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Standard energetics of greater white-toothed shrews (*Crocidura russula*, Soricidae) from temperate and Mediterranean environments

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Abstract

Climate is an important factor affecting the standard energetics of mammals. Once body mass is accounted for, thermal conductance tends to be lower in mammals from colder regions. Basal rate of metabolism (*BMR*) is predicted to be low in species or populations inhabiting warm, arid and unproductive habitats and high in those exposed to cold climates. Surprisingly, data available on the greater white-toothed shrew (*C. russula*), a recent colonizer of the temperate zone in Europe, suggest an inverse trend for *BMR* across the species' geographical range. Rate of metabolism, body temperature and thermal conductance were measured at different ambient temperatures in a *C. russula* population from Southern France and a population from Switzerland, two localities with strikingly different climates ("Mediterranean" *vs* temperate climate).

The French shrews were on average lighter than the Swiss shrews (8.2 g *vs* 10.8 g). Their absolute *BMR* was also lower, but when body mass variation was accounted for, locality did not significantly affect *BMR*. Thus *BMR* of French and Swiss shrews represented, respectively, 160 and 158 % of the value expected on the basis of body mass, and the results for the French population contrast with the much higher earlier data on *C. russula* from the Mediterranean region. Minimal thermal conductance depended both on body mass and locality. Swiss shrews tended to have a lower minimal thermal conductance than French shrews (98 % *vs* 108 % of the expected value, respectively). Besides increased thermogenic capacity and expression of torpor, as well as social thermoregulation and nest-site selection, an increase in body mass and a reduction of thermal conductance should facilitate winter survival of the greater white-toothed shrew in the colder regions of the temperate zone.

Keywords: basal metabolic rate, climate, body temperature, thermal conductance, intraspecific variation, scaling, Mammalia.

Genoud M., 2019. Paramètres énergétiques chez des musaraignes musettes (*Crocidura russula*, Soricidae) de milieux tempéré et méditerranéen. *Bulletin de la Société Vaudoise des Sciences Naturelles* 98: 77-91

Résumé étendu

Le coût énergétique de la maintenance est particulièrement élevé chez les endothermes (mammifères et oiseaux), qui régulent leur température corporelle à un niveau élevé en variant la production interne de chaleur. Le métabolisme basal (*BMR*), la température corporelle et la conductance thermique (facilité à perdre de la chaleur) sont des paramètres physiologiques fondamentaux, qui déterminent largement le niveau du métabolisme énergétique de repos à diverses températures ambiantes. Ces paramètres sont influencés par de nombreux facteurs, parmi lesquels le climat joue

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un rôle important. La conductance thermique est généralement plus basse chez les mammifères des régions froides, qui ont un pelage plus isolant. Le métabolisme basal (*BMR*) tend à être plus bas chez les populations ou espèces vivant dans des habitats chauds, arides et peu productifs et plus élevé chez celles qui vivent sous des climats froids.

La musaraigne musette (*C. russula*), une colonisatrice récente des zones tempérées d'Europe, est soumise à des conditions climatiques très différentes selon la localisation : climat méditerranéen pour les populations du Sud et climat tempéré pour celles du Nord. Or, les données physiologiques disponibles pour différentes populations suggèrent pour le *BMR* l'inverse de la tendance générale observée chez les mammifères : le *BMR* des populations méditerranéennes est en effet décrit comme beaucoup plus élevé. Une procédure expérimentale identique a été appliquée pour mesurer le métabolisme énergétique, la température corporelle et la conductance thermique à différentes températures ambiantes chez des individus de deux populations différentes : une population du sud de la France (climat méditerranéen) et une population de Suisse (climat tempéré).

Les musaraignes du sud de la France étaient en moyenne plus légères que celles de Suisse (8,2 g *vs* 10,8 g). Leur *BMR* était également plus faible, mais cette différence était explicable par la variation du poids : en contrôlant l'effet du poids corporel, la localité (France *vs* Suisse) n'avait pas d'effet significatif sur le *BMR*. Ainsi, le *BMR* des musaraignes de Suisse et du sud de la France représente respectivement 158 % et 160 % de la valeur attendue sur la base du poids corporel, et les résultats pour la population française contrastent avec les valeurs précédemment connues pour des musaraignes musettes de la région méditerranéenne. La conductance thermique minimale était affectée à la fois par le poids corporel et par la localité. Les musaraignes suisses avaient une conductance thermique inférieure à celle des individus français (98 % *vs* 108 % de la valeur attendue).

Des données précédentes ont montré qu'une augmentation de la capacité de thermogenèse, une utilisation accrue de la torpeur journalière et de la thermorégulation sociale (repos en groupe) ainsi que la sélection de microclimats cléments facilitent la survie hivernale de la musaraigne musette dans les régions froides de la zone tempérée. Les résultats de la présente étude suggèrent qu'à ces ajustements, il faut ajouter un abaissement de la conductance thermique et une augmentation de la taille corporelle.

Mots-clés : taux de métabolisme basal, climat, stratégie énergétique, temperature corporelle, conductance, variation intraspécifique, effet d'échelle, musaraigne, Mammalia.

INTRODUCTION

The energy cost of self-maintenance is an essential component of an animal's energy budget, along with the costs of growth and reproduction (e.g. WITHERS 1992). It is also very high in endotherms, which regulate their body temperature at a high level by varying internal heat production (MCNAB 2002, 2012). Basal rate of metabolism (*BMR*), body temperature (T_b) and thermal conductance (*c*, a measure of the easiness to loose heat) are fundamental physiological parameters, as they largely determine the resting rate of metabolism of an endotherm at a given ambient temperature (MCNAB 1980). Being measured in standardized conditions, they allow meaningful comparisons among populations or species. Yet comparative analyses have revealed that these "standard" energetics parameters vary strongly among species, even when body mass differences are accounted for (ASCHOFF 1981, MCNAB 1988, 2008, CLARKE & ROTHERY 2008, GENOUD *et al.* 2018). Besides many other influential factors, climate explains a substantial part of this interspecific residual variation (SCHOLANDER *et al.* 1950a, LOVEGROVE 2003, MCNAB 2008).

Climate affects the energetics of mammals in various and complex ways, particularly because it includes several important variables (e.g. temperature, rainfall, and their seasonal variations) and because it is tightly linked to other influential factors such as food habits, local productivity, or altitude (MCNAB 2002). In cold environments, rate of heat loss is often decreased through increased fur insulation (i.e. lowered thermal conductance; SCHOLANDER *et al.* 1950a, 1950b). Maximum rate of heat production also tends to be higher, which may require an increase in *BMR* as well (REZENDE *et al.* 2004). A trend towards higher *BMR* in colder environments has indeed been described (LOVEGROVE 2003). In contrast, mammals from arid and hot environments with low primary productivity often exhibit low *BMR*, which limits evaporative water loss, helps avoid overheating and/or leads to a frugal use of the scattered or unpredictable energy resources (MCNAB & MORRISON 1963, DEGEN *et al.* 1998, MUELLER & DIAMOND 2001, BOZINOVIC *et al.* 2009, GENOUD 2014). While the above trends have been revealed essentially by interspecific comparative analyses, they might also explain part of the variation in energetics among different conspecific populations. The latter variation has received much less attention than the interspecific variation, but some studies have described trends similar to the broad interspecific trends mentioned (e.g. HAYES 1989, BOZINOVIC *et al.* 2009, CASTELLANOS-FRÍAS *et al.* 2015).

The greater white-toothed shrew (*Crocidura russula*: Soricomorpha, Soricidae) is a common small mammal of Western Europe and the Western Mediterranean region (POITEVIN *et al.* 1986, GENOUD & HUTTERER 1990). It is a recent member of the continental Europe's fauna that reached the Iberian peninsula from Morocco about 60'000 years ago (COSSON *et al.* 2005) and probably extended its range to the North during the last 10'000 years (POITEVIN *et al.* 1986). This shrew is exposed to diverse environmental conditions over its present range, the climate of the southern parts being classified as temperate "Mediterranean" (Csa) by the Köppen-Geiger climate classification, that of the northern and north-eastern parts as temperate (Cfb) and even cold (Dfb) (BECK *et al.* 2018). *C. russula* occurs in a wide variety of habitats in the Mediterranean region, including shrubland (different types of garrigue, maquis), oak forest, coastland dunes as well as fallow land, cultivated fields (e.g. vineyards, olive orchards) and other anthropogenic habitats (FONS 1975, POITEVIN *et al.* 1987). The synanthropy of this shrew tends to increase in colder regions (GENOUD & HUTTERER 1990). Thus in Switzerland, lowland populations inhabit hedges, shrubland as well as gardens, but greater white-toothed shrews are usually restricted to the vicinity of farms and houses above 600 m elevation (Genoud & Hausser 1979, Genoud 1982). In the Mediterranean region, *C. russula* tends to be slightly smaller than in more northern regions (Genoud & Hutterer 1990).

The thermal energetics of *C. russula* has been examined repeatedly (Fons & Sicart 1976, Nagel 1985, 1991, 1994, Sparti 1990, 1992, Fontanillas *et al.* 2005, Magnanou *et al.* 2005, Cretegny & Genoud 2006, Oliveira *et al.* 2016). Contrasting results were sometimes obtained, suggesting an appreciable intraspecific variation. In particular, estimates of the *BMR* of shrews from southern parts of the species' range (Fons & Sicart 1976, Magnanou *et al.* 2005, Oliveira *et al.* 2016) are much higher than those of shrews from more northern areas (Sparti 1990, Nagel 1991, 1994, Fontanillas *et al.* 2005, Cretegny & Genoud 2006). This difference appears confusing, both in magnitude and direction, especially if one considers the interspecific patterns yet described. In order to compare their standard energetics' parameters (*BMR*, T_b and *c*), I measured resting rate of metabolism and body temperature of greater white-toothed shrews from Southern France and Switzerland at different ambient temperatures with the same methodology.

MATERIAL AND METHODS

Animals and maintenance

Greater white-toothed shrews were captured in the fall (October – December) in the vicinity of Lausanne (Western Switzerland, $N = 17$) and at Tour du Valat (Camargue, Southern France, $N = 12$). These two populations experience very different climatic conditions as can be inferred from the data gathered by the nearby meteorological stations of Geneva and Montpellier (Peel *et al.* 2007). The Mediterranean climate is warmer than that of the Swiss lowlands (mean annual temperature 14.3 *vs* 9.8 °C) with a milder coldest month (5.9 *vs* 0.2 °C) and a hotter warmest month (23.5 *vs* 19.3 °C). It is also globally drier (mean annual precipitation 762 *vs* 933 mm) and characterized by a warm season (April – September) that is much drier than the cold one (312 *vs* 452 mm), whereas in the Swiss lowlands the warm season receives even more precipitation than the cold one (501 *vs* 432 mm).

All captured individuals were born the same year. They were transferred to Lausanne University where they were maintained for several weeks in identical conditions. They were reared singly in cages of 25 x 40 cm of which the bottom was covered with earth. A small box filled with dry hay was provided for nesting. Lighting followed a photoperiod similar to that of both Southern France and Switzerland during the experimental period (lights on between 07:30 and 18:00) and ambient temperature ranged between 18 and 20 °C. Food, consisting of minced meat mixed with carrots and a supplement of vitamins and minerals (Genoud & Vogel 1990), and water were provided *ad libitum*.

Experiments

Animals were acclimated for 10 – 14 days to the rearing conditions before being measured within three additional weeks. They were measured only once per day and each experiment was done at a single experimental temperature. The chosen experimental temperatures were expected to provide values of body temperature and rate of metabolism both within the thermoneutral zone (i.e. the thermal range within which resting metabolic rate remains constant and minimal) and below thermal neutrality, hence permitting to estimate the normothermic body temperature (resting T_b maintained below thermal neutrality), minimal thermal conductance (*cmin*) and *BMR* of each individual. Since previous work on *C. russula* reported a lower limit of the thermoneutral zone located between 27.5 and 30 °C and an upper limit at slightly less than 35 °C (Nagel 1985, 1991, Sparti 1990), each shrew was randomly measured at 20 °C, 25 °C, 30 °C, 32.5 °C and 35 °C. Minimal resting rates of metabolism corresponding to the *BMR* were expected to occur at 30 and 32.5 °C.

Rate of metabolism was measured as oxygen consumption (VO_2) with a flow-through respirometry system. Fresh outside air was pushed through a 0.5 l respirometry chamber placed in a water bath at a regulated temperature. Flow rate was set at 8 – 16 l/h depending on the experimental temperature. Ambient temperature (T_a) within the metabolic chamber was not measured during the experiments, but preliminary tests showed that despite the presence of a shrew, T_a within the chamber always remained within 0.5°C of the regulated temperature. Immediately after the chamber, CO_2 and water vapour were successively scrubbed. Then, flow rate was measured with a rotameter (Sho-Rate, Brooks Instruments, Ede, Netherlands) calibrated in the experimental conditions of temperature and pressure. Volumes were converted to STPD conditions (standard temperature and pressure of dry gas). Finally, the O_2 fraction was measured with a paramagnetic oxygen analyser (Taylor Servomex OA 273) of which the output was recorded continuously with a chart recorder. Rate of oxygen consumption (VO_2) was calculated using equation 11.1 in Lighton (2008) and wet thermal conductance (*c*) was calculated using corresponding values of T_a, T_b and VO_2 (McNab 1980) as $c = VO_2 / (T_b - T_a)$.

Neither food nor water was available during the experiments, which lasted 1 – 3 h. A run was terminated when the O_2 consumption reached a minimal level that was relatively stable for at least 5 min, indicating that the shrew was resting. The shrew was rapidly removed from the respirometry chamber and its body temperature was measured within 1 min with a BAT–12 telethermometer (mouse rectal probe BAT–3, inserted 1 cm deep into the rectum). Since food was withheld 1 h before each run, it can be assumed that shrews were postabsorptive at the end of the experiments, when measurements were made (McNab 1991). Body mass (*m*) was measured at the beginning and at the end of each run. The latter value is hereafter referred to as the experimental body mass, as it corresponds to the physiological measurements. In a few cases, a resting phase ended shortly before the shrew was removed such that resting T_b and *c* could not be obtained. In those cases, the experimental body mass corresponding to the resting rate of metabolism was calculated by linear interpolation between the initial and final body masses. When no rest was observed for 3 h, the experiment was stopped and was done again on a subsequent day.

Statistics

Although only individuals born the same year were captured, age could not be assessed precisely and included as an explanatory variable. However, after weaning, greater white-toothed shrews typically reach a stationary body mass until the end of the winter (Jeanmaire-Besançon 1984, Genoud & Hutterer 1990), such that any age related weight effect can be excluded. An average body mass was calculated for each shrew as the mean of all experimental body masses. In order to check that shrews from both localities reacted in roughly similar ways to captivity, the captivity-induced body mass change was also calculated for each individual as $\partial m = m_f - m_i$, where m_i is the body mass measured upon arrival at Lausanne University and m_f is that measured at the end of the last run. Linear models were used to test for the effect of locality (France *vs* Switzerland) on average body mass and ∂m. Because sexual size dimorphism was previously observed in populations from both Switzerland (Bouteiller-Reuter & Perrin 2005, Fontanillas *et al.* 2005) and the Mediterranean region (Sans-Coma *et al.* 1976), sex was included as an additional explanatory factor in these models.

The study was not designed to define precisely the limits of the thermoneutral zone. However, the following procedure was applied to check whether the data were in agreement with the previously established thermoneutral zone (Nagel 1985, 1991, Sparti 1990). Firstly, the T_a at which the lowest rate of metabolism was observed for each individual was identified. Secondly, paired *t*-tests were performed to test for differences in average rate of metabolism between adjacent pairs of experimental temperatures within the expected thermoneutral zone (30 *vs* 32.5 °C) as well as across its expected limits (i.e. 25 *vs* 30 °C and 32.5 *vs* 35 °C). *P*-values were adjusted using a Bonferroni correction. Only shrews for which measurements were available at both of each pair's experimental temperatures were selected for this purpose.

For *BMR* and *cmin* (a single value per individual) the effect of locality was tested using linear models. Both physiological parameters depend on body mass, hence experimental body mass was included in these models as a covariate in addition to the factors locality and sex. Body mass, *BMR* and *cmin* were $\log_{10}$-transformed to linearize the relationships and remove heteroscedasticity. The effect of locality on the T_b regulated at rest below thermal neutrality was tested using a mixed effects linear model (Zuur *et al.* 2009) to account for the different contributions of the different individuals (one or two measurements per individual). Shrew identity was entered as a random effect and locality, sex and T_a were included as fixed effects. Non-significant interactions were removed from all models (Engqvist 2005) and the normality assumption was checked with the Shapiro-Wilk test. The level of significance was set at 0.05.

RESULTS

Body mass

Average body mass significantly depended on both locality ($t_{26} = 8.4$, $P < 0.001$, $N = 29$) and sex ($t_{26} = 3.1$, $P = 0.005$). Individuals from France were on average lighter than those from Switzerland, and females were lighter than males (table 1). On average, shrews maintained

Table 1. Body mass and energetic parameters of *C. russula* from Southern France and Switzerland. Means ± standard deviations are reported. *N* (number of individuals) is indicated in parentheses. *m* is average body mass, whereas m_{BMR} and m_{cmin} are the body mass corresponding to the *BMR* estimate and to the *cmin* estimate, respectively. "Overall" reports the average of male and female averages, except for T_b, where an average of all individuals is indicated.

	Population from Southern France			Population from Switzerland		
	Females	Males	Overall	Females	Males	Overall
m (g)	7.4±0.9 (7)	8.9±1.0 (5)	8.2±1.1 (12)	10.5±0.8 (11)	11.1±0.8 (6)	10.8±0.4 (17)
BMR ($mlO_2\ h^{-1}$)	19.3±2.8 (7)	22.9±1.6 (5)	21.1±2.5 (12)	24.5±2.3 (11)	26.5±1.0 (6)	25.5±1.4 (17)
m_{BMR} (g)	7.4±1.0 (7)	9.1±1.1 (5)	8.3±1.2 (12)	10.4±0.8 (11)	11.3±0.9 (6)	10.9±0.6(17)
T_b (°C)	34.9±0.2 (7)	34.8±0.6 (5)	34.9±0.4 (12)	34.7±0.9 (8)	34.0±0.7 (5)	34.4±0.9 (13)
cmin ($mlO_2\ h^{-1}\ °C^{-1}$)	2.83±0.27 (7)	3.16±0.12 (5)	3.00±0.23 (12)	3.18±0.37 (8)	3.05+0.11 (5)	3.12±0.09 (13)
m_{cmin} (g)	7.4±1.0 (7)	8.8±0.7 (5)	8.1±1.0 (12)	10.5±1.0 (8)	10.7±0.6 (5)	10.6±0.1 (13)

their initial body mass during the experimental session (∂m = -0.1 ± 0.6 g, N = 29), although appreciable individual variation was observed (∂m-range: -1.3 – 1.4 g). ∂m was not significantly affected by locality (t_{26} = -0.46, P = 0.65) or sex (t_{26} = -1.20, P = 0.24).

Thermal energetics of *Crocidura russula*

All individuals from both localities reacted as typical endotherms when exposed to various T_a (figure 1). Short episodes of torpor (≤ 1 h) occurred during three runs with two different

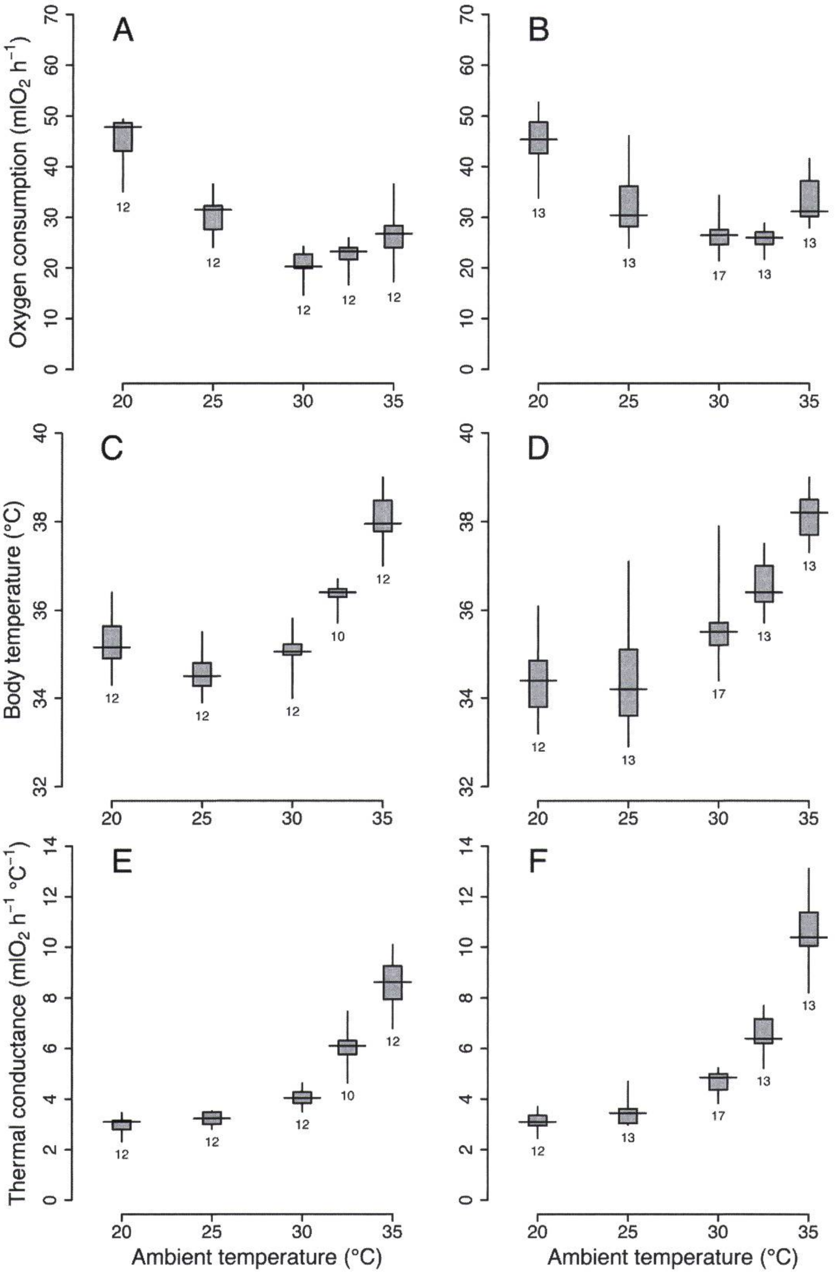

Figure 1. Resting rate of metabolism measured as oxygen consumption (A, B), body temperature (C, D) and wet thermal conductance (E, F) in *C. russula* from Southern France (left hand graphs: A, C, E) and Switzerland (right hand graphs: B, D, F) at different ambient temperatures. Data are shown as box and whiskers plots (median ± 25/75 % and range). Sample size (representing both the number of individuals and the number of measurements) is given below each lower whisker.

shrews from Switzerland. A value of the euthermic resting metabolic rate could still be obtained during two of these experiments, whereas the third had to be repeated on the next day. No data on torpid shrews are considered in this paper.

Mean rate of oxygen consumption (VO_2) did not differ significantly between 30 and 32.5 °C in the Swiss shrews ($t_{12} = 1.02$, $P = 0.99$). Seven of them exhibited their lowest VO_2 at 30 °C and the remaining 6 individuals had their lowest metabolic rate at 32.5 °C. A marginal tendency ($t_{11} = 2.7$, $P = 0.07$) was observed among the French shrews for a slightly higher metabolic rate at 32.5 °C than at 30 °C (figure 1). Even if most ($N = 10$) of these individuals had their lowest VO_2 at 30 °C, two individuals exhibited their lowest rate at 32.5 °C, suggesting that, at least for these two individuals, the thermoneutral zone extended above 32.5 °C. The lowest stable VO_2 measured for each shrew at 30 or 32.5 °C was therefore selected as an estimate of its *BMR*. In agreement with earlier estimations of the limits of the thermoneutral zone (Nagel 1985, 1991, Sparti 1990), metabolic rate was significantly higher at 25 °C than at 30 °C in both populations ($t_{12} = 3.3$, $P = 0.02$ and $t_{11} = 10.3$, $P < 0.001$ for the Swiss and the French populations, respectively) and it was also higher at 35 °C than at 32.5 °C ($t_{12} = 7.4$, $P < 0.001$ and $t_{11} = 3.4$, $P = 0.02$ for the Swiss and the French populations, respectively; figure 1). Within and above thermal neutrality, *c* and T_b increased strongly with T_a (figure 1). The lowest value of wet thermal conductance (*c*) was obtained for each shrew at either 20 °C or 25 °C. This value was taken as an estimate of its minimal thermal conductance (*cmin*, table 1).

Comparison between populations

Locality significantly affected the T_b maintained below thermal neutrality through its interaction with T_a (table 2). This interaction was due to the slightly higher average T_b maintained by shrews from France at 20°C, as compared both to their T_b at 25°C and to the T_b maintained by the Swiss shrews (figure 1). The same pattern also explains the negative effect of T_a on T_b when both populations are considered (table 2). These effects remain small, though, especially when considering the relatively large thermolability of the Swiss shrews (extreme values 32.9 – 37.1 °C, figure 1).

Average absolute *BMR* was larger in the Swiss than in the French population and was also larger in males than in females (table 1). This variation could be explained by the concomitant variation in body mass among populations and sexes (figure 2, table 1). Indeed, only *m* had a significant effect on *BMR* in a model also including locality and sex as explanatory factors (table 2). Discarding locality and sex, the following scaling equation was obtained for shrews from both localities ($N = 29$, figure 2):

$$\log_{10} BMR = 1.478\ (\pm\ 0.087) + 0.648\ (\pm\ 0.089)\ \log_{10} m$$

Standard errors are given in parentheses, *BMR* is expressed in mlO_2/h and *m* is in g. This equation explained 66 % of the observed variation in *BMR*.

Average absolute *cmin* was also higher in the Swiss than in the French population (table 1). Males had on average a higher conductance in the French population, but the reverse was true in the Swiss population despite the males being also heavier in this locality. Minimal thermal conductance was affected significantly by body mass and locality but not by sex (table 2). Accounting for body mass differences, the Swiss shrews had a significantly lower *cmin* than their French counterparts (figure 3).

Table 2. Effect of locality on energetic parameters of *C. russula* from Southern France and Switzerland. Response variables are the standard energetics parameters T_b (body temperature below thermal neutrality), *BMR* (basal metabolic rate) and *cmin* (minimal thermal conductance). Sex is included as an explanatory variable besides locality in all models. T_b variation is analysed with a mixed-effects model also including ambient temperature (T_a) as an explanatory variable, whereas linear models including body mass (*m*) as a covariate are used for *BMR* and *cmin*. *BMR*, *cmin* and *m* were $\log_{10}$-transformed for analysis. Non-significant interactions between explanatory variables were removed from the models. Reference locality is the French locality and reference sex is female.

T_b	Estimate		SE	df	*t*	*P*
Intercept	38.00	±	1.03	22	36.90	< 0.001
T_a	-0.13	±	0.04	22	-2.91	0.008
Locality	-3.66	±	1.45	22	-2.54	0.02
Sex	-0.44	±	0.27	22	-1.63	0.12
T_a: Locality	0.14	±	0.06	22	2.25	0.03
$\log_{10}$ *BMR*						
Intercept	0.872	±	0.147	25	5.94	< 0.001
$\log_{10} m$	0.478	±	0.167	25	2.87	0.008
Locality	0.027	±	0.026	25	1.03	0.31
Sex	0.025	±	0.018	25	1.37	0.18
$\log_{10}$ *cmin*						
Intercept	-0.092	±	0.128	21	-0.72	0.48
$\log_{10} m$	0.630	±	0.144	21	4.36	< 0.001
Locality	-0.055	±	0.022	21	-2.51	0.02
Sex	-0.011	±	0.014	21	-0.75	0.46

DISCUSSION

The standard energetics' patterns observed in this study for greater white-toothed shrews from Western Switzerland are in accord with those reported by SPARTI (1990). They agree well with the limits of the thermoneutral zone estimated by this author (lower limit between 27.5 and 30 °C, and upper limit below 35 °C). Previous data were insufficient to describe the region of thermal neutrality of shrews from the southern parts of the species' range. The data reported here for individuals from Southern France suggest a thermoneutral zone extending over a range of T_a similar to that of the Swiss shrews (figure 1). They do not validate the suggestion made by FONS and SICART (1976) of a zone of thermoneutrality not extending below 35 °C.

On an absolute scale, shrews from Southern France had a lower *BMR* than those from Switzerland. However, this difference was largely explained by the variation in body mass, neither locality nor sex affecting the *BMR* significantly when body mass was accounted for. Therefore, the use of a standardized procedure (season, year, acclimation procedure, feeding status, respirometry set-up and experimental protocol) failed to confirm the *BMR* difference between northern and Mediterranean populations of *C. russula* suggested by previous reports. When expressed as a percentage of the value expected on the basis of body mass for Eutherians ($BMR = 2.85\ m^{0.726}$, with *BMR* in mlO_2/h and *m* in g; GENOUD *et al.* 2018), the *BMR* of the shrews from the Swiss

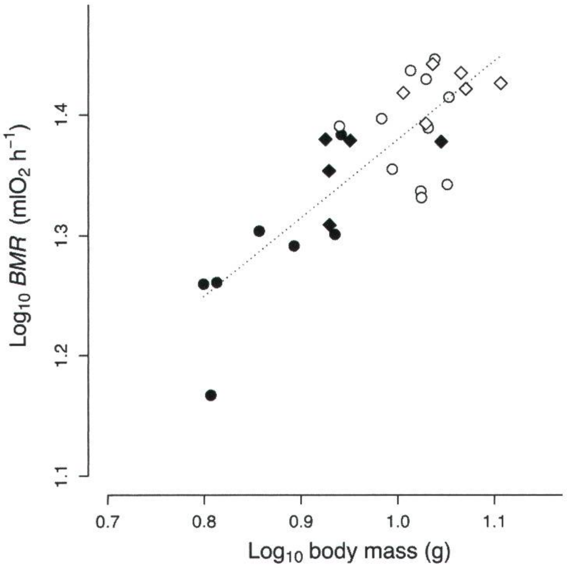

Figure 2. Relationship between basal rate of metabolism (*BMR*) and body mass among *C. russula* from Southern France (closed symbols) and Switzerland (open symbols). Circles represent females and diamonds represent males. The dotted line is the scaling relationship fitted to the entire data set (equation given in the text).

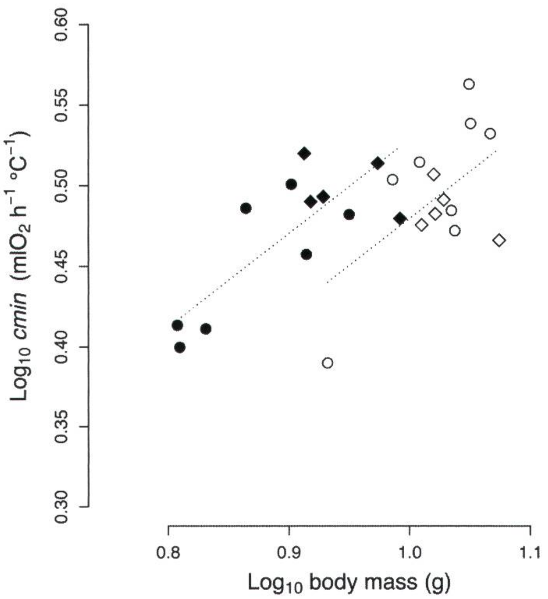

Figure 3. Relationship between minimal thermal conductance (*cmin*) and body mass among *C. russula* from Southern France (closed symbols) and Switzerland (open symbols). Circles represent females and diamonds represent males. The dotted lines are the scaling relationships for the two populations (details in table 2).

and French localities are very similar (158 % and 160 %, respectively). German shrews had basal rates between 159 % and 160 % of the expected value (Nagel 1985, 1991, 1994). Slightly lower estimates were previously obtained for wintering individuals from Western Switzerland (147 %; Sparti 1990). Even lower rates (123–135 %) were obtained in Switzerland on non-reproductive adult females maintained for several months in captivity (Cretegny & Genoud 2006) and on individuals kept for an entire winter in captivity and measured in March, at the onset of reproduction (Fontanillas *et al.* 2005). In contrast, the previous estimates reported for shrews from Southern France (194 %; Fons & Sicart 1976) and Portugal (256 %; Oliveira *et al.* 2016) are much higher. The data obtained by Magnanou *et al.* (2005) on individuals from the Mediterranean region are difficult to compare in this context, as these authors provided only a linear regression equation of metabolic rate *vs* T_a. However, at a T_a of 32.5°C (i.e. within thermal neutrality) their equation would yield a rate corresponding to 257 % of the predicted value.

The causes of the discrepancy between present and previous results on individuals from Southern Europe are unclear. Developmental or seasonal variations do not explain the discrepancy at least for the non-reproductive shrews sampled in October, November and January by Magnanou *et al.* (2005) and Oliveira *et al.* (2016). Fons and Sicart (1976) measured three adult shrews, but information is lacking on season and reproductive stage. It is also unlikely that differences in the feeding status would be a major cause. Even small amounts of food given during runs have only a limited effect on the metabolic rate in shrews, presumably because they process food very rapidly (McNab 1991). Thus withholding food during runs surely ensures a postabsorptive state unless the duration of the experiments is very short. The respirometry set-up is a more important factor to be considered. Fons and Sicart (1976) and Magnanou *et al.* (2005) used a closed-circuit respirometer with which rate of metabolism is averaged over some time period, presumably making it difficult to avoid the effects of activity. Hence non-biological causes may be involved in this discrepancy.

The absence of a significant difference in mass-independent *BMR* between shrews from localities experiencing strikingly different climates might be surprising, especially when considering the trends observed in interspecific comparative analyses (DEGEN *et al.* 1998, MUELLER & DIAMOND 2001, LOVEGROVE 2003, REZENDE *et al.* 2004, GENOUD 2014). Indeed, some studies have reported lower *BMR* in small mammal populations from warmer and/or more arid habitats (MCNAB & MORRISON 1963, CASTELLANOS-FRÍAS *et al.* 2015). However, others have described similar basal rates for small mammal populations originating from very different climates (HAIM & FAIRALL 1986; BOZINOVIC *et al.* 1999), suggesting that the effect of climate on the *BMR* may be counteracted by many other factors (e.g. MCNAB 2008). Furthermore, the present study has been conducted during the cold season, when shrews from both localities experience ambient temperatures well below the thermoneutral zone. Again, the general interspecific trend might have led to the prediction of a higher *BMR* and higher maximum rate of thermogenesis in shrews from the Swiss locality. Indeed, survival of *C. russula* in mountain areas of Switzerland is crucially affected by NST (non-shivering thermogenesis), which accounts for an important part of the thermogenic response (FONTANILLAS *et al.* 2005). In addition, maximum rate of thermogenesis is correlated positively with *BMR* among rodents (REZENDE *et al.* 2004). However, European crocidurine shrews (including *C. russula*) exhibit higher maximum rates of thermogenesis than African crocidurines, without having higher basal rates (SPARTI 1992). Also, in greater white-toothed shrews from Switzerland, mtDNA haplotype variants showing different altitudinal distributions affected NST in interaction with sex, but were characterized by similar basal rates (FONTANILLAS *et al.* 2005). Thus maximum rate of thermogenesis might be increased adaptively in shrews without affecting much the *BMR*.

Thermal conductance differed significantly between the two populations. The average *cmin* of the Swiss shrews corresponds to 98 % of the value expected on the basis of body mass for a mammal during the resting phase ($cmin = 1.022\ m^{0.481}$, *cmin* in $mlO_2\ h^{-1}\ °C^{-1}$ and *m* in g; ASCHOFF 1981). Previous estimations for the same population during the cold season are only slightly lower (90 – 94 %; LARDET 1989, SPARTI 1990). In comparison, the minimal thermal conductance of shrews from Southern France averaged 108 % of the expected value. Estimates based on the slope of the metabolic rate *vs* T_a relationship (NAGEL 1977, 1980, 1985, 1991, 1994, MAGNANOU *et al.* 2005) can hardly be compared to the above values as this slope often differs from true conductance (MCNAB 1980).

The effect of climate on fur insulation and thermal conductance has long been demonstrated: mammals from cold regions tend to have a lower conductance than tropical ones (SCHOLANDER *et al.* 1950a, 1950b) and generally exhibit lower conductance in winter (HART 1956). This pattern tends to be weaker among small mammals, partly because they are more limited in the amount of fur they can carry (HART 1956, MCNAB 2002). Thus, conspecific small mammal populations that were examined within the same study usually exhibited only minor differences in thermal conductance, even when coming from distant locations and different climates (e.g. ROSENMANN & MORRISON 1974, BOZINOVIC *et al.* 1999). However, either lower (MCNAB & MORRISON 1963) or higher (HAIM & FAIRALL 1986) conductance values were found in desert populations of some species of rodents and *cmin* tends to be higher in African than in European shrews (SPARTI 1990). Despite being relatively small, the observed difference between the two

C. russula populations can be seen as an adjustment to their different climates. At the same body mass and body temperature, a 10 % difference in *cmin* (98 *vs* 108 %) would translate into a similar difference in resting rate of metabolism below thermal neutrality, hence improving survival during winter. Lardet (1989) has demonstrated that in Western Switzerland, *C. russula* undergoes seasonal changes in *cmin* of similar amplitude, whereby wintering shrews have a lower conductance (94 %) than summer individuals (103 %). It must be noted that the observed difference between the two populations does not necessarily represent differential adaptation to their respective climate. It could also be due to differential acclimatization to the climatic conditions experienced by the shrews at the time they were captured.

As it colonized the temperate regions of Europe, *C. russula* made a number of morphological, anatomical, physiological and behavioural adjustments that allowed it to balance an energy budget in progressively colder environments. Firstly, reduction of heat loss was achieved through increased reliance on daily torpor, social thermoregulation and nest-site selection (Genoud & Hausser 1979, Genoud 1985, 1988). Results of this paper (see also Sparti 1990) suggest that heat loss was further reduced by a decrease in thermal conductance (increased insulation), at least in winter. Secondly, maximum rate of thermogenesis increased, but this increase was not accompanied by a concomitant rise in *BMR* (Sparti 1992).

Increasing body mass was probably a third important adjustment. The body mass variation observed in the greater white-toothed shrew over its range appears to agree with "Bergmann's rule", according to which endothemic animals tend to be larger in colder regions. This trend has been shown to occur in a small majority of the studied mammal species (Ashton *et al.* 2000, but see McNab 1971, 2002), although there are notable counter-examples, including several Palearctic shrews of the genus *Sorex* (Ochocinska & Taylor 2003). The original explanation that larger animals are favoured in cold climates because they have lower relative (i.e. mass-specific) heat losses due to a smaller surface to volume ratio should clearly be rejected, as larger animals do in fact expend more energy and require more food on an absolute scale despite their smaller surface to volume ratio (McNab 1971, 2002). The positive link between body mass and energy expenditure is illustrated in the present study by the positive effect of body mass on both absolute *cmin* and *BMR* (table 2, figs. 2 and 3). A correlation between body mass and latitude or thermal conditions in endotherms can be explained in many different ways, including by adducing some of the numerous effects that body mass has on energetics (e.g. reviewed by Ashton *et al.* 2000, McNab 2002). On one hand, a larger body mass leads to larger energy requirements, which is suggested as the principal cause for the tendency exhibited by shrews of the genus *Sorex* to be smaller in colder areas (Ochocinska & Taylor 2003). But on the other hand, larger body mass is associated with larger fasting endurance time (maximum time between "refuelling"), because the amount of fat varies with body mass raised to a power that is larger than that for rate of metabolism (Lindstedt & Boyce 1985, McNab 1991, 2002). Larger body mass may also allow larger amounts of brown fat to be carried (Fontanillas *et al.* 2005), a tissue that is responsible for most of the NST (non-shivering thermogenesis). Indeed, small size was associated with lower survival in Swiss wintering *C. russula* maintained in semioutdoor conditions (Fontanillas *et al.* 2005). Thus in the greater white-toothed shrew, larger size could be favoured in colder regions because its negative consequences (larger potential energy requirements) are minimized by adjustments reducing heat loss and outbalanced by advantages derived in particular from larger fasting endurance.

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