Self-organization in the dynamics of huddling behavior in *Octodon degus* in two contrasting seasons

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Abstract In small mammals, huddling appears as an efficient response to low temperature with important consequences in energy saving, which in turn affect individual fitness. It has been proposed that this behavior is a self-organized process. However, to prove self-organization, it is necessary to study the dynamics of huddling, ruling out the presence of leaders. The objectives of this study were to determine the dynamics of huddling at different temperatures in *Octodon degus*, documenting the presence or absence of leaders, and to study the consistency of this behavior in two contrasting seasons. We found that huddling dynamics did not indicate the presence of leader initiators of the clustering at lower temperatures. There was no deterministic pattern in huddling dynamics, in any period or at any temperature, suggesting a behavior triggered spontaneously without any order, hierarchy, or recipes. The effect of temperature on huddling behavior was marked and similar in both seasons. The variability of the huddled groups was greater at higher temperatures, which is explained by a greater movement of individuals and more frequent variations in the number and size of the groups at higher temperatures. The results describe huddling as a self-organized behavior, more economical than other physiological processes and therefore preserved by natural selection. This increases its importance for survival and fitness given the significant reduction in energy expenditure achieved under conditions of low temperatures and reduced availability of food, such as during the breeding season of *O. degus*.

Keywords Huddling · Self-organization · Leaders

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Introduction

In the last few years, there is increasing evidence that self-organization (i.e., a process where some form of global order arises out of the local interactions between the components of an initially disordered system) plays an important role in the behavior and development of biological systems (Halley and Winkler 2008). Several forms of social aggregation and sociability have been suggested as self-organized pattern formations, such as the clustering of whirling beetles, firebug overwintering aggregations, sow bug aggregations, aggregations of bees, larval aggregation (Camazine et al. 2001), and huddling behavior (Schank and Alberts 1997), among others.

To compensate for the increased energy expenditure caused by exposure to low temperatures, individuals may exhibit behavioral responses such as social grouping or huddling

(Canals et al. 1998; Gilbert et al. 2010). Thermoregulatory huddling has developed in several taxonomic groups (Gilbert et al. 2007, 2008, 2012), appearing as an efficient response to low temperature with important consequences to energy saving and allocation, which in turn affect survival, rates of food ingestion, and in consequence the individual fitness (Sealander 1952; Trojan and Wojciechowska 1968; Springer et al. 1981; Andrews and Belknap 1986; Bozinovic et al. 1988; Arnold 1988, 1990; Canals et al. 1989, 1997, 1998; Gilbert et al. 2007, 2010, 2012). Also, huddling prevents an increase in basal metabolic rate when animals are acclimated to cold conditions, exerting a modulator effect on thermal acclimation of the basal metabolic rate (Nuñez-Villegas et al. 2014). Among small rodents, huddling occurs within the nest and among pups and mothers. In this case, group sizes are between five and ten individuals, which appear to be associated with a decrease in the proportion of energy saved when the group is larger than five individuals (Canals et al. 1997). Nevertheless, among bats and birds, huddling group sizes are larger (Gilbert et al. 2007). Huddling induces metabolic depression without hypothermia (Gilbert et al. 2010) and is mainly attributed to the reduced surface area/volume ratio of the huddling group. Recently, Gilbert et al. (2012) reported through thermal images that at 14°C, the mean surface temperature of the huddle was higher than the mean temperature of isolated pups. Thus, huddling behavior reduces energy costs by reducing the metabolic rate and average thermal conductance of each individual in the group mainly because of the reduction in surface area and altering the thermal environment experienced by animals exposed to the cold. Nevertheless, there are alternative explanations for this reduction such as the increase in ambient temperature caused by huddling itself (Gilbert et al. 2007, 2012) and adjustments in body temperature during huddling and psycho-physiological effects (Martin et al. 1980). However, adjustments of body temperature and psycho-physiological effects appear to have minor importance (Contreras 1984). Thus, temperature-induced microenvironment changes by individuals inside a group may effectively 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.

There is evidence that this behavior is a self-organized process. Indeed Schank and Alberts (1997) showed that huddling—as an aggregative behavior—can emerge as a self–organizing process from autonomous individuals following simple sensorimotor rules. Among rodent species, huddling becomes spontaneous at low environmental temperature (T_a), with groups of two to three individuals in close contact without any reported group leader or pre-established configurations. The main environmental trigger of this behavior seems to be low T_a; nevertheless, in rats, there are some reports that other non-thermal cues, such as olfactory and contact cues,

could elicit huddling (Alberts 2007). Previous results support all predictions for systems under continuous phase transition triggered by low temperatures, a phenomenon recently reported for the first time in a biological system (Canals and Bozinovic 2011). These authors suggested that huddling behavior in social animals, a recognized adaptive behavior, may be considered to be a self-organized system coupled with an external driving parameter.

However, to prove self-organization, it is necessary to study huddling behavior discounting the presence of leaders and of deterministic patterns in its dynamics (Camazine et al. 2001). These dynamics can also be affected by hormonal cycles typical of the breeding season, in which the behavior of different species is well documented (Solís and Rosenmann 1990; Adkins-Regan 2005). In this study, we analyze the dynamics of huddling in Octodon degus, a social species that exhibits this behavior, in order to test the hypothesis that if huddling is a self-organized behavior, there will not be initiator leaders and deterministic patterns during huddling dynamics. If huddling is a self-organized behavior triggered by thermal stimuli, then it will occur in the absence of a leader. If not, it will be possible to distinguish some pattern of aggregation and a specific individual leading this behavior.

Materials and methods

Study animals

The rodent O. degus (Octodontidae), endemic to Chile, was used as experimental model. This species inhabits the regions from Atacama to the O'Higgins Region, in the area between Vallenar and Rapel in Chile (Muñoz-Pedreros 2000). O. degus typically exhibits crepuscular activity, with two peaks of maximum activity at 08:30 and 19:30 in periods ranging from 05:00–10:00 and 17:00–21:00 (Muñoz-Pedreros 2000). The rest of the time individuals rest in their burrows connected by trails. O. degus is a highly social rodent (Ovtscharoff and Braun 2001; Ebensperger and Wallem 2002) that lives in family groups (one male and one or more females and their offspring) within their burrows (Ebensperger et al. 2004). The breeding season begins in May–June and runs through August–September. Births usually occur during the spring, but a second pupping can occur in December (Muñoz-Pedreros 2000; Colby et al. 2012).

Wild adult individuals of O. degus used in this study were captured during March 2009 in Rinconada de Maipú, Santiago (33°31′ S, 70°50′ W) by using Sherman traps. The rodents were weighed with a balance (Shimadzu, AUX 220± 1 g) and identified by drawing capillary patterns with a mark, that is, fading the fur of the back-lumbar area with bleach. They were moved to the laboratory where they were kept in individual cages at 20±2 °C, 12:12 light/dark period, and with

ad libitum food until the experimental trials were finished in November. The body mass (M_b: average±1 standard deviation) of the individuals were M_b=180.29±25.42 g in total and 173.86±27.32 and 181.08±23.01 for males and females, respectively.

Experimental design

Thirteen individuals were introduced into an experimental arena, a circular chamber 60 cm deep and 110 cm in diameter, with the floor and internal walls painted black. The arena was placed inside a thermoregulated chamber of 3.90×1.49 m with no windows. The individuals were sequentially exposed to eight temperatures in separate trials every 2 days: 35, 32, 28, 24, 20, 16, 12, and 5 °C. Thus, a complete run took 22 days.

As stated previously, individuals should be grouped randomly in no specific order and without learning effect if huddling is a self-organized behavior. For this reason, huddling behavior was recorded twice: first in May (autumn time) and subsequently in November (spring time). In this way, comparisons between these two runs of experimental trials permitted to check for requirements of self-organization. During the time elapsing between the first and second experimental run of trials, the individuals were kept in individual cages and with food ad libitum at the same initial conditions. The same 13 individuals were used in the two periods with the exception of individual number 7, which died and was replaced by a new individual (X) bred in the animal vivarium. At the start of the experimental trials of the second run, individuals were marked and weighed again.

In each experimental trial, the individuals were recorded in the morning, which is during the period of activity of this species. The experimental trials lasted 1 h, starting after 30 min of adaptation. The recordings were made with a digital video camera (Panasonic PV-GS90), which was located 2 m above the arena. The arena was covered with a glass plate to prevent the animals from escaping.

Each video recorded was studied in full, recognizing each of the individuals by its mark. For analyses of distances and dispersion among individuals, 20 segments of 1 min from the second half hour of recording were randomly selected in each recording. Then, we selected the most representative image of the activities of each 1-min segment.

Analyses

We define a cluster as a group in which the animals were in physical contact. In the full analysis of each film, the proportion of cases in which each individual was part of (a) the first cluster (= times in which a particular individual was part of the first cluster/number of experimental trials) and (b) any cluster (= times in which a particular individual was part of any

cluster in 30 observations in each trial/number of observations) were recorded. We operatively define a leader as an individual or a pair of individuals which always or in a statistically significant proportion participate in the first group in both experimental periods. The individual proportions were compared with the forest plot in which these are plotted with the confidence interval for the average proportion. Sex differences were studied with a Λ-Wilks test for repeated measurements (arcsin-transformed). Following the methodology described by Alberts (2007), the dynamics of clustering at each temperature was characterized by describing the groupings at each instant of time. Combinations of groups of individuals and isolated individuals were called "aggregons" (following Alberts (2007)). For example, a (7-3-1-1-1) aggregon means a group of seven individuals, a group of three individuals, and three isolated individuals. Each of the possible aggregons was associated with a particular value that we called the aggregon value (AV). The AVs depend primarily on the number of individuals in the largest cluster and secondarily on the other clusters ordered from largest to smallest (Table 1). Thus, for each experimental temperature, we obtained a time series of AVs that represents quantitatively the huddling dynamics.

For analyses of distance and dispersion among individuals, a grid of 8×8 square cells was overlaid on each image. The following two variables were determined in each image:

1. The distance between the individuals was determined using the following rules (Canals and Bozinovic 2011): (a) for the distance between two individuals, the shortest distance without considering the tail was considered, (b) for the distance from an isolated individual to a group, the shortest distance between the individual and the group, (c) the distance between individuals of the same group is considered to be zero, and (d) the distance from an individual within a group to another outside of the group was determined as in rule b. Thus, for each image 78=13!/(2! 11!) (all combinations of two obtained from a total of 13 individuals) values were recorded, and the average distance of these values was obtained.

2. The variance/mean ratio of the number of individuals per grid cell, called the index of dispersion (I_d), was calculated for each image, which allows determining whether a distribution of individuals is random (I_d=1), grouped (I_d>1) or regular (I_d <1) (Canals and Bozinovic 2011).

To study the effect of temperature on the response variables—average distance between individuals, the I_d, and the average aggregon value and how these variables vary across the two time experimental periods, we performed two-way analyses of variance (in STATA 11.2 software). We previously tested the assumptions of the ANOVA: normality with Shapiro–Wilks test, and homoskedasticity with Bartlett test. The average aggregon value was log-transformed because the variances were not homogenous.

Table 1 Table of conversion from aggregons (A_i) to an aggregon value (AV), ordered from largest to smallest

A1	A2	A3	…	…	…	…	…	…	…	…	…	…	AV
1	1	1	1	1	1	1	1	1	1	1	1	1	1
2	1	1	1	1	1	1	1	1	1	1	1		2
2	2	1	1	1	1	1	1	1	1	1			3
2	2	2	1	1	1	1	1	1	1				4
2	2	2	2	1	1	1	1	1					5
2	2	2	2	2	1	1	1						6
2	2	2	2	2	2	1							7
3	1	1	1	1	1	1	1	1	1	1			8
3	2	1	1	1	1	1	1	1	1				9
3	2	2	1	1	1	1	1	1					10
3	2	2	2	1	1	1	1						11
3	2	2	2	2	1	1							12
3	2	2	2	2	2								13
3	3	1	1	1	1	1	1	1					14
…	…	…	…	…	…	…	…	…	…	…	…	…	…
…	…	…	…	…	…	…	…	…	…	…	…	…	…
9	1	1	1	1									90
9	2	1	1										91
9	2	2											92
9	3	1											93
9	4												94
10	1	1	1										95
10	2	1											96
10	3												97
11	1	1											98
11	2												99
12	1												100
13													101

Additionally, to search for temporal patterns, time series of aggregon values were analyzed by autocorrelation (ACF) and partial autocorrelation functions (PACF) for each temperature and each experimental run. If any deterministic pattern exists, it would produce a significant peak in ACF or in PACF. Non-significant autocorrelations and partial autocorrelations indicate a totally random process (white noise). Significance level for all tests was $\alpha = 0.05$.
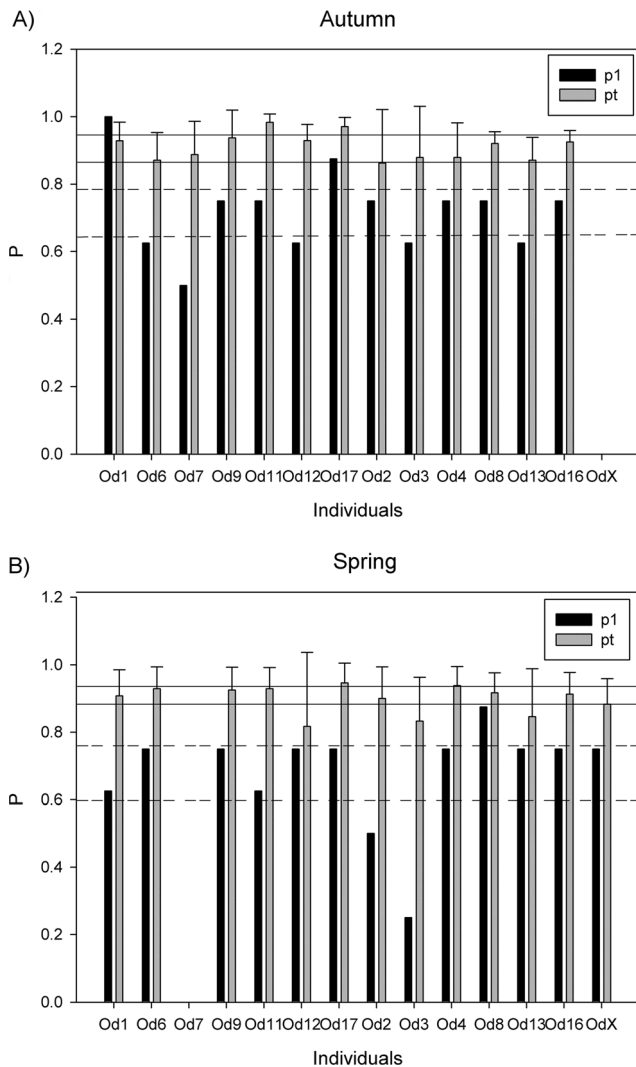
Results

The chance to be part of the first group was high in both experimental series of trials: 0.721 ± 0.127 (mean ± standard deviation) in the first and 0.683 ± 0.158 in second run, respectively. Overall probability was 0.696 ± 0.112, and there were no consistent differences between specific individuals. We note that while in May (first run) individuals 1 and 17 seem to have had more participation, in November (second run) individual 8 participated more in the first group. Similarly, the probability in the entire experiment of belonging to any group was even higher: 0.911 ± 0.039 in the first, 0.899 ± 0.042 in the second run of experimental series, and 0.904 ± 0.032 overall, with no animals that clearly had greater participation than others in a group. No differences were detected between sexes: Λ-Wilks$=0.47$, $p=0.16$ and Λ-Wilks$=0.87$, $p=0.53$ for the probability of belonging to any group and to be part of the first group, respectively. Thus, while in the first experimental run individuals Od11 and Od17 (both females) appeared to be more grouped, in the second there were several other individuals who were in groups more often, such as the male Od8 (Fig. 1).

The time series of aggregon values for all temperatures and both experimental runs followed a white noise pattern (Fig. 2). There was no effect of the period on aggregon average value ($F_{1, 315}=2.61$, $p=0.11$), but there was a clear temperature effect ($F_{7, 315}=73.29$, $p<0.001$) and temperature–period interaction effect ($F_{15, 315}=7.60$, $p=0.006$), indicating a more pronounced effect in the first than in the second run (Fig. 3). The variance of the aggregon values was greater at higher temperatures (Bartlett test$=284.98$, $p<0.001$) and was higher in the first (CV$=0.221$) than in the second run (CV$=0.16$) (Bartlett test$=11.94$, $p=0.0006$).

Average distances between individuals were reduced as the function of temperature decreased ($F_{7, 316}=115.3$, $p<0.001$) with no difference between experimental runs ($F_{1, 316}=0.332$, $p=0.565$) or interaction ($F_{15, 316}=0.679$, $p=0.411$). Conversely, the I_d values were higher (greater clustering) at lower temperatures ($F_{7, 315}=91.55$, $p<0.001$) without effects of period ($F_{1, 315}=0.989$, $p=0.321$) and without interaction ($F_{15, 315}=1.026$, $p=0.312$) (Fig. 4).
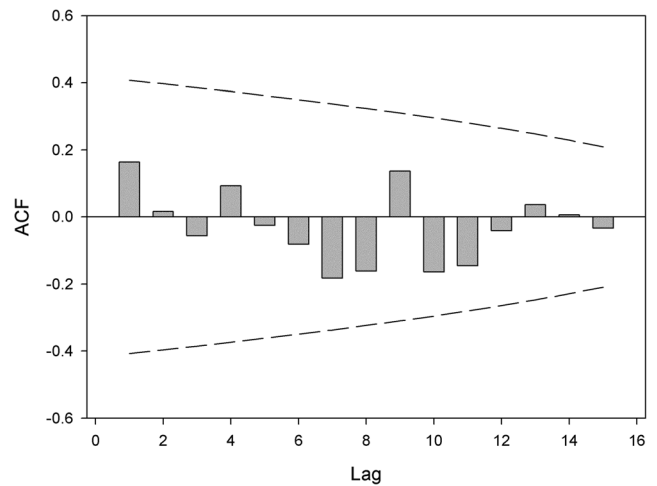
Discussion

The analysis of huddling dynamics did not indicate the presence of leaders initiating the clustering at lower temperatures. While there were individuals who most often formed part of the first group, this trend was not maintained from one temperature to another; the initiators of the first aggregons were different in the first and second run of experimental trials. These results are confirmed by considering the probabilities of each individual to be part of a group because, independent of the time, all individuals showed similar odds of huddling and a high tendency to huddle, which suggests that the behavior of huddling in *O. degus* is not initiated by leaders. This contrasts with the behavior reported in some vertebrates, in which the presence of one or more individuals who are experienced or have prior information makes the rest of the group follow and produces a consensus among the individuals in the

group (Couzin et al. 2005) or in which there is a hierarchy in the spatial arrangement of individuals in the group (Nagy et al. 2010).

The absence of leaders resembles the dynamics observed in the emperor penguin (*Aptenodytes forsteri*), in which there are waves of motion that occur during thermoregulation clustering; although they seem coordinated, they do not follow a hierarchical order or movements initiated by one or more leaders (Zitterbart et al. 2011). The presence of a leader in the formation of a group would require the group leader to have knowledge of the desired pattern and to be able to maintain a synoptic view of the emerging structure and communicate instructions to the rest of the group. In the context of huddling behavior, this would have meant finding one or a
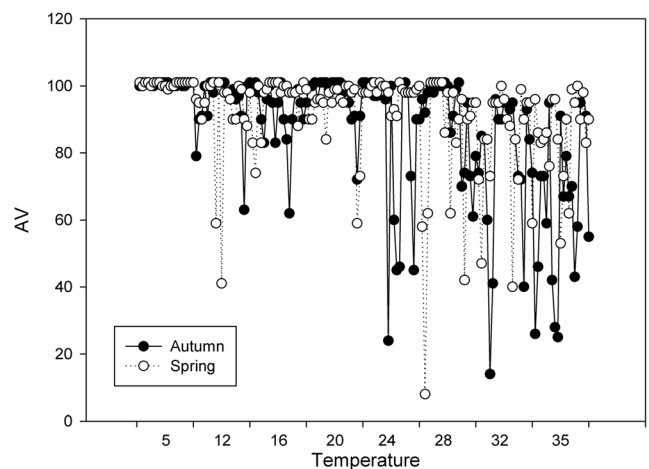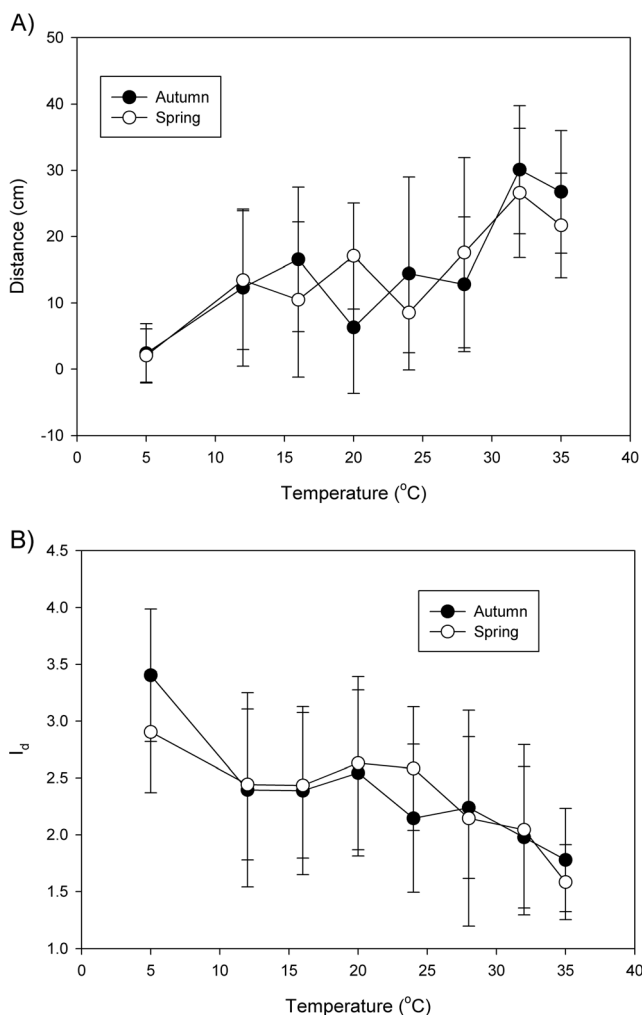

Fig. 2 Example of an autocorrelation function (*ACF*) of time series of aggregon values. All autocorrelations were within the confidence bands of 0, which is characteristic of a white noise time series. The series shown was obtained at 24 °C in autumn

pair of initiator individuals with such behavior, which did not happen in this research. But there are other possibilities, such as blueprints, which means that each member of a group has a personal copy or idea of the pattern to build. Other possibilities are sequences of actions that lead to the formation of a pattern (recipes; sensu Camazine et al. 2001) and templates which require a form that serves as a template for the formation of the group (Camazine et al. 2001). In the huddling behavior observed in our study, there were no environmental elements that could serve as templates. The groups were highly variable in size and shape as we could observe in the variability of the AV values, ruling out the possibility of blueprints. The existence of recipes leads to the recognition of deterministic patterns in the dynamics of huddling. This fact did not occur in our results at any temperature or in any period. Thus, the absence of leaders, coupled with these facts, implies a self-organized behavior (sensu Camazine et al. 2001)

Fig. 1 Plot of the probability to be part of the first group (*p1*, *black bars*) and to be part of any group (*pt*, *gray bars*) for individuals of *O. degus* during huddling behavior in two seasons: autumn (**a**) and spring (**b**) at different temperatures. The individuals were named with the *letters Od* and a reference *number*: *Od1*, *Od6*, *Od7*, *Od9*, *Od11*, *Od12* and *Od17* were females. *Lines* represent the confidence interval for p1 (*dashed line*) and for pt (*continuous line*)

Fig. 3 Variation of aggregon values at different temperatures in two seasons: autumn and spring

Fig. 4 Variation of the distance (**a**) and of the dispersion index (**b**) among individuals at different temperatures in two seasons: autumn and spring. *Bars* represent standard deviations

initiated spontaneously without any order, hierarchy, or recipes. These results are consistent with other group behaviors in this species such as the collective detection of predators. Some studies revealed that collective predator detection is also a random process without coordination in their anti-predator group vigilance, preventing temporal overlapping among individuals, and independent of group attributes such as genetic relatedness (Ebensperger et al. 2006; Quirici et al. 2008, 2013).

In *O. degus*, we observed a progressive reduction in the distance among individuals and a progressive increase of the dispersion index as a function of temperature, without a clear break in the curves of these variables. This contrasts with the huddling dynamics shown by *Mus musculus* in the same conditions, where a sharper breakpoint at temperatures between 15 and 20 °C was observed (Canals and Bozinovic 2011). This could be explained because *O. degus* has greater sociability and more tendency to huddle than *M. musculus*. Average distances between individuals observed in *M. musculus* were

markedly greater than those of *O. degus* when exposed to the same temperatures used in this study (Canals et al. 1998; Canals and Bozinovic 2011). For example, at 24 °C, a temperature below the thermoneutral zone for both species, the average distance recorded in *M. musculus* was 44.3 cm (Canals and Bozinovic 2011) and for *O. degus* was 14.4 cm; at the lowest temperature (5 °C), these were 5.2 and 2.3 cm, respectively. This behavior increased in intensity as the temperature decreased, which is shown as greater dispersion indexes at low temperatures. However, huddling was evident at all temperatures in *O. degus*.

In addition, the season when the experimental tests were carried out (May and November) appears to have no effect on the high tendency of grouping, the average distance between individuals, or the average variance–mean ratio during huddling. This happened even though the groups were composed of males and females, which could indicate that the aggregation tendency of this species especially at low temperatures overcomes the interference caused by intersexual and intrasexual interactions. These interactions almost certainly occurred mainly in the first run of experimental trials because they coincided with the time of mating season in the field (May-June; Soto-Gamboa 2005), and there is evidence that *O. degus* maintains in captivity its physiological and behavioral characteristics associated with breeding (Solís and Rosenmann 1990; Soto-Gamboa 2005; Soto-Gamboa et al. 2005). Moreover, the lack of differences between the two experimental moments does not appear to be explained by the light/dark cycle used in this study. Soto-Gamboa et al. (2005) showed that *O. degus* maintained with L/D 12:12 cycle in laboratory at temperatures similar to those used in our experiments (15–25°C) have the same variation in blood testosterone and cortisol levels as field animals despite great differences between agonistic and non-agonistic differences between these periods.

However, the variability of aggregon values was greater at higher temperatures, which is explained by greater movement of individuals and more frequent variations in the number and size of the aggregons at these temperatures. We also found greater variability in the AV values in the first experimental trials that could be related to the reproductive conditions of the individuals. In captivity, changes in gonadal activity and plasma levels of testosterone in males during the breeding season (Soto-Gamboa 2005) can be observed as reduced sociability, expressed in a larger number of agonistic behaviors, and lower affinity, demonstrated by a lower approach frequency between males and fewer interactions between males, as well as a decrease in the duration of these interactions (Solís and Rosenmann 1990). The difference in variability between the two experimental times was more marked with increasing temperature. The low variability observed in the aggregons at lower temperatures in experimental periods allows us to suggest that testosterone levels of *O. degus* do not affect the

effectiveness of huddling behavior when the temperature is low. The latter would be very beneficial, considering that during the reproductive season cortisol levels in males increase, especially in males defending a harem or territory (Soto-Gamboa et al. 2005), which would act to the detriment of energy balance by increasing the metabolic rate and reducing body energy reserves (Brillon et al. 1995). On the other hand, it is in this period (May–June) that the temperature is the lowest of the year at the sampling site of *O. degus*. Taking these conditions into account, the energetically economical character of huddling behavior becomes more important; it becomes an efficient tool to meet the energy requirements of the breeding season.

The importance of abiotic factors, mainly environmental temperature, in determining the characteristics of behavior in *O. degus* and other species has been documented in several studies (Bozinovic and Vásquez 1999; Bozinovic et al. 2000), but the processes by which these factors drive this behavior remain poorly understood. However, there is increasingly more evidence emerging that self-organization plays an important role in the behavior and development of biological systems (Halley and Winkler 2008) and together with natural selection would be part of the evolutionary process of these systems (Kauffman 1993; Camazine et al. 2001; Halley and Winkler 2008). Clustering as behavioral strategy in which the adaptive value is evident has been reported in several animal taxa including invertebrates such as honeycomb worm, serpulids, flies and mayflies, beetles, spiders, and caterpillars (Camazine et al. 2001), for example, overwintering aggregation of firebugs (*Pyrrhocoris apterus*) and collective feeding of bark beetle larvae (*Dendroctonus micans*). When larvae feed cooperatively, they are able to overwhelm and outmaneuver the reaction of the host tree: the secretion of large quantities of resin that can entrap and kill the larvae (Grégoire 1988; Camazine et al., 2001).

The results obtained in this study are consistent with those of Canals and Bozinovic (2011), who described huddling as a self-organized behavior triggered when the temperature decreases to a critical value. Self-organizing means that the huddling behavior is energetically more economical in physiological processes than alternative mechanisms such as leaders, blueprints, recipes, and templates and therefore more likely to be preserved by natural selection (Kauffman 1993; Camazine et al. 2001; Halley and Winkler 2008), which increases its importance for survival and fitness given the significant reduction in energy expenditure achieved under conditions of low temperatures and reduced availability of food, such as those which occur during the breeding season of *O. degus* in the wild.

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