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ORIGINAL ARTICLE

Social thermoregulation in Mediterranean greater white-toothed shrews (*Crocidura russula*)

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Abstract

Social thermoregulation is the huddling of two or more individuals that share endogenous warmth to reduce thermoregulation costs. Strategies vary widely depending on the species' social behavior and the ambient ecological conditions. In greater white-toothed shrews (*Crocidura russula*), huddling is employed in communal nests only in the colder months, which suggests that temperature is an important factor in the species' social thermoregulation strategy. To test this hypothesis, we analyzed the behavior and physiology of five groups of shrews from winter, acclimated to 14 °C, and four groups from summer, acclimated to 24 °C. Each group consisted of six captive males that were first housed singly for 2 days and later allowed to interact with other shrews of the same group. Our analysis revealed all group mates were frequently found huddling in the same shelter, regardless of acclimation temperature. However, mass-adjusted resting metabolic rate decreased in winter shrews with larger huddle sizes and remained constant in summer shrews in huddles with three or more individuals. Body temperature was also significantly lower and more varied in winter shrews. After being group-housed, winter shrews used less torpor and significantly increased their body mass and food intake in the first days. Our results suggest that temperature had a small influence in huddling behavior but a large one in physiological factors, such as metabolism, body temperature, and food intake, after shrews started interacting socially. Therefore, social thermoregulation provides benefits to *C. russula* besides energy savings.

Significance statement

Small mammals often huddle to reduce thermoregulation costs during cold. Previous studies in wild greater white-toothed shrews suggested that this species only employs social thermoregulation in the colder months of the year. We captured wild shrews and assessed the energetic advantages of this social thermoregulation strategy under controlled conditions. We confirmed that social thermoregulation indeed has more energetic benefits to shrews in winter than in summer. However, huddling between individuals still occurs at warm temperatures, when energetic benefits are no longer significant. Such observations suggest that huddling is advantageous to shrews in multiple ways beyond thermoregulation. Furthermore, social interaction between individuals influenced daily torpor, body mass, and feeding, further supporting the hypothesis that sociality in greater white-toothed shrews has direct and indirect effects on their energy budget.

Keywords Heterothermy · Huddling effectiveness · Resting metabolic rate · Seasonal changes · Social organization · Soricidae

Introduction

Ambient temperature has a strong impact on the daily energy expenditure of mammals. Cold temperatures increase the energetic costs of homeothermy, as more energy is required to maintain body temperature. This has led mammals to develop several behavioral, morphological, and physiological adaptations to compensate the costs of thermoregulation (Merritt 2010; Tattersall et al. 2012).

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One behavioral adaptation which has received widespread attention is social thermoregulation. It involves the huddling of two or more individuals, usually in a sheltered area, that take advantage of their endogenous warmth to reduce thermoregulatory costs. Indeed, daily energy expenditure can be reduced by about one-third, depending on the species, number of huddling individuals, and local shelter temperature (reviewed in Gilbert et al. 2010). Social thermoregulation has been described in several species, such as primates (Eppley et al. 2017), carnivores (Graw et al. 2019), small birds (Douglas et al. 2017), and emperor penguins (Ancel et al. 2015), and has been studied more frequently in captivity, where monitoring and experimental procedures can be controlled (Gilbert et al. 2010). Thus, small mammals have been the preferred targets for these studies because they can be maintained in captivity with relative ease (Merritt and Zegers 2014; Nuñez-Villegas et al. 2014; Groó et al. 2018).

Social thermoregulation strategies vary widely between species and ecological conditions. Many huddle with conspecifics only under minimal ambient temperatures (Webster and Brooks 1981; Wolton 1985; Perret 1998; Rhind 2003; Ruf and Bieber 2020), when the energetic advantages of huddling are higher (Canals et al. 1998). More social species huddle with conspecifics under a broader range of temperatures (i.e., in winter and summer), a behavior more associated with cooperative breeding or group-bonding (Nuñez-Villegas et al. 2014; Chappell et al. 2016; Groó et al. 2018). Food shortages also trigger energy saving mechanisms, one of which can be huddling more frequently with conspecifics (Perret 1998). However, this strategy may be compromised by intraspecific competition for territories and other resources (Vickery and Millar 1984). Another energy-saving mechanism triggered by food shortage is daily torpor, which can be used together with huddling to optimize energy savings (Jefimow et al. 2011; Tomlinson et al. 2014; Sukhchuluun et al. 2018) and to facilitate rewarming rate on arousal (Willis 2008; Eto et al. 2014). Some daily heterotherms even forego torpor entirely when its costs outweigh the energetic gains acquired from social thermoregulation and nest insulation (Nowack et al. 2013; Douglas et al. 2017). The advantages of torpor must be balanced against the costs associated with nest sharing. For example, larger group sizes deplete resources near the nest faster and increase foraging time for each group member (Vickery and Millar 1984; West and Dublin 1984).

The greater white-toothed shrew *Crocidura russula* (Hermann, 1780) is a small mammal whose social organization, like many other shrew species, is dependent on season (Valomy et al. 2015). During the cold, winter season, shrews are more social towards conspecifics and nest communally in mixed-sex groups; during the warm, breeding season, they form monogamous and territorial pairs which exclude other conspecifics from their home range (Frank 1983; Cantoni and Vogel 1989; Rychlik 1998). Observations in captivity have confirmed the formation of reproductive pairs which are aggressive towards conspecific strangers (Vogel 1969). However, non-paired shrews, regardless of their sex, can be kept in the same cage, and even share the same nest, after an initial habituation period (Vogel 1969).

Crocidura russula can enter daily torpor to reduce thermoregulation costs, with body temperatures going as low as 22 °C (Nagel 1977). Laboratory studies have successfully induced torpor in *C. russula* by reducing food supply (Genoud 1985) or exposing shrews to low ambient temperatures (Oliveira et al. 2016). But knowledge of the influence of social thermoregulation on torpor use is still lacking.

Here, we investigated the influence of season on the social thermoregulation of Mediterranean *C. russula*. We compared the behavior and physiology—namely huddle size and frequency, resting metabolic rate, body temperature, body mass, and food intake—of *C. russula* in groups of six individuals from winter and from summer. If season has a strong influence in the social thermoregulation of this species, we predict that winter shrews will (1) huddle in larger group sizes and more frequently; (2) save more energy with increasing huddle sizes; (3) use daily torpor more often; and (4) increase food intake and, consequently, body mass.

Methods

Animal capture and housing

Greater white-toothed shrews were trapped in the summer of 2017 (July and September, $n = 24$) and winter of 2017 (January, $n = 6$), 2018 (January and February, $n = 18$), and 2019 (January, $n = 6$). Trapping places were located in Sintra-Cascais Natural Park, Portugal (lat, 38.78; long, −9.40) and were characterized by a wet climate, open mixed forest with *Quercus* spp., and Mediterranean shrubby-type vegetation. Wooden-box live traps (16.5 × 8.0 × 9.5 cm; produced by PPUH A. Marcinkiewicz, Rajgród, Poland) were set before sunset and checked every 3 h until 01h00. Bait was provided only in winter, because traps tend to be invaded by ants in summer, which reduces trapping success (FGO pers. obs.). Only males were used for the study to avoid the formation of male–female monogamous pairs that would interfere with behavioral observations (Vogel 1969). Captured males of similar size (7–9 g) were transferred to the animal facility of the Faculty of Sciences, University of Lisbon. Other trapped individuals, including female shrews, were released on site immediately after capture.

Shrews were housed individually in white plastic terraria (PVC) (38 × 28 × 17 cm), covered with a grid mesh on top to allow ventilation. Terraria were enriched with a mixture of sand and soil as substrate, half of an eggbox and cardboard sheets as shelter, and some natural vegetation collected at the trapping site. Shrews captured in winter (herein referred to as winter shrews) were acclimated to 14 ± 1 °C, and shrews captured in summer (herein referred as summer shrews) were acclimated to 24 ± 1 °C. These temperatures correspond to the daily average high temperatures found at the shrews' trapping site in winter and summer, respectively (Weather Spark 2020). Photoperiod was 12D:12L with lights on between 07h00 and 19h00. As *C. russula* is a species that is active mainly at night (Vogel and Genoud 1981; Magnanou et al. 2009; Oliveira et al. 2016), the use of natural photoperiod (long night in winter and short night in summer) could influence the time spent by shrews huddling in shelters (see below) and thus mask the effect of season. Therefore, we decided to test winter and summer animals in the same photoperiod to reveal the influence of other seasonally changing factors (e.g., ambient temperature, social behavior). Shrews were fed daily around 18h00 with 1.0 g of mealworms, 1.5 g of blowfly pupae, and 3.5 g of minced meat. Winter shrews were supplied with an additional 0.5 g of minced meat to compensate their larger thermoregulatory costs. Food and water were changed at the same time.

Prior to experiments, shrews were marked by fur bleaching with hydrogen peroxide to allow individual identification (Ohayon et al. 2013). Shrews were restrained by hand, and bleach was applied on top of the fur to avoid skin irritation. The bleach was rinsed thoroughly after 20 min using a cloth embedded in warm water. Fur was then dried with a cloth, and the shrew was put back in its home cage. None of the shrews showed any sign of distress during or after the bleaching procedure.

Experimental terrarium

After an acclimation period of at least 1 week to captivity, shrews were assigned into five groups of six winter individuals and four groups of six summer individuals and transferred to a new experimental terrarium (100 × 100 × 40 cm). This terrarium was initially divided, using opaque wooden barriers, in seven compartments: six small compartments (33 × 40 × 40 cm), one for each shrew, and one long compartment in the center of the terrarium inaccessible to shrews (100 × 20 × 40 cm, neutral zone) (Fig. 1). Each compartment had one cylindrical cardboard shelter (15 cm long; 4.5 cm diameter), food and water bowls, and part of the substrate belonging to the individual cage where each animal was previously housed.

Shrews were housed singly in the experimental terrarium, in their respective compartment, for 2 days. On the third day, barriers were removed, and shrews had full access to all areas of the terrarium and could interact with other individuals. Body mass and body temperature, measured using a rectal thermometer (Digitron 2088 T), were monitored daily, in the morning (10h00–11h00), for 2 days prior to barriers being removed (baseline measurements) and for 10 consecutive days after removing the barriers. In total, 12 observations were made per individual, two when housed singly and 10 when housed in a group. At the same time in the morning, shelters were checked to assess the location of each shrew, in a total of 10 observations per group.

On the first, third, and tenth night after barriers were removed, shrews from each season were exclusively fed with live mealworms – 4.5 g for each individual in the terrarium. Such amount of food has been previously observed to exceed the required to sustain the shrews' energy requirements (Oliveira et al. 2021b). In the following morning, mealworms left in the bowl (3.2 cm high to avoid mealworms to escape) were weighed to quantify food intake. Shrews' body mass was also measured at the same time and whenever food was provided. After each trial, the usual diet and feeding routine was restored. This procedure was part of a larger behavioral experiment that is outside the scope of this study.

Due to differences in the single housing period, huddling data from one of the winter groups could not be analyzed and was removed. However, metabolic data from this group was included in the study (see below).

Huddling energetics

After huddling observations were concluded (10 days after barriers were removed), the resting metabolic rate (RMR) of all shrews was measured. Shrews were tested singly and with group mates ranging from two to six animals (sample sizes in Table 1). Each individual was used only once per group size to avoid pseudoreplication. Group mates were chosen based on the individuals that were observed sharing a shelter in the morning. If the target group sizes were not observed (e.g., in one terrarium a shelter with three individuals was never observed), random individuals from the same terrarium were chosen instead.

Metabolic measurements were done during the day, between 09h00 and 17h00 h, when shrews are less active (Oliveira et al. 2016). Oxygen consumption was measured in an open flow respirometry system using a Servomex (series 4100) oxygen analyzer. Shrews were placed inside a small acrylic cylindrical chamber (length, 25 cm; diameter, 7 cm). The chamber was placed horizontally inside an incubator (Sanyo 089A) set to 14 °C for winter shrews and 24 °C for summer shrews. Atmospheric dried air was pumped through the chamber with a flow rate of 500 ml min^{-1}. Flow rate was controlled and measured continuously at the chamber inlet by a calibrated mass flow controller (Sierra Instruments 840L connected to a Sierra Instruments Cal-Bench for readouts). Air was dried using silica gel columns twice: before entering the chamber and before entering the oxygen analyzer. To minimize error in the conversion of oxygen

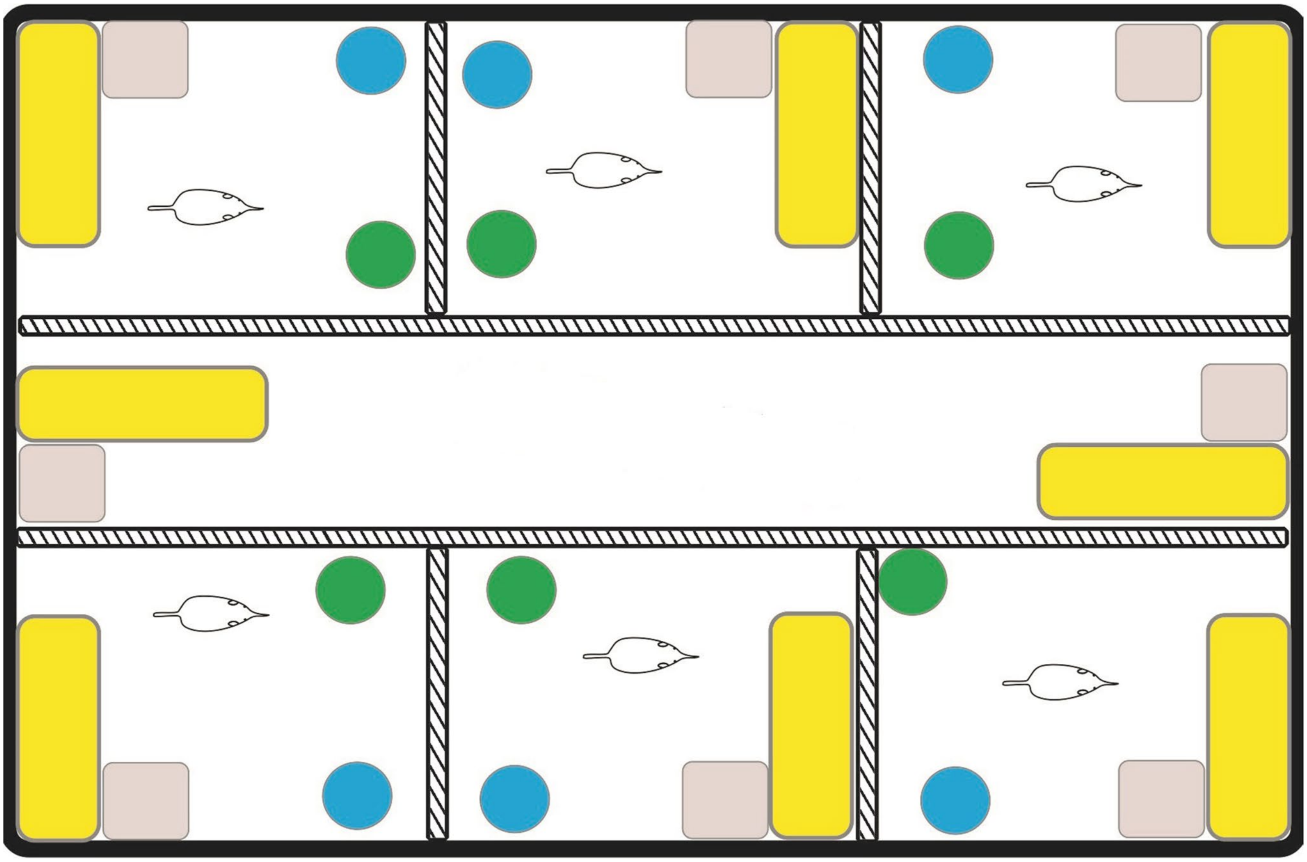

Fig. 1 Terrarium scheme before barriers (diagonal stripes) were removed, and shrews were group-housed. Each territory had a long cylindrical shelter (yellow rectangle), food and water bowls (green and blue circles, respectively), a stone (gray square) to prevent shelters from being moved, sand and soil as substrate, and some sticks as environmental enrichment. The middle area had two additional shelters but no shrews. Sticks and stones were present as environmental enrichment in addition to the same substrate

consumption to energy expenditure when the respiratory quotient (RQ) is unknown, carbon dioxide was not removed from the air entering the metabolic chamber (Koteja 1996). Readings from the oxygen analyzer were digitized approximately 35 times per second. The accumulated data was then averaged over a period of 15 s, meaning each 15 s measurement was based on a total of about 500 actual readings. Metabolic rate was calculated as the average of the ten lowest and consecutive values registered, corresponding to 2.5 min of stable oxygen measurements inside the chamber. Shrews inside the chamber were checked every few minutes through a plexiglass window until they had settled down and—if two or more individuals were measured—formed an aggregated group. This procedure allowed the interruption of measurements in case of excessive aggressive interactions between shrews. Oxygen consumption (VO_2) was obtained from the following equation: $VO_2 = V_2(F_1O_2—F_2O_2)/(1—F_1O_2)$, where V_2 is the flow rate measured at the outflow of the chamber and F_1O_2 and F_2O_2 are the oxygen concentrations measured at the inflow and outflow of the chamber, respectively (Depocas and Hart 1957). All VO_2 measurements were corrected to standard temperature and pressure and converted to energy units assuming 1 ml $O_2 = 20.1$ J and 1 J $\text{min}^{-1} = 16.667$ mW.

Table 1 Sample sizes used in metabolic measurements

Huddle size	Winter shrews	Summer shrews
1	30	24
2	15	12
3	9[a]	8
4	5	4
5	5	4
6	4[a]	4

[a] One individual died before his group's metabolic measurements could be completed

Before and after each measurement, baseline values of atmospheric oxygen were obtained by performing a 30 min measurement without any animal inside the chamber and averaging the VO_2 of these measurements. Shrews' body mass (g) was registered before and after entering the metabolic chamber using a digital pocket scale PPS200 with an accuracy of 0.01 g. The mean of these two values was used in statistical analysis. After metabolic measurements, shrews returned to their terraria with individuals of the same group.

Data was not recorded blind in this study because the measured variables were not subjected to observer bias.

Data analysis

Data exploration followed the protocol described in Zuur et al. (2010). To analyze the relationship between huddling behavior and temperature, two linear mixed models were fitted: one for maximum huddle size, the maximum number of shrews sharing a shelter in each observation, and another for proportion huddled, the proportion of individuals that were not alone in a shelter (Tomlinson et al. 2014). To examine the influence of social behavior on individual thermal response, two other linear mixed models were fitted for body mass and body temperature. Shrews with a body temperature below 28.0 °C were considered to be in torpor (Brigham et al. 2011). This threshold was chosen based on the frequency of temperature measurements of winter shrews, which maintained a lower body temperature than summer shrews (Appendix; see also the "Results" section). Another model was fitted to analyze the effect of time and temperature on food intake. Because we could not discriminate how much food each individual ate, food intake was quantified as the total amount of food eaten by a shrew group and divided by the number of individuals (i.e., six) in that group. Since the previous variables were measured repeatedly in the same individuals within the same groups, individual identity, or group identity when appropriate, was added as random terms to these models. Finally, to access the energetic advantage of huddling, a generalized additive model was fitted for mass-adjusted RMR. A linear model was additionally fit to confirm the generalized additive model results numerically. Data exploration and statistical models were carried out in the software R version 4.0.3 (R Core Team 2020). Models were fitted using the "nlme" package for linear mixed models with a Gaussian distribution (Pinheiro et al. 2019), the "glmmTMB" package for generalized linear mixed models (Brooks et al. 2017), and the "mgcv" package for the generalized additive model (Wood 2017).

Model selection was employed to find the optimal fit for each model. First, we applied several models with different residual structures to find the optimal random component. Then, we assessed each model graphically for patterns in the normalized residuals. From among models without obvious residual patterns, we chose the best model based on their AICc (Akaike's Information Criterion corrected for small sample sizes) obtained through restricted maximum likelihood estimation (REML) (Zuur et al. 2009) (Online Resource 1, Table S1). The next step in model selection was to find the optimal fixed component, using the "MuMIn" package (Bartoń 2020). The combination of fixed terms obtained through maximum likelihood estimation (ML) that produced the model with the lowest AICc from among all the possible models (i.e., the top model) (Online Resource 1, Table S2) was chosen. Finally, models were refitted with REML to obtain unbiased variance estimates. Both the starting and the final fixed components of each model, as well as a description of the final model, can be found in Table 2.

Descriptive statistics are presented as mean ± SE.

Results

Huddling behavior

The most frequent number of shrews sharing a shelter in each observation was six, i.e., the maximum possible. Huddles

Table 2 Model description for each response variable

Response variable	Starting fixed component	Final fixed component	Random effect	Statistical model
Maximum huddle size	Season * day	Season	Group	Linear mixed model
Proportion huddled	Season * day	Intercept	Group	Linear mixed model
Mass-adjusted RMR	Season * huddle size	Season * huddle size	None	General linear model with gamma distribution and identity link
Body mass	Season * day * housing[a]	Day + season * housing	Individual	Linear mixed model with an AR-1 correlation structure for day[b]
Body temperature	Season * day * housing[a]	Day * (season + housing)	Individual	Linear mixed model with different variances per season[c]
Food intake	Season * day * body mass difference	Body mass difference + season * day	None	Generalized least squares

[a] Housed singly or in groups

[b] Body mass was shown to increase daily during exploratory analysis

[c] Residual spread was larger in winter shrews than in summer shrews

with six individuals were observed 35 times in winter shrews (87.50%) and 26 times in summer shrews (65.00%), while huddles with five or four individuals were more commonly observed in summer shrews (Fig. 2a). Yet, no significant differences were detected in huddle sizes between winter and summer (Table 3). Similarly, the proportion of huddling individuals was marginally lower in summer shrews (0.95 ± 0.01) than in winter shrews (0.97 ± 0.01) (Fig. 2b, Table 3). Maximum huddle size and proportion huddled were consistent over time and were significantly correlated (Kendall rank correlation = 0.605, $p < 0.001$).

Huddling energetics

Resting metabolic rate was consistently higher at 14 °C than at 24 °C, even when adjusted for body mass. Individual RMR was 33.91 ± 1.06 mW g^{-1} at 14 °C and 18.22 ± 0.69 mW g^{-1} at 24 °C. Our generalized additive model revealed significant smoothers for temperature (14 °C, $F_{1.86} = 42.30$, $p < 0.001$; 24 °C, $F_{2.71} = 30.27$, $p < 0.001$). Plotting these smoothers revealed a large decrease in metabolic rate with an increase in huddle size up to three individuals (Fig. 3). At huddle sizes between 3 and 6 individuals, results diverged slightly. In shrews at 14 °C, decrease in mass-adjusted RMR was continuous, with maximum energy savings of 38.58% ± 3.71% observed in huddles with six individuals; in shrews at 24 °C, this decrease in metabolic rate stopped at huddles with three individuals (energetic savings of 36.54% ± 1.55%), with maximum energy savings of 39.58% ± 5.94% observed in huddles with five individuals. These results were supported by a mixed model with huddle size as a categorical variable: huddle sizes between 3 and 6 individuals did not show a significant difference in mass-adjusted RMR at 24 °C but did so at 14 °C (Table 3).

Body temperature

Body temperature measurements revealed 14 winter shrews (4.86%) in torpor (body temperature below 28 °C). Nine of these measurements were made in single-housed individuals (18.75% of all single-housed observations); the other five were made in individuals sharing a shelter with all group mates (2.08% of all group-housed observations).

Body temperature of group-housed winter shrews (32.0 ± 0.1 °C) was significantly lower than group-housed summer shrews (35.4 ± 0.1 °C; Fig. 4, Table 3). Both group-housed winter shrews and group-housed summer shrews had a significantly higher body temperature than single-housed shrews (29.9 ± 0.5 °C and 34.7 ± 0.1 °C, respectively; Fig. 4, Table 3). Time had a small, non-significant effect on body temperature in both acclimation groups, with an estimated increase of 0.03 °C day^{-1} (Table 3).

Body mass

Body mass was significantly larger in winter shrews (9.76 ± 0.08 g) than summer shrews (8.50 ± 0.10 g; Fig. 4; Table 3). Body mass was also significantly larger in group-housed shrews, regardless of the acclimation group (single shrews, 8.68 ± 0.13 g; grouped shrews, 9.22 ± 0.08 g; Fig. 4, Table 3). There was a significant

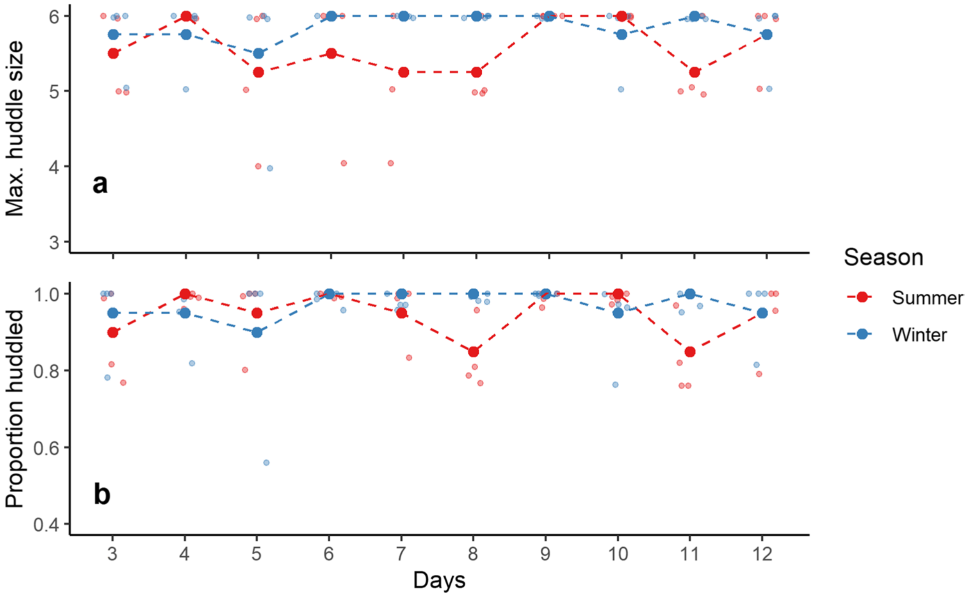

Fig. 2 Maximum huddle size (**a**) and proportion of huddling shrews (**b**) acclimated to 24 °C (summer) and 14 °C (winter). Observations were done every morning in four groups of six shrews from each temperature treatment. Each point represents one group observation. Some random noise was added to prevent point juxtaposition. Large points connected to dashed lines represent the mean of observations for each day

Table 3 Linear model estimates for maximum huddle size, proportion huddled, mass-adjusted resting metabolic rate (RMR), body temperature, body mass, and food intake. Confidence intervals (CI 95%) of terms in bold do not cross 0

Term	β	SE	z	CI 95%
Maximum huddle size				
Intercept	5.85	0.125	46.851	**[5.601, 6.099]**
Summer	−0.275	0.189	−1.457	[−0.737, 0.187]
Group variance (SD)	0.214			[0.085, 0.540]
Residual variance		0.585		[0.463, 0.740]
Proportion huddled				
Intercept	0.958	0.015	62.484	**[0.927, 0.988]**
Group variance (SD)	0.035			[0.015, 0.079]
Residual variance		0.082		[0.070, 0.097]
Mass-adjusted RMR (mW)[a]				
Intercept	23.600	1.233	19.138	**[21.183, 26.017]**
Summer	−12.144	1.433	−8.477	**[−14.952, −9.336]**
Huddle size 1	10.282	1.499	6.859	**[7.344, 13.220]**
Huddle size 2	4.254	1.597	2.664	**[1.124, 7.384]**
Huddle size 4	−3.123	1.813	−1.723	[−6.675, 0.430]
Huddle size 5	−2.638	1.834	−1.438	[−6.232, 0.957]
Huddle size 6	−4.130	1.869	−2.209	**[−7.794, -0.466]**
Summer:huddle size 1	−3.527	1.709	−2.063	**[−6.877, -0.176]**
Summer:huddle size 2	−2.589	1.799	−1.439	[−6.114, 0.937]
Summer:huddle size 4	3.418	2.104	1.625	[−0.706, 7.542]
Summer:huddle size 5	1.907	2.091	0.912	[−2.190, 6.005]
Summer:huddle size 6	3.719	2.131	1.745	[−0.459, 7.896]
Group variance (SD)	0.817			[0.278, 2.402]
Body temperature (ºC)				
Intercept	31.801	0.407	77.158	**[31.353, 32.248]**
Summer	3.326	0.451	8.367	**[2.850, 3.803]**
Day	0.032	0.048	1.751	[−0.001, 0.064]
Single	−1.948	0.444	−3.677	**[−2.642, −1.254]**
Summer:single	1.499	0.474	2.408	**[0.789, 2.208]**
Individual variance (SD)	0.642			[0.476, 0.865]
Residual variance		0.795		[0.729, 0.865]
Body mass (g)[b]				
Intercept	8.821	0.335	26.298	**[8.162, 9.480]**
Day	0.133	0.020	6.657	**[0.093, 0.172]**
Summer	−0.275	0.462	−0.595	[−1.204, 0.655]
Single	0.072	0.114	0.629	[−0.153, 0.296]
Day:summer	−0.115	0.027	−4.330	**[−0.167, −0.063]**
Day:single	−0.127	0.049	−2.536	**[−0.221, −0.028]**
Correlation structure (φ)	0.979			[0.967, 0.986]
Residual variance		1.568		[1.271, 1.934]
Food intake (g)				
Intercept	4.059	0.209	19.419	**[3.649, 4.469]**
Body mass difference	0.858	0.302	2.844	**[0.267, 1.449]**
Summer	−1.566	0.182	−8.616	**[−1.922, −1.210]**
Day 5	−0.674	0.226	−2.980	**[−1.117, −0.231]**
Day 12	−1.212	0.178	−6.805	**[−1.561, −0.863]**
Summer:day 5	0.246	0.278	0.885	[−0.299, 0.790]
Summer:day 12	0.812	0.246	3.294	**[0.329, 1.294]**

Reference group: winter season. β = estimate; *SE* = standard error; *SD* = standard deviation

[a] Huddle size was coded as a categorical variable. Huddles with three individuals were used as the reference

[b] Individual variance could not be estimated due to large confidence intervals

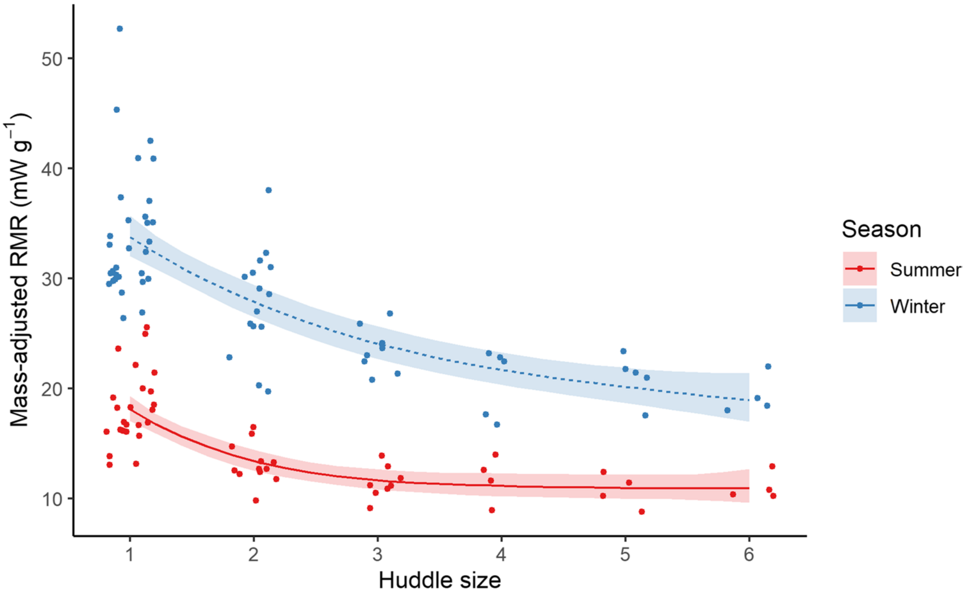

Fig. 3 Mass-adjusted resting metabolic rate (RMR) of shrews acclimated to 24 °C (summer) and 14 °C (winter). Huddle size represents the number of individuals inside the metabolic chamber at time of measurement (see Table 1 for sample sizes). Lines (±95% CI) represent the smoothers obtained through a general additive model for each season group (see "Data analysis")

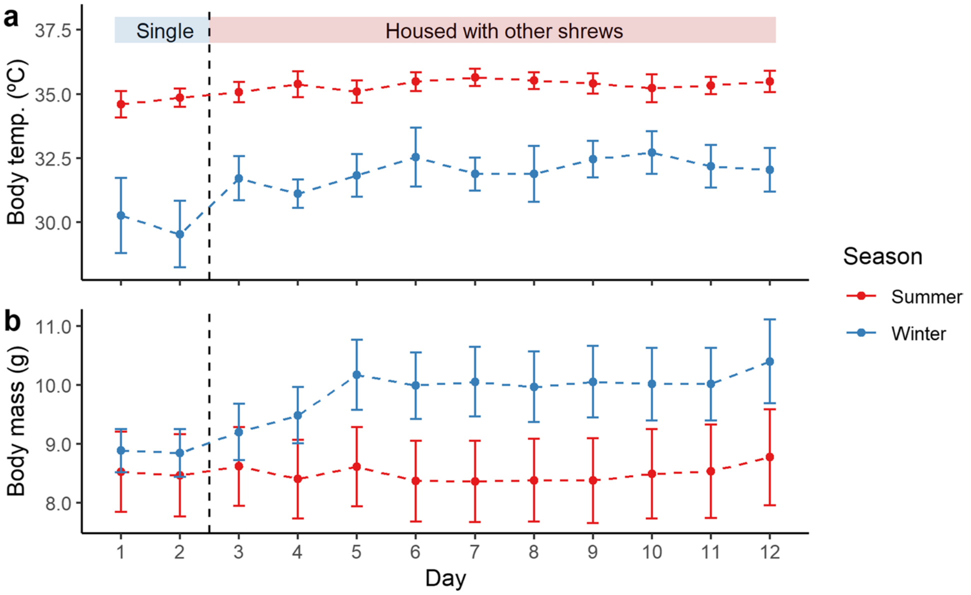

Fig. 4 Mean (±95% CI) body temperature (**a**) and body mass (**b**) measured in the morning in shrews acclimated to 24 °C (summer) and 14 °C (winter). Shrews were housed singly in the first 2 days of measurements and then housed with five other individuals in the following days. *n* = 24 for each season in each day

temporal autocorrelation between measurements (Online Resource 1, Table S1) originating from a significant and positive effect of time in the body mass of winter shrews, with an estimated increase of 0.13 g day^{-1} (Table 3). This increase was more evident until the fifth day, after which body mass stabilized (Fig. 4). Such a time effect was not found in summer shrews (Table 3).

Food intake

Winter shrews consumed all the mealworms on day 3, nearly all on day 5, and then dropped food intake by 17.95% between days 5 and 12 (Fig. 5). Summer shrews consumed significantly less mealworms than winter shrews (Fig. 5, Table 3). A positive relationship was found between body mass difference and food intake (Table 3), meaning shrews gained weight with increased food intake. Consequently, winter shrews gained considerably more body mass than summer shrews on days 5 and 12, but not on day 3 (Fig. 5). Contrastingly, gains in body mass and consumption of mealworms by summer shrews were similar in all 3 days (Fig. 5). Individuals decreased body mass only in seven observations, four in the summer season (range 0.02–0.22 g), and three in the winter season (range 0.11–0.55 g).

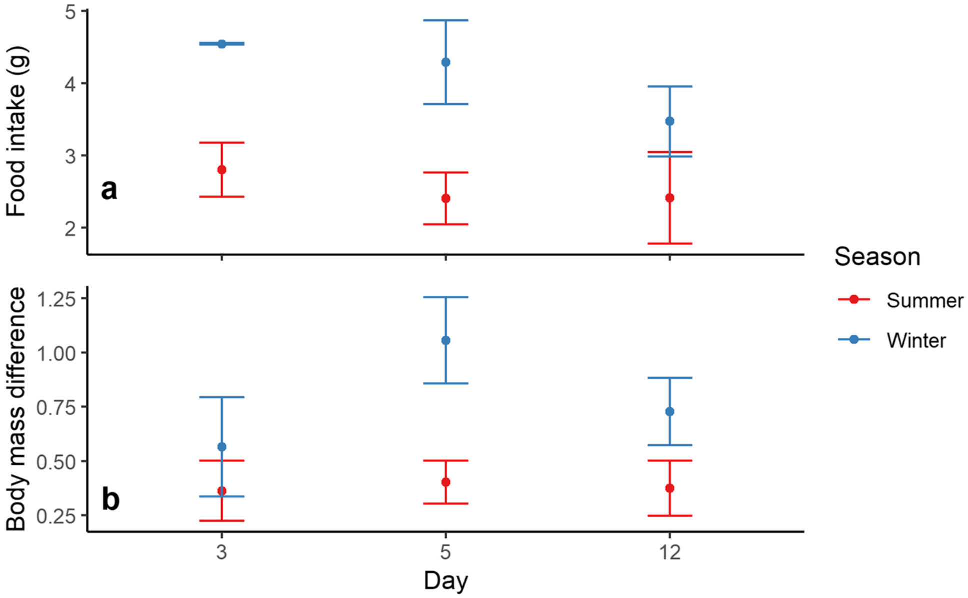

Fig. 5 Mean (±95% CI) food intake (**a**) and body mass difference (**b**) quantified in the morning in shrews acclimated to 24 °C (summer) and 14 °C (winter). Observations were made in experimental days 3, 5, and 12 (group-housed shrews). Food intake, $N=4$ groups from each season; body mass difference, $n=24$ individuals from each season

Discussion

Huddling behavior

Contrary to our initial hypothesis, our results suggest that season has a small influence in the huddling behavior of Mediterranean *C. russula*. Huddle size and huddle frequency were not significantly different between winter shrews and summer shrews, which contradict previous field observations where non-paired shrews only shared nests with conspecifics in winter (Cantoni and Vogel 1989).

We advance two possible explanations for this contradiction. The first is the presence of females triggering aggressive behaviors and reproductive competition between male *C. russula*. Mate competition between same-sex individuals is often triggered by the presence of opposite-sex individuals in both females (Scheibler et al. 2004; Rusu and Krackow 2004) and males (delBarco-Trillo and Ferkin 2006; Ewaldsson et al. 2016). Observations made in captive *C. russula* by Vogel (1969) showed serious fights between individuals only if a stranger was added to a cage with an established couple, but not when same-sex individuals were kept together. Therefore, the absence of females may have favored sociality between males and promoted communal sheltering at both temperatures.

Our second explanation is based on competition for resources. Sociality is positively driven by food availability and population density, factors that have been thoroughly studied in four-striped grass mice (*Rhabdomys pumilio*) (Schradin et al. 2012, 2020). Previous research into the social behavior of *C. russula* has been made in central Europe (Vogel 1969; Cantoni and Vogel 1989), where *C. russula* faces competition from other shrew species such as *Sorex araneus* and *C. leucodon* (Vogel et al. 2002; Neves et al. 2019). In these conditions, the formation of territorial breeding pairs may be advantageous to defend resourceful territories from other shrews (Cantoni and Vogel 1989, but see Bouteiller and Perrin 2000). Conversely, in southwestern Europe, *C. russula* is the dominant shrew species and can be found in comparatively high numbers (Mitchell-Jones et al. 1999). Thus, competition among shrew species should not be so pervasive. Less marked seasonal variations in our study area point to little changes in invertebrate abundance throughout the year (e.g., Lino et al. 2014), which translates into reduced competition for food resources and larger sociality between conspecifics than previously observed in central Europe.

Huddling energetics

Perhaps more surprising than the abovementioned changes are the energetic implications of sharing a shelter with group mates. At a huddle size of six individuals, both winter and summer shrews reduced their metabolic rate by nearly 40% each, slightly higher energy savings than similar studies for other small mammals (Gebczynski 1969; Vogt and Lynch 1982; Pillay and Rymer 2017). Huddling effectiveness—the maximum amount of energy saved during huddling (Canals et al. 1997)—was reached around six individuals at 14 °C and three individuals at 24 °C. Similar results have been found for the least shrew, *Cryptotis parva*, with huddling effectiveness being reached around six individuals at 14 °C and two individuals at 24 °C (Merritt and Zegers 2014). Canals et al. (1998) have previously demonstrated that huddling effectiveness decreases when ambient temperature reaches 5 °C below the species' critical temperature. Since the thermoneutral zone of *C. russula* lies between 27.5 and 30 °C (Sparti 1990), it is likely the collective temperature of three huddling individuals at 24 °C reaches values near the species' thermoneutral zone. In fact, temperatures inside the shelter in summer reached 28–29 °C when individuals were isolated and 31–32 °C when all six individuals were sharing a shelter (FGO et al., unpublished data). In winter, this was no longer the case: shelters reached temperatures of 17–19 °C when a single individual was inside and 26–28 °C when all six individuals were inside (FGO et al., unpublished data). Therefore, results on metabolic rates suggest that huddling shrews may benefit in ways other than thermoregulation (e.g., safety from predators, social bond maintenance), particularly at warmer temperatures.

Body temperature

Winter shrews maintained a lower body temperature than summer shrews throughout the experiment. Although previous literature has reported a large variation in homeothermic body temperature in white-toothed shrews (Churchfield 1990; Taylor 1998), our results suggest this variation may have a seasonal influence. This should allow shrews to save some energy during cold and optimize metabolic performance when temperatures are warmer. Other studies have reported lower body temperatures in homeothermic mammals exposed to cold temperatures (Glanville and Seebacher 2010; Jefimow et al. 2011; Zhang et al. 2018), although rarely to the extent reported here, a 3.5 °C difference between winter and summer shrews. This large seasonal variance in body temperature might be related with the species' ability to use heterothermy. Indeed, 4.86% of winter shrews had body temperatures below 28 °C, strongly suggesting that these individuals were in torpor (Nagel 1977). Such observations support previous theoretical evidence that torpor is an important physiological strategy used by *C. russula* to reduce energy expenditure when exposed to low temperatures (Genoud 1985; Oliveira et al. 2016).

Most shrews found in torpor were housed singly. Indeed, shrews did not enter torpor when huddling with conspecifics in a possible effort to optimize energy savings. Such observations match results found in white-browed babblers and African lesser bush babies (Nowack et al. 2013; Douglas et al. 2017), but contrast with observations made in Japanese field mice and Siberian hamsters, in which huddling and torpor are used together to reduce energetic demands (Jefimow et al. 2011; Eto et al. 2014). It is likely the energetic advantages provided by social thermoregulation in *C. russula* are sufficient to balance the energy budget. A reduction of torpor frequency after shrews interacted, and nested, with conspecifics may also have a hormonal base. Torpor can be inhibited by an increase in testosterone levels (Goldman et al. 1986; Lee et al. 1990) resulting from the presence of other males (Wingfield et al. 1990; Soto-Gamboa et al. 2005). Although torpor can provide significant energetic savings, it is not without disadvantages. For instance, torpor can delay the ability to react to threats (Luo et al. 2014; Nowack et al. 2016), such as aggressive behavior from other males.

It must be noted these observations were limited to an ambient temperature of 14 °C in a captive setting where food was readily available, which could explain the reduced number of individuals found torpid. More dedicated research is needed to investigate the complementary role of heterothermy and huddling in the energetic strategy of shrews, particularly in wild animals or at lower temperatures.

Body mass and food intake

Body mass measurements revealed winter shrews gained weight during the first 3 days after being housed with other shrews. This effect matched the period when winter shrews ate all the available mealworms during the food intake experiment. Many red-toothed shrews (subfamily Soricinae) in the wild decrease body mass in winter to reduce total energy requirements (Pucek 1963; Merritt 1995; Kardynia and Rychlik 2011). However, shrews in captivity, like other mammals (Lutz and Woods 2012), accumulate fat reserves from ad libitum access to food (Churchfield 1981; Oliveira et al. 2016). We hypothesize winter shrews increased their body mass rapidly after being housed with other conspecifics because of the energetic savings provided by social thermoregulation and an increased voracity caused by strong competition between individuals for food resources (Barnard and Brown 1985). Larger body sizes also reduce the surface-to-volume ratio and, consequently, the amount of energy required to maintain homeothermy (see Bergmann's rule, Meiri and Dayan 2003). This gain in body mass cannot be explained alone by the extra food provided to winter shrews. First, both winter and summer shrews maintained their body mass when housed singly, which means the food provided was adequate to the acclimation regime of each group. Second, in the food intake experiment, group-housed winter shrews had higher food intake and accumulated more body mass than summer shrews. Conversely, food intake and body mass were constant throughout measurements in summer shrews, likely because the warmer temperature exerted less pressure on shrews to feed.

Conclusion

Our results show the importance of social thermoregulation in reducing the daily energy expenditure of *Crocidura russula* exposed to cold. Despite previous knowledge that shrews are territorial in the breeding season—when temperatures are higher—in our experiment, both winter and summer shrews engaged in communal sheltering. Moreover, summer shrews often huddled in groups of 5–6 individuals, even though no further energetic benefits were registered in huddles with more than three individuals. Beyond social thermoregulation, other strategies proved relevant against cold temperatures. Winter shrews resorted to daily torpor in the absence of huddling individuals to reduce daily energy expenditure and maintained low homeothermic temperatures to reduce costs associated with thermoregulation. Body mass and food intake increased in winter shrews after being group-housed, which could evidence changes in behavior associated with resource competition and/or accumulation of fat reserves to conserve body heat. Overall, the adaptive variation of *C. russula*'s social organization remains largely unexplored (Valomy et al. 2015). Even though our study has limitations regarding ecological conditions and cannot fully replicate parameters found in the wild, it hints towards intraspecific variation in the social behavior of shrews depending on environmental factors such as temperature range, resource availability, reproductive competition, and interspecific competition. We encourage further studies on the species' social behavior along its distribution range while accounting for the factors previously mentioned. Moreover, behavioral data should be combined with biochemical and physiological descriptors to unveil if the factors regulating the huddling behavior of shrews are ecologically and/or genetically determined.

Appendix

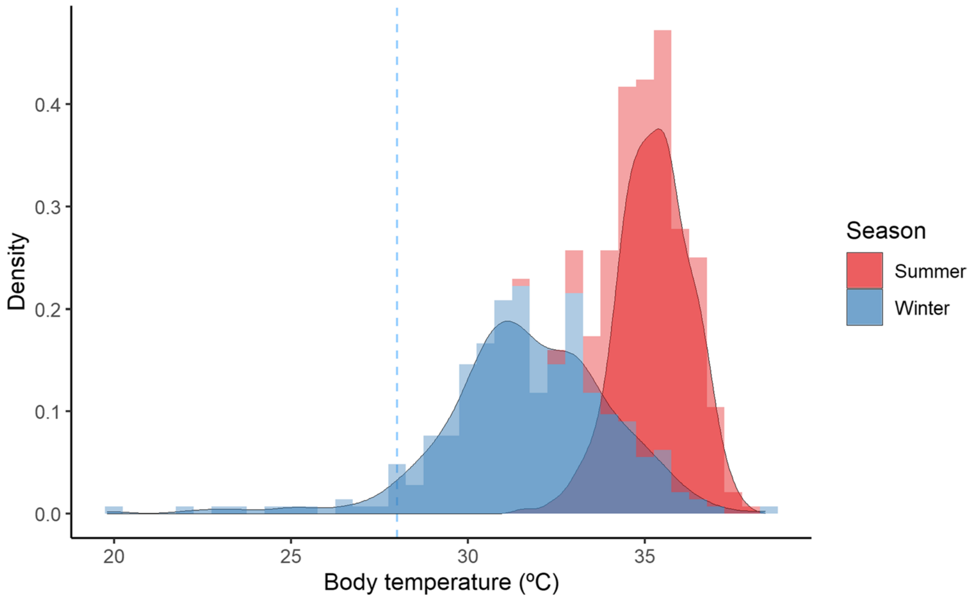

Fig. 6 Histogram and frequency density of body temperatures registered during the morning in shrews acclimated to 24 °C (summer) and 14 °C (winter). Individuals to the left of the dashed line (body temperatures below 28 °C) were considered to be in torpor

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00265-021-03072-7.

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Data availability The datasets generated and analyzed during the current study are available in the Figshare repository (Oliveira et al. 2021a).

Declarations

Ethics approval All the experimental procedures were stated by a competent authority (ORBEA 3/2017) to be in accordance with the requirements following the European guidelines (Directive 2010/63/EU) transposed to the Portuguese law (Decreto-Lei n.º 113/2013). Capture, handling, and transportation of shrews were authorized by the

Institute for Nature Conservation and Forests (ICNF, license numbers 13/2017/CAPT and 163/2018/CAPT). Shrews were cared for in accordance with the Animal Behaviour guidelines for the treatment of animals in behavioral research and teaching (ASAB/ABS 2020). Methods and results are reported according to the ARRIVE guidelines (Percie du Sert et al. 2020). After the conclusion of experimental procedures, shrews were released at their capture location.

Competing interests The authors declare no competing interests.

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