABLE 2

Changes in the α Exponent at Different Values of Critical Temperature (T_c) and Different Numbers (*n*) of Points Near T_c

15	0.153 ± 0.011*	0.163 ± 0.006*	0.164 ± 0.01*
16	$0.272 \pm 0.038^{*}$	$0.303 \pm 0.039^{*}$	0.331 ± 0.059
17	$0.238 \pm 0.029^{*}$	$0.261~\pm~0.026^{*}$	0.280 ± 0.043

rodent species, huddling became spontaneous at low T_a with groups of two to three individuals in close contact without any, already reported, group leader or preestablished configurations, because each group is different.

The main environmental trigger of this behavior seems to be low T_a ; nevertheless, in rats there are some reports that other nonthermal cues could elicit huddling [39]. Our results suggest that critical temperature is round about 16 and 20°C, as all statistical analyses of the relationships CVM versus T_a and the evolution of group size showed that at 16°C there was a change in these variables and also in the fractal dimension. In fact, between 20 and 28°C, the median group size was about 4, whereas at 16° C it increased to 9. These $T_{\rm a}$ values seem reasonable, as the lower limit of thermoneutrality in mice is 25-30°C [40]. Interestingly, and considering that in mice $\phi = 0.58$ [26], the group size observed at temperatures of 16° C or less (S = 9.3, 8.0, and 14.5) is near the intersection between autosimilar and small mammal solutions (Figure 2), showing that at these group size the geometrical assemble of the group is roughly autosimilar, which is one of the main characteristics of a fractal geometry. Also, the fractal dimension changed in the transition zone from 1.3 to nearly 1.45, as expected in a spontaneous fractal organization. The actual fractal dimension of the group can be estimated as the calculated dimension plus one ($F_{\rm D} = f_{\rm d}$ +1; see Ref. 41) because silhouettes were a two-dimensional section of the group, but the group is three dimensional. In the huddling dynamics, there was a transition from a situation mainly governed by dimensions near the topological dimension of a planar surface (dimension = 2), for example, $F_{\rm D}$ = 2.2 at 35°C, to a more complex figure with fractal-like groups, for example, $F_D = 2.52$ at 5°C. This is surprising because fractals exhibit larger area for a given volume, exactly the opposite of the biological function of huddling. However, as our models shown, at a given group size, animals in groups cannot break their own geometrical constraints, showing a fractal-like geometry instead of a Euclidean geometry.

As expected for a second-order phase transition of a thermodynamic system, the variance-mean coefficient of the individuals in each grid cell followed a sigmoid curve. Nevertheless, we chose to estimate the critical temperature from the relationships CVM versus T_a because it is an independent criterion of our main function of interest, which is the distance between individuals. This has the advantage of being a continuous variable that, under our conditions, is 0 when individuals are in contact. Also, the power law obtained showed an adequate data adjustment for a critical temperature of 16°C. Nevertheless, the sensitivity analysis also showed a significant adjustment at critical temperatures between 14 and 17°C without a large variation in the α exponent. The same analysis revealed

that the variability in the α exponent was low when changing the number of points near T_c , which is relevant because the critical exponent should be estimated only near the critical temperature.

In summary, we tested the hypothesis that thermoregulatory huddling behavior, a self-organized phenomenon, behaves as a system with continuous (second-order)-phase transition called critical when the environmental temperature (driving parameter) is near a critical value. Our results support all predictions for critical systems under phase transition [9]: (1) A transition from nongrouped individuals at high T_a to huddling at low T_a s. This change was represented by a sigmoid change in CVM of the number of individuals in each grid cell, as expected for that continuous-phase transition; (2) the main descriptor of huddling behavior (D) followed a power law as a function of T_a near the critical environmental temperature, and (3) in the transition-phase zone, the group size did not differ from autosimilar behavior and became spontaneously organized in fractals. This suggests that huddling behavior may be considered as a transition between two states (nonordered at high temperature and ordered at low temperature). Each state has their own thermodynamics characteristics, where the system falls into one of universal classes defined by its critical exponent. Near the continuous-phase transition the system could be not very sensitive to the nature of the constituents or the details of the interactions subsisting among the individuals during the huddling dynamics. We predict that huddling dynamics in other species will be represented by the same exponent (i.e., falling in the same universal class).

During the last few years, there is increasing evidence that self-organization plays an important role in the behavior and development of biological systems [2]. Also, self-organization acting in concert with natural selection may be part of the whole evolutionary process [2, 42-45]. The importance of abiotic factors, mainly the thermal environment, in determining behavioral traits has been a central issue of discussion [46-48]. Physiological and environmental constraints are determinant in the relationship between abiotic variables and the spatial distribution of individuals and populations, but the processes driving such patterns remain poorly understood. We believe that our results help to visualize behavioral social thermoregulation, a recognized adaptive behavior as a self-organized second-order thermodynamic system coupled with an external driving, which to our knowledge has not been reported in biological systems.

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REFERENCES

- 1. Schroeder, M. Fractal, Chaos, Power Laws; WH Freeman & Co: New York, 1991; p 429.
- 2. Halley, J.D.; Winkler, D.A. Critical-like self-organization and natural selection: Two facets of a single evolutionary process? Biosystems 2008, 92, 148–158.
- 3. Shimada, I.; Kawasoe, Y.; Hara, H. A temporal model of animal behavior based on a fractality in the feeding of *Drosophila melanogaster*. Biol Cyber 1991, 68, 477–481.
- 4. Alados, C.L.; Escós, J.M.; Emlen, J.M. Fractal structure of sequential behavior patterns: An indicator of stress. Anim Behav 1996, 51, 437–443.
- 5. Alados, C.L.; Huffman, M.A. Fractal long-range correlations in behavioral sequences of wild chimpanzees: A non invasive analytical tool for the evaluation of health. Ethology 2000, 106, 105–116.
- 6. María, G.A.; Escós, J.; Alados, C.L. Complexity of behavioral sequences and their relation to stress conditions in chickens (*Gallus gallus domesticus*): A non-invasive technique to evaluate animal welfare. Appl Anim Behav Sci 2004, 86, 93–104.
- 7. Canals, M.; Solís, R. Geometry of living system and its importance in medicine. Rev Med Chile 2005, 133, 1097–1107.
- 8. Camazine, M.; Deneubourg, J.-L.; Franks, N.R.; Sneyd, J.; Theraulaz, G.; Bonabeau, E. Self-Organization in Biological Systems; Princeton University Press: New Jersey, 2001; pp 5–93.
- 9. Gisiger, T. Scale invariance in biology: Coincidence or footprint of a universal mechanism? Biol Rev 2001, 76, 161–209.
- 10. Deneubourg, J.L.; Gregoire, J.C.; Le Fort, E. Kinetics of the larval gregarious behavior in the bark beetle *Dendroctonus micans*. J Insect Behav 1990, 3, 169–182.
- 11. Deneubourg, J.L.; Aron, S.; Goss, S.; Pasteels, J.M. The self-organizing exploratory pattern of the Argentine ant *Iridomyrmex humilis*. J Insect Behav 1990, 3, 159–168.
- 12. Schank, J.C.; Alberts, J.R. Self-organized huddles of rat pups modeled by simple rules of individual behavior. J Theor Biol 1997, 1, 11–25.
- 13. Gilbert, C.; Robertson, G.; Le Maho, I.; Naito, Y.; Ancel, A. Huddling behavior in emperor penguins: Dynamics of huddling. Physiol Behav 2006, 88, 479–488.
- 14. Gilbert, C.; Blanc, S.; Le Maho, Y.; Ancel, A. Energy saving process in huddling emperor penguins: From experiments to theory. J Exp Biol 2007, 211, 1–8.
- 15. Gilbert, C.; Blanc, S; Giroud, S.; Trabalon, M.; Le Maho, Y.; Perret, M.; Ancel, A. Role of huddling on the energetic of growth in a newborn altricial mammal. Am J Physiol 2007, 293, R867–R876.
- 16. Sealander, J.A. The relationship of nest protection and huddling to survival in *Peromyscus* at low temperature. Ecology 1952, 33, 33–71.
- 17. Trojan, R.; Wojciechowska, B. The effect of huddling on the resting metabolism rate of the European common vole *Microtus arvalis* (Pall). Bull Acad Pol Sci 1968, 16, 107–109.
- 18. Gebczynski, M. Social regulation of body temperature in the bank vole. Acta Theriol 1969, 4, 427–440.
- 19. Fedyk, A. Social thermoregulation in Apodemus flavicollis (Melchior, 1834). Acta Theriol 1971, 16, 221–229.
- 20. Tertil, R. The effect of behavioral thermoregulation on the daily metabolism of *Apodemus agrarius*. Acta Theriol 1972, 22, 328–332.
- 21. Springer, S.; Gregory, P.; Barret, W. Importance of social grouping on bioenergetics of the golden mouse, *Ochrotomys nutalli*. J Mammal 1981, 62, 628–630.
- 22. Vogt, D.F; Lynch, G.R. Influence of ambient temperature, nest availability, huddling and daily torpor on energy expenditure in the white footed mouse *Peromyscus leucopus*. Physiol Zool 1982, 55, 56–63.
- 23. Andrews, R.V.; Belknap, R.W. Bioenergetic benefit of huddling by deer mice *Peromyscus maniculatus*. Comp Biochem Physiol A 1986, 87, 345–348.
- 24. Bozinovic, F.; Rosenmann, M.; Veloso, C. Termorregulación conductual en *Phyllotis darwini* (Rodentia: Cricetidae): Efecto de la temperatura ambiente, uso de nidos y agrupamiento social sobre el gasto de energía. Rev Chil Hist Nat 1988, 61, 81–86.
- 25. Canals, M.; Rosenmann, M.; Bozinovic, F. Energetics and geometry of huddling in small mammals. J Theor Biol 1989, 141, 181–189.
- 26. Canals, M.; Rosenmann, M.; Bozinovic, F. Geometrical aspects of the effectiveness of huddling in small mammals. Acta Theriol 1997, 42, 321–328.
- 27. Canals, M.; Rosenmann, M.; Novoa, F.F.; Bozinovic, F. Modulating factors of the energetic effectiveness of huddling in small mammals. Acta Theriol 1998, 43, 337–348.
- 28. Gilbert, C.; McCafferty, D.; Le Maho, I.; Martrette, J.M.; Giroud, S.; Blanc, S.; Ancel, A. One for all and all for one: The energetic benefit of huddling in endotherms. Biol Rev 2010, 85, 545–569.
- 29. Ancel, A.; Visser, H.; Handrich, Y.; Masman, D.; Le Maho, Y. Energy saving in huddling penguins. Nature 1997, 385, 304–305.
- Batcheler, P.; Kinney, R.O.; Demlow, L.; Lynch, C.B. Effect of temperature and social interactions on huddling behavior in *Mus musculus*. Physiol Behav 1983, 31, 97–102.
- 31. Hayes, J.P.; Speakman, J.R.; Racey, P.A. The contribution of local heating and reducing exposed surface area to the energetic benefit of huddling by short tailed field voles (*Microtus agrestis*). Physiol Zool 1992, 64, 742–762.
- 32. Sato, H.; Kawamura, Y.; Ogawa, T.; Murakami, Y.; Ossumi, H.; Mizumaki, M.; Ikeda, N. Critical phenomena in helical magnet β-MnO₂: X-ray magnetic scattering study. Physica B 2003, 329, 757–758.
- 33. Herreid, C.F; Kessel, B. Thermal conductance in birds and mammals. Comp Biochem Physiol A 1967, 21, 405-414.
- 34. Bozinovic, F.; Rosenmann, M. Comparative energetics of South American cricetid rodents. Comp Biochem Physiol A 1988, 91, 195–202.

- 35. Kleiber, M. The Fire of Life; Wiley: New York, 1961; p 454.
- 36. Contreras, L.C. Bioenergetics of huddling: Test of a psychophysiological hypothesis. J Mammal 1984, 65, 256-262.
- 37. Vickery, W.L.; Millar, J.S. The energetics of huddling by endotherms. Oikos 1984, 43, 88–93.
- 38. Martin, R.A.; Fiorentini, M.; Connors, F. Social facilitation of reduced oxygen consumption in *Mus musculus* and *Meriones unguiculatus*. Comp Biochem Physiol A 1980, 65, 519–522.
- 39. Alberts, J.R. Huddling by rats pups: Multisensory control of contact behavior. J Comp Physiol Psychol 1978, 92, 220–230.
- 40. Gebczynski, A.K. Daily variation of thermoregulatory costs in laboratory mice selected for high and low basal metabolic rate. J Therm Biol 2005, 3, 187–193.
- 41. Rigaut, J.P. An empirical formulation relating boundary lengths to resolution in specimens showing "non-ideally fractal" dimensions. J Microsc 1984, 133, 41–54.
- 42. Kauffman, S.A. Antichaos and adaptation. Sci Am 1991, 265, 78-84.
- 43. Kauffman, S.A. The origins of order: Self-organization and selection in evolution; Oxford University Press: New York, 1993; p 740.
- 44. Solé, R.V.; Manrubia, S.C.; Benton, M.; Kauffman, S.; Bak, P. Criticality and scaling in evolutionary ecology. TREE 1999, 14, 156–160.
- 45. Weber, B.H. Origins of order in dynamical models. Biol Philos 1998, 13, 133-144.
- 46. Bozinovic, F.; Vásquez, R.A. Patch use in a diurnal rodent: Handling and searching under thermoregulatory costs. Funct Ecol 1999, 13, 602–610.
- 47. Bozinovic, F.; Lagos, J.A.; Vásquez, R.A.; Kenagy, G.J. Time and energy use under thermoregulatory constraints in a diurnal rodent. J Therm Biol 2000, 25, 251–256.
- 48. Vásquez, R.A.; Ebensperger, L.A.; Bozinovic, F. The effect of microhabitat on running velocity, intermittent locomotion, and vigilance in a diurnal rodent. Behav Ecol 2002, 13, 182–187.