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Rate of metabolism during lactation in small terrestrial mammals (*Crocidura russula*, *Mus domesticus* and *Microtus arvalis*)

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Abstract

Basal rate of metabolism (BMR) and resting maternal rate of metabolism around peak lactation (RMR_L) were measured in *Crocidura russula*, *Mus domesticus* and *Microtus arvalis*. These species have a moderate or high BMR relative to the scaling relationship of Kleiber. One goal of the study was to check whether females of these species show elevated rates of metabolism during lactation. A second goal was to test for a possible intraspecific correlation between the level of BMR and the change in rate of metabolism associated with lactation. RMR_L was significantly higher than BMR in all species when changes in body mass between the two states were taken into account. Data available on other small mammals are in accordance with this finding, which does not support the hypothesis that low-BMR mammal species increase their rate of metabolism during reproduction because Kleiber's relationship represents an optimal level for therian reproduction. Within *C. russula* and *M. domesticus*, a significant and negative correlation was found between the level of BMR and the change in rate of metabolism associated with lactation. This pattern is presumably due to the fact that low-BMR females undergo more extensive physiological and anatomical changes during lactation than high-BMR females.

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1. Introduction

The energetic cost of reproduction is a central aspect of reproduction in small mammals. When they are pregnant or lactating, females channel appreciable (and often very large) amounts of the ingested energy into new tissues or milk that is distributed to the offspring (Randolph et al., 1977; Weiner, 1987; Mover et al., 1989; Genoud and Vogel, 1990; Thompson, 1992; Rogowitz and McClure, 1995; Künkele and Trillmich, 1997; McNab, 2002; Liu et al., 2003). This energy, which is allotted to production, is not considered when measuring rate of metabolism. However, there are two aspects of the energy cost of production: energy must be sequestered into the new tissues or milk, and additional energy is required for the work of production (Gessaman, 1973). Thus, the rate of metabolism of reproducing females may be more or less affected by the physiological changes associated with reproduction.

Basal rate of metabolism (BMR) is defined as the minimum rate of metabolism of an endothermic animal measured under a number of restrictive conditions: individuals must be adults resting within the thermoneutral zone, neither digesting food nor (for females) being involved in reproduction (McNab, 1997). Despite such a precise definition, this physiological parameter exhibits a large degree of variation among mammals, only part of which is linked to body mass (Kleiber, 1961; McNab, 1988). Allometric equations (e.g. Kleiber, 1961 or McNab, 1988) are commonly used to calculate the “relative BMR” of a species under study by expressing its BMR as a percentage of the value expected on the basis of its body mass. The variation in relative BMR among mammals has been analyzed by many authors and its interpretation remains controversial (see McNab, 2002, for a review). In particular, McNab (1980) proposed that a high relative BMR may permit a high reproductive output, through higher growth rate of pups, higher milk production, higher fecundity or a combination of these. This proposal has been the subject of an ongoing debate, either at an interspecific level or at an intraspecific level (Hennemann,

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1983; Hayssen, 1984; Glazier, 1985; Derting, 1989; Derting and McClure, 1989; Earle and Lavigne, 1990; Harvey et al., 1991; Hayes et al., 1992; Stephenson and Racey, 1993a; Speakman and McQueenie, 1996; McLean and Speakman, 2000; Johnson et al., 2001a; McNab, 2002; Krol et al., 2003).

Thompson and Nicoll (1986) and Nicoll and Thompson (1987) observed that females of three mammalian species with a low BMR (*Monodelphis domestica*, *Echinops telfairi* and *Elephantulus rufescens*) strongly increased their rate of metabolism during reproduction, with maximum values achieved during lactation. In contrast, data from the literature suggested no such increase in a few species with a moderate or high BMR. This difference between low-BMR and high-BMR species led Thompson and Nicoll (1986) to hypothesize that predicted BMR according to the Kleiber equation ($BMR = 3.42 m^{0.75}$, where BMR is in $mLO_2 h^{-1}$ and m is body mass in g) may reflect an “advantageous or essential energetic regime” for therian reproduction and to propose that this is the reason why mammals with a low BMR relative to the Kleiber equation must increase their rate of metabolism during reproduction. Indeed, their hypothesis is supported by the increased rate of metabolism of low-BMR species during reproduction only if high-BMR species do not show such an increase. However, more recent studies showed diverse patterns of metabolic change during reproduction in species with a moderate or high BMR, including maternal rates of metabolism clearly above nonreproductive levels (Thompson, 1992; Stephenson and Racey, 1993a; Speakman and McQueenie, 1996; Antinuchi and Busch, 2001).

It has also been suggested that the rate of metabolism for a whole individual can be increased in reproducing female mammals as a consequence of the increase in size and/or activity of specific organs or tissues, such as the mammary glands or the intestine (Hammond and Diamond, 1992; Thompson, 1992; Hammond et al., 1994; Speakman and McQueenie, 1996). If this was the main cause of elevated maternal rate of metabolism, low-BMR and high-BMR species should not exhibit the drastically different patterns of metabolic change during reproduction that have been hypothesized by Thompson and Nicoll (1986). Furthermore, appreciable intraspecific variation in BMR or maternal rate of metabolism has often been noticed (Derting and McClure, 1989; Earle and Lavigne, 1990; Hayes et al., 1992; McLean and Speakman, 2000), but the possible relationship between the level of BMR and the pattern of change in maternal rate of metabolism among conspecific females has yet to be examined.

In the present study, we provide new data on the BMR and the maternal rate of metabolism measured during lactation ($=RMR_L$; Thompson, 1992) in three species of small terrestrial mammals, the white-toothed shrew *Crocidura russula* (Soricidae, Eulipotyphla) the (wild) house mouse *Mus domesticus* (Muridae, Rodentia) and the common vole *Microtus arvalis* (Cricetidae, Rodentia). These small mammals have a BMR that is either close to or above the value predicted by the Kleiber equation (Rosenmann and Morrison, 1974; Sparti, 1990; Richardson et al., 1994; Cretegy, 1997). We address two main questions: firstly, does RMR_L differ from BMR in these three

species? Secondly, is the variation in metabolic change between the two states (lactating vs. neither pregnant nor lactating) correlated with variation in BMR among conspecific females? Because females may exhibit a different body mass in these two reproductive states and because body mass is known to affect rate of metabolism, it is obviously necessary to control for the confounding effects of body mass to answer these questions.

2. Materials and methods

2.1. Animals and maintenance conditions

Nineteen female *C. russula* (average body mass, $m = 11.3 \pm 1.5$ g (SD)), 24 female *M. domesticus* ($m = 22.8 \pm 2.2$ g) and 11 female *M. arvalis* ($m = 33.9 \pm 7.9$ g), were used in this study. The shrews were caught in winter in the vicinity of Lausanne (western Switzerland, 400–600 m elevation). In this region, the reproductive season of *C. russula* normally extends from early spring to fall (Jeanmaire-Besançon, 1988) and females participate only exceptionally in two successive reproductive seasons (Jeanmaire-Besançon, 1986), so that the individuals caught can be assumed to be nulliparous and born in the previous summer or fall. All mice and voles were first-generation offspring of individuals caught in the vicinity of Lausanne. The reproductive season of *M. arvalis* is similar to that of *C. russula* in this region (personal observations, C.C.), that of *M. domesticus* extending probably throughout the year where favourable conditions are met (Hübner, 1995). The taxonomy of the European mice is still debated, but populations from Switzerland belong to the West-European long-tailed commensal form usually referred to as *M. domesticus* (Hübner, 1995; Macholan, 1999). Females of all three species were kept individually or paired with males originating from the same populations (see below for details) in cages of 38×22 cm in an animal room with an ambient temperature of 20–22 °C and a long-day photoperiod (16L:8D) corresponding to summer conditions. Cage floors consisted of earth for shrews and wood shavings for rodents. Hay was given as nesting material to all species and a nest box was provided to the shrews and voles. Food and water were given ad libitum. In the case of shrews, food consisted of minced horsemeat mixed with grated carrots, and a mineral and vitamin supplement for insectivores (Eberle Nafag, Gossau, Switzerland). The rodents received dry pellets (type 924/25W10, Eberle Nafag, Gossau, Switzerland), but they also consumed variable quantities of the dry hay given as nesting material. In addition, voles received seeds and a piece of carrot on a daily basis.

2.2. Experiments

The rate of metabolism of each female was measured during the reproductive season in two reproductive states: (1) while neither pregnant nor lactating (hereafter referred to as the NL state), and (2) around peak lactation (the L state). All measurements were made under conditions meeting the requirements for BMR, except for the reproductive activity in the L state. Rates of metabolism measured during lactation are therefore referred to

as resting rates of metabolism (RMR_L ; Thompson, 1992). Throughout this paper, the NL state corresponds to the condition shown by adult females within the reproductive season, which are ready to reproduce but are neither pregnant nor lactating. This eliminates a number of potential sources of variation in rate of metabolism, including particularly seasonal variations (Genoud, 1990; Merrit et al., 2001). In order to avoid the difficulty of determining whether a nulliparous female was in a physiological state appropriate for reproduction or not, BMR was not measured in nulliparous females, but in females that had successfully raised at least one litter. It was measured at least one week after weaning of the preceding litter and subject to the condition that the female was not pregnant (male removed before parturition of the preceding litter).

The RMR_L was measured during the second to sixth litter of each female, during summer or fall. The first litter was never used since primiparous females differ from more experienced females in their patterns of energy acquisition and allocation (e.g. see Genoud and Vogel, 1990, for *C. russula*; Cretegny, 1997, for *M. arvalis*). *C. russula* and *M. domesticus* mothers were not pregnant at the time of RMR_L measurement (males removed at parturition), but in *M. arvalis* males were not separated at parturition, such that most mothers were simultaneously pregnant and lactating. Furthermore, in order to standardize reproductive effort, litters were adjusted at parturition to 4 young, which is a little below average litter size for all three species in the region of Lausanne (Genoud and Vogel, 1990; Cretegny, 1997; personal observations). RMR_L measurements took place around peak lactation (Genoud and Vogel, 1990; Cretegny, 1997; personal observations), between days 7 and 11 postpartum (the day of parturition is day 0) in *C. russula*, between days 8 and 12 in *M. domesticus* and during day 10 in *M. arvalis*. Litters were weighed on the day of RMR_L measurement. In addition, they were also weighed on day 10 in *C. russula* and *M. domesticus*, when RMR_L was measured on a different day.

2.3. Rate of metabolism

Rate of metabolism was measured as oxygen consumption and is hereafter expressed in $mLO_2 h^{-1}$. Experiments were conducted at 31 °C, which is within the thermoneutral zone for all three species (Sparti, 1990 for *C. russula*; Rosenmann and Morrison, 1974 and Genoud, unpublished data for *M. domesticus*; Cretegny, 1997 for *M. arvalis*). Females were removed from their cages in the morning and introduced into the respirometric chamber. Values were taken only after a period allowing for the digestion of the food that the animals may have eaten in the morning, i.e. after 3 h for the shrews and 6 h for the two rodent species. After this time lapse, a measure was taken during a period of at least 15 min of stable and minimal oxygen consumption corresponding to a period of inactivity of the individual.

The respirometric system used is an open air-flow system that has been described previously (Sparti and Genoud, 1989; Genoud and Ruedi, 1996). Animals were placed in a 1.0 L (*C. russula*) or 3.5 L (*M. domesticus* and *M. arvalis*) respirometric chamber submersed in a water bath at 31 °C. Air was pushed through this chamber by a pump at a regulated flow rate of 15–

27 $L h^{-1}$ STPD depending on the size of the animal. After the chamber, the air passed through soda lime and silica gel to remove carbon dioxide and water, and then through a Brooks Sho-Rate flow meter (Veenendaal, Netherlands) calibrated for the operating temperature and pressure conditions. Part of the air was then passed through a two-way oxygen analyser (OA184 Taylor Servomex, Crowborough, England or S-3A/11 Ametek, Pittsburgh, PA, USA) to measure its oxygen concentration. Oxygen consumption was calculated according to formula 10 in Depocas and Hart (1957).

2.4. Statistics

Unless otherwise stated, values are expressed as means and standard deviation. Relative BMR is BMR expressed as a percentage of the value expected according to Kleiber's equation (Kleiber, 1961), because this was the scaling equation used by Thompson and Nicoll (1986). Equations derived more recently from a much larger number of mammal species (McNab, 1988) would not change any of the conclusions of the present paper. All statistical tests were carried out on \log_{10} -transformed data to prevent heteroscedasticity and to linearize the relationship between rate of metabolism and body mass.

As every female had been measured in both reproductive states, the effect of reproductive state on rate of metabolism in each species was tested with a repeated measures ANCOVA. The software "R" (or "GNU S"; Ihaka and Gentleman, 1996) was used: it allows for a variation of the covariable across the factor within subjects. \log_{10} rate of metabolism was the dependent variable and \log_{10} female body mass was the covariable. Reproductive state was a within-subjects factor, individual females being the "subjects". There are two levels of analysis in such ANCOVAs: a "between-subjects" level and a "within-subjects" level. In this case, the null hypothesis was that \log_{10} rate of metabolism would not be affected by reproductive state within subjects (individuals). Litter mass may have affected RMR_L even if litter size was standardized and although such an influence has generally not been found in earlier studies (e.g. see Krol et al., 2003). Because RMR_L was not necessarily measured on the same day in *C. russula* and *M. domesticus*, litter mass measured on the day of RMR_L measurement depended strongly on the age of the young in these species. It was not correlated with RMR_L ($P > 0.1$ in both cases). Litter mass measured on day 10 ($=m_Y$) was used instead as a comparative index of the energetic load imposed on the female by its litter. However, m_Y was significantly correlated with female mass (see below), which is the covariable. Thus, when RMR_L was correlated with m_Y independently of female body mass (partial correlation analyses), residuals of the linear regression between $\log m_Y$ and $\log m_L$ were calculated ($=res_{m_Y}$; m_L is female body mass during lactation) and a similar ANCOVA was done on RMR_L values corrected for an average residual.

At the intraspecific level, testing of the hypothesized correlation between the change in rate of metabolism between the two reproductive states (RMR_L –BMR) and the level of BMR compared to other conspecific females was done with partial correlation analyses controlling for body mass effects.

Table 1
Body mass, BMR (NL state) and RMR_L during peak lactation (L state) in three species of small mammals

	<i>Crocicidura russula</i>	<i>Mus domesticus</i>	<i>Microtus arvalis</i>
<i>N</i>	19	24	11
<i>NL state</i>			
Body mass (g)	11.3±1.5	22.8±2.2	33.9±7.9
BMR (mL O ₂ h ⁻¹)	22.4±2.0	35.3±4.8	61.4±7.1
Relative BMR (%)	106	99	128
logBMR=	0.84+0.48 log <i>m</i>	0.28+0.93 log <i>m</i>	1.20+0.38 log <i>m</i>
SE _a ; SE _b ; r ² ; P	0.13; 0.12; 0.47; 0.001	0.30; 0.22; 0.45; <0.001	0.14; 0.09; 0.65; <0.01
<i>L state</i>			
Body mass (g)	12.8±1.3	24.9±2.0	28.6±6.7
RMR _L (mL O ₂ h ⁻¹)	32.1±3.6	44.4±3.7	66.3±8.2
Relative RMR _L (%)	139	116	157
logRMR _L =	0.52+0.89 log <i>m</i>	0.58+0.76 log <i>m</i>	1.14+0.47 log <i>m</i>
SE _a ; SE _b ; r ² ; P	0.19; 0.17; 0.61; 0.0001	0.24; 0.17; 0.48; <0.001	0.16; 0.11; 0.67; <0.01

Relative BMR and RMR_L are rates of metabolism expressed as a percentage of the value predicted on the basis of body mass (*m*) according to the equation of Kleiber (1961; BMR=3.42 *m*^{0.75}, where BMR is in mL O₂ h⁻¹ and *m* in g). The linear regressions of BMR and RMR_L against body mass are also given (log₁₀-transformed values), with the standard errors of the constant (SE_a) and slope (SE_b) as well as *r*² and the significance level *P* of the regression.

The analyses were complicated by the fact that this metabolic change may be influenced by female body mass, by body mass changes of the female between the two states, as well as by litter mass. Five variables were therefore used: log*m*_{NL}, where *m*_{NL} is female body mass in the NL state; logΔ*m*=log(*m*_L-*m*_{NL}); res*m*_γ; resBMR, the residual of the linear regression between logBMR and log*m*_{NL}; and logΔMR=log(RMR_L-BMR). The

partial correlation between logΔMR and resBMR was then calculated, while controlling for the other variables.

Differential degrees of relatedness within a population might lead to conflict with the statistical requirement of independence between individuals in both the ANCOVA and the partial correlation analysis. Unfortunately, no information was available on the relatedness between the individuals measured. However, despite some heritable variation appears to be present for BMR in laboratory mice, rate of metabolism and other related physiological traits have been shown to exhibit low heritabilities (for a discussion see Ksiazek et al., 2004). This suggests that the confounding effect of differential degrees of relatedness among individuals should be small in our analyses.

3. Results

3.1. BMR and RMR_L

Average BMR was slightly above the value expected on the basis of Kleiber's equation in *C. russula*, close to the predicted value in *M. domesticus*, and appreciably higher than the expected value in *M. arvalis* (Table 1 and Figs. 1–3). Slightly higher values would be obtained by using McNab's (1988) equation for 272 Eutherians (112%, 107% and 140% of expected, respectively). Metabolic variability within each species was large, the coefficient of variation being respectively 8.9%, 13.6% and 11.6% in the three species (Table 1). Even relative BMR varied strongly, with ranges of 95–127% of the predicted value in *C. russula*, 80–122% in *M. domesticus*, and 109–151% in *M. arvalis*. Lactation had a roughly similar effect on rate of metabolism in the three species (Figs. 1–3). On average, RMR_L exceeded BMR by 9.7, 9.1 and 4.9 mL O₂ h⁻¹ in *C. russula*, *M. domesticus* and *M. arvalis*, respectively (Table 1). It remained higher than the BMR even when expressed as a percentage of Kleiber's equation (Table 1), with ranges of 117–154% of

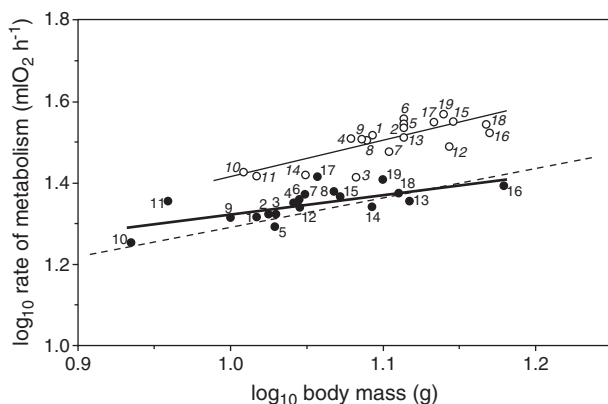


Fig. 1. Rate of metabolism (measured as oxygen consumption) as a function of body mass in 19 adult female *Crocicidura russula* measured while neither pregnant nor lactating (NL state; closed symbols=BMR) and around peak lactation (L state; open symbols=RMR_L). Individuals are numbered (NL state in standard type, L state in italics). Thick and thin continuous lines are the linear regressions through BMR and RMR_L values (Table 1), respectively, and dashed line is the scaling equation of Kleiber (1961).

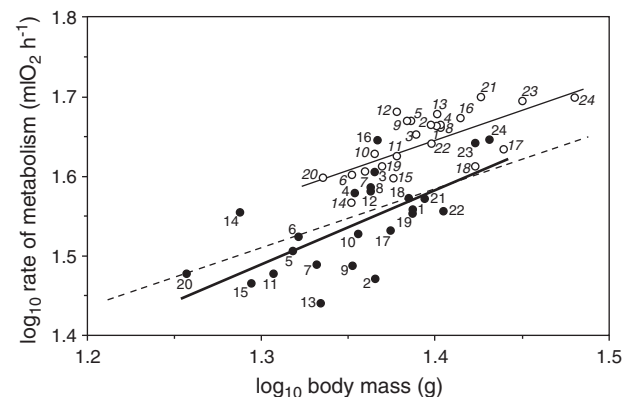


Fig. 2. Rate of metabolism (measured as oxygen consumption) as a function of body mass in 24 adult female *Mus domesticus* measured while neither pregnant nor lactating (NL state; closed symbols=BMR) and around peak lactation (L state; open symbols=RMR_L). Individuals are numbered (NL state in standard type, L state in italics). Thick and thin continuous lines are the linear regressions through BMR and RMR_L values (Table 1), respectively, and dashed line is the scaling equation of Kleiber (1961).

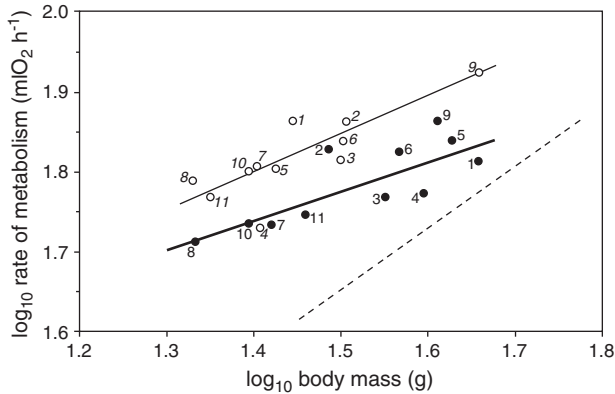


Fig. 3. Rate of metabolism (measured as oxygen consumption) as a function of body mass in 11 adult female *Microtus arvalis* measured while neither pregnant nor lactating (NL state; closed symbols=BMR) and around peak lactation (L state; open symbols=RMR_L). Individuals are numbered (NL state in standard type, L state in italics). Thick and thin continuous lines are the linear regressions through BMR and RMR_L values (Table 1), respectively, and dashed line is the scaling equation of Kleiber (1961).

predicted in *C. russula*, 102–130% in *M. domesticus*, and 138–181% in *M. arvalis*.

In *M. arvalis*, female body mass was slightly lower during lactation than in the NL state (Table 1; paired samples *t*-test; $t=2.52$, $df=10$, $P<0.05$). In contrast, it was higher during lactation in both *C. russula* ($t=6.08$, $df=18$, $P<0.001$) and *M. domesticus* ($t=7.31$, $df=23$, $P<0.001$). Therefore, at least in the two latter species, changes in body mass might account for all or part of the metabolic difference between reproductive states. Indeed, BMR was significantly related to body mass within each species, with body mass explaining 47%, 45% and 65% of the overall BMR variation in *C. russula*, *M. domesticus* and *M. arvalis*, respectively (linear regressions; Table 1). The same was true for RMR_L, with body mass making similar contributions to the metabolic variation among the lactating females (61%, 48% and 67% for the three species; Table 1). This confirmed that changes in body mass must be controlled for when comparing BMR and RMR_L.

The repeated measures ANCOVA gave similar results in the three species (Table 2). The reproductive state had a highly significant effect on rate of metabolism at the “within-individuals level” of analysis ($P<0.01$ in all species). The effect of body mass was also highly significant in all species at the “between-individuals” level ($P<0.001$). At the “within-individuals level” it was significant in *C. russula* and *M. domesticus* ($P<0.0001$), but not in *M. arvalis* ($P>0.05$). The interaction between reproductive state and body mass was never significant ($P>0.05$) but it approached the significance limit at the “between-individuals” level in *C. russula* and *M. arvalis*. Litter mass on day 10 ($=m_Y$; all litters adjusted to 4 young) averaged 27.7 ± 2.9 g in *C. russula*, 30.2 ± 3.1 g in *M. domesticus* and 28.7 ± 5.1 g in *M. arvalis*. It was correlated with female body mass in the three species ($r=0.83$, 0.65 and 0.65 , respectively; all $P<0.05$). RMR_L was correlated with m_Y in all species, but the partial correlation between RMR_L and litter mass, while controlling for female mass, was significant only in *C. russula* ($r=0.57$; $t=2.78$; $df=16$; $P<0.05$). Thus a

second ANCOVA was done in this species on RMR_L values corrected for the effect of litter mass. The results of this analysis were very similar and are not given here.

3.2. Individual variation in metabolic change between the two reproductive states

The difference between BMR and RMR_L showed large individual variation: (RMR_L–BMR) ranged from 3.4 to 15.4 $\text{mLO}_2 \text{h}^{-1}$ in *C. russula*, from 1.1 to 20.0 $\text{mLO}_2 \text{h}^{-1}$ in *M. domesticus* and from –6.0 to 11.1 $\text{mLO}_2 \text{h}^{-1}$ in *M. arvalis* (Figs. 1–3). When expressed as a percentage of the BMR measured in the same female, RMR_L varied from 115% to 179% in *C. russula*, 103% to 173% in *M. domesticus* and 90% to 115% in *M. arvalis*.

The change in rate of metabolism between the NL and L states, $\log\Delta\text{MR}$, was significantly and negatively correlated with the level of BMR (resBMR) in the mice (Pearson’s $r=-0.75$; $P<0.001$) but not in the shrews ($r=-0.24$; $P=0.32$) and the voles ($r=0.26$; $P=0.44$). However, as already suggested, variations in female body mass, in female body mass change between the two states and/or in litter mass may affect this relationship. The partial correlation between $\log\Delta\text{MR}$ and resBMR, while controlling for $\log m_{\text{NL}}$, $\log\Delta m$ and $\text{res}m_Y$, was highly significant and negative in *C. russula* ($r=-0.73$; $t=3.97$; $df=14$; $P<0.01$) and *M. domesticus* ($r=-0.78$; $t=5.49$; $df=19$; $P<0.001$). In *M. arvalis* it was not significant ($r=0.004$; $t=0.01$; $df=6$; $P>0.9$), but the sample size in this species was much

Table 2

Tests of the effect of the reproductive state on the rate of metabolism in the three species under study

	<i>Crocidura russula</i>	<i>Mus domesticus</i>	<i>Microtus arvalis</i>
N	19	24	11
Error: factor (individual)			
logm	1; 0.031; 29.3 ; <0.0001	1; 0.049; 37.3 ; <0.0001	1; 0.031; 28.5 ; 0.0007
logm*factor (reproductive state)	1; 0.004; 3.55 ; 0.08	1; 0.0001; 0.08 ; 0.78	1; 0.042; 3.89 ; 0.08
Residuals	16; 0.017	21; 0.027	8; 0.009
Error: within			
logm	1; 0.188; 223 ; <0.0001	1; 0.104; 68.4 ; <0.0001	1; 0.000003; 0.005 ; 0.94
Factor (reproductive state)	1; 0.042; 50.1 ; <0.0001	1; 0.023; 14.9 ; 0.009	1, 0.01; 19.5 ; 0.002
logm*factor (reproductive state)	1; 0.002; 2.23 ; 0.15	1; 0.0008; 0.54 ; 0.47	1; 0.003; 0.51 ; 0.50
Residuals	16; 0.013	21; 0.032	8; 0.004

For each species, full results of the repeated measures ANCOVA are given with, for each source of variation, the degrees of freedom (*df*), the sum of squares and, when appropriate, the *F* value (in bold) and its associated probability level (*P*, in italics). Two levels are considered in such analyses: the “between-individuals” level (Error: factor (individual)) and the “within-individuals” level (error: within).

smaller. Thus, other things being equal, female shrews and mice with a lower than average BMR tended to show a larger than average increase in rate of metabolism during lactation.

The pattern detected in shrews and mice can be easily illustrated with *M. domesticus*, in which the intraspecific scaling exponent for BMR was close to 0.75 (0.93, with 95% confidence intervals ranging between 0.34 and 1.36; Table 1 and Fig. 2). The studied population can be divided into two metabolic groups, characterized by a BMR of less than 100% and more than 100% of predicted by the Kleiber equation, respectively (mice on each side of the dashed line on Fig. 2). The low-BMR group would have increased its relative rate of metabolism from an average BMR of 94% to an average RMR_L of 117% of Kleiber's equation. A smaller average increase would have been exhibited by lactating females of the high-BMR group (BMR = 113%; RMR_L = 121% of predicted).

4. Discussion

4.1. Basal rate of metabolism

The average basal rate of metabolism obtained in this study for *C. russula* (Table 1) is only slightly lower than the value published by Sparti (1990) on shrews of the same population (106% vs. 116% of predicted by the Kleiber equation). Part of the slight difference may be due to seasonal variation in both rate of metabolism and body mass, since Sparti (1990) measured wintering shrews which were on average slightly lighter (10.4 g). Rosenmann and Morrison (1974) and Richardson et al. (1994) provided data compatible with BMR determination on wild caught house mice. Their relative BMR estimates (102–113%) are close to our values for *M. domesticus* (99%), despite the fact that they were obtained with smaller mice from very distant regions. In laboratory mice, measurements meeting the requirements for BMR estimation provided relative average values ranging from slightly less than 100% to 148% (Rosenmann and Morrison, 1974; Lacy and Lynch, 1979; Hayes et al., 1992; Konarzewski and Diamond, 1994; Richardson et al., 1994; Speakman and McQueenie, 1996; Johnson et al., 2001a). Given that the various strains of the laboratory mouse have been submitted to long-lasting artificial selection, these data can hardly be compared with values on wild caught mice (e.g. see Richardson et al., 1994). As for *M. arvalis*, BMR estimates available for individuals from eastern Europe (60.2 mL O₂ h⁻¹ or 163% of predicted for animals weighing on average 23.9 g; Jansky, 1959; Trojan and Wojciechowska, 1967) are much higher than ours (128%). Part of this discrepancy may be due to technical problems (e.g. the use of a closed-circuit respirometer by these authors, which makes it difficult to eliminate the effect of activity), but differences in body mass and other local adaptations in this wide ranging species may also be involved.

4.2. Comparison between average BMR and average RMR_L

Resting rate of metabolism during lactation (RMR_L) was higher than BMR in *C. russula*, *M. domesticus* and *M. arvalis*,

the difference between these two rates being in each species larger than could be accounted for by changes in body mass. These results do not fit into Thompson and Nicoll's (1986) analysis, according to which species with a BMR higher than expected show little increase in reproductive RMR.

Many studies have been carried out on the metabolic changes associated with reproduction in mammals (e.g. see the review of Thompson, 1992). However, only few of them allow a comparison between the BMR and the maternal rate of metabolism during either gestation or lactation. Indeed, the first condition that must be met for such a comparison is that the measurements of the rate of metabolism must meet the criteria for BMR, except for the reproductive state of the mothers when measuring maternal RMR. For example, metabolic measurements made on resting individuals below thermal neutrality (e.g. on *Suncus murinus*, Dryden et al., 1974; on *M. arvalis*, Trojan and Wojciechowska, 1967; on *Sigmodon hispidus*, Randolph et al., 1977), which have been cited by Thompson and Nicoll (1986), include energy expended for thermoregulation and depend to a large extent on ambient temperature, body temperature and minimal thermal conductance (McNab, 2002). They are therefore inadequate to detect a metabolic shift from basal levels. In addition, as already pointed out by McNab (1997), some species of mammals normally do not maintain a normothermic body temperature when resting and do not exhibit a thermoneutral zone, such that they cannot be assigned a basal rate of metabolism. Some tenrecs (e.g. *Microgale dobsoni*, Stephenson and Racey, 1993a; *Geogale aurita*, Stephenson and Racey, 1993b) may fall into this category (but see below).

A comparison between maternal RMR and BMR also rests on the condition that both parameters are measured during the same study, with the same population and, if possible, on the same individuals, because there is now ample evidence that intraspecific variation in rate of metabolism can be large (Earle and Lavigne, 1990; Hayes et al., 1992; McLean and Speakman, 2000; this study). Values of BMR and maternal RMR obtained on different individuals of the same population are adequate when sample size is sufficiently large. But studies providing only values for maternal RMR (e.g. on *Didelphis virginiana*, Fleming et al., 1981) which have to be compared with BMR data obtained by other authors and/or on other populations include sources of variation (geographical, technical) that should clearly be controlled. Even if sources of variation are reduced to a minimum, within-individual variation in body mass, which may be appreciable in small mammals (McLean and Speakman, 2000), should be considered when comparing different reproductive stages, because body mass is a major determinant of the rate of metabolism.

Another complication comes from the fact that rate of metabolism varies along a reproductive event, a variation which partly depends on the species (Thompson and Nicoll, 1986; Nicoll and Thompson, 1987; Mover et al., 1989; Stephenson and Racey, 1993a; Garton et al., 1994; Harder et al., 1996; Künkele and Trillmich, 1997; McLean and Speakman, 2000). In the present study, RMR_L has been measured only once around peak lactation, both to permit a comparison across individuals or species in a state of maximum reproductive effort (Genoud

Table 3
Body mass, BMR and RMR during lactation in small mammals

Species	NL state			L state			References
	N	Mass (g)	BMR (mLO ₂ h ⁻¹)	N	Mass (g)	RMR _L (mLO ₂ h ⁻¹)	
<i>Metatheria</i>							
<i>Monodelphis domestica</i>	19	64.1	49.1*	63			Harder et al., 1996
<i>Monodelphis domestica</i>	5	82.0	59.5*	64			Thompson and Nicoll, 1986
<i>Eutheria (wild)</i>							
<i>Echinops telfairi</i>	1	141	39.1*	28		119*	Thompson and Nicoll, 1986
<i>Echinops telfairi</i>	1	153	40.1*	27		77*	Nicoll and Thompson, 1987
<i>Plecotus auritus</i>	14	10.7	14.7	73	4	19.9	McLean and Speakman, 2000
<i>Microgale talazaci</i>	3	47.1	46.6* ⁺	76	2	60*	Stephenson and Racey, 1993a
<i>Ctenomys talarum</i>	9	118	95.5	78	9	144	Zenuto et al., 2002
<i>Elephantulus rufescens</i>	3	84.1	77.9	82		110*	Thompson and Nicoll, 1986
<i>Akodon azarae</i>	8	26.3	39.0	98	7	86.7	Antinuchi and Busch, 2001
<i>Mus domesticus</i>	24	22.8	35.3	99	24**	44.4	This study
<i>Crocidura russula</i>	19	11.3	22.4	106	19**	32.1	This study
<i>Mesocricetus auratus</i>	21	112	125++	106	16	164++	Garton et al., 1994
<i>Microtus arvalis</i>	11	33.9	61.4	128	11**	66.3	This study
<i>Crocidura suaveolens</i>		9.0	22.9	129		30.2*	Mover et al., 1989
<i>Microgale cowani</i>	2	10.3	27.0 ⁺	137	1	37.1	Stephenson and Racey, 1993a
<i>Eutheria (laboratory form)</i>							
<i>Mus musculus</i>	71	27.1	44.6	110	71**	97.6	Johnson et al., 2001a,b
<i>Mus musculus</i>	9	24.8	56.2	148	8	141	Speakman and McQueenie, 1996

NL state: neither pregnant nor lactating adult females. L state: lactating females. Species are ranked according to relative BMR. % = rate of metabolism expressed as a percentage of the rate predicted on the basis of Kleiber's (1961) equation ($BMR = 3.42 m^{0.75}$, where m is in g). No attempt is made to distinguish different stages of lactation. When longitudinal data are available during lactation, average RMR_L for peak lactation is indicated. In some cases, no specific N value is available for the data indicated; when no specific body mass data is given for RMR_L, relative RMR_L (%) is calculated on the basis of the NL body mass.

*Value recalculated or estimated from a figure. ⁺Thermoneutral zone uncertain. **Same individuals as for the NL state.

++Values corrected to an average body mass of 111.9 g and an average body temperature of 36.6 °C.

and Vogel, 1990; Cretegy, 1997; personal observations) and to avoid multiple disturbances of the lactating females and their litter. During gestation, small mammals show variations in the RMR that largely reflect variations in body mass. However, both positive and negative deviations from the value predicted for a nonreproductive female of the same mass and species have been found (Mover et al., 1988; Stephenson and Racey, 1993a; Garton et al., 1994; Harder et al., 1996; McLean and Speakman, 2000; Antinuchi and Busch, 2001; Zenuto et al., 2002). Further interspecific and intraspecific studies on the RMR of pregnant small mammals would clearly be of interest, especially if these studies would also control for the effects of body mass. In addition, Mover et al. (1989) have shown for *C. suaveolens* that the RMR of lactating females was strongly increased above the nonreproductive level, whereas that of females which were simultaneously pregnant and lactating remained close to BMR. When compared to lactation alone, simultaneous pregnancy and lactation was also associated with a significantly lower RMR in female laboratory mice, once body mass effects were controlled for (Johnson et al., 2001b). In our study, female common voles still exhibited an elevated RMR_L although most of them were simultaneously pregnant and lactating.

With the above restrictions, data permitting comparison of RMR_L with BMR in small mammals are quite scarce, although they are already scattered across major taxonomic groups (Table 3). RMR_L tends to be higher than BMR in all species

included, such that there seems to be no reason, at this stage, to explain the increased maternal rate of metabolism of low-BMR species in a way that is specific to them. Therefore, this limited data set does not provide much support for Thompson and Nicoll's (1986) hypothesis that predicted BMR according to the Kleiber equation may reflect an "advantageous or essential energetic regime" for therian reproduction. At least, the increased maternal rate of metabolism in low-BMR species can hardly be considered as support for this hypothesis.

Among the measurements that were discarded from Table 3, it is worth mentioning those published on tenrecs by Stephenson and Racey (1993a,b). These authors examined the relationship between RMR and ambient temperature in *Microgale dobsoni* and *Geogale aurita*, and showed that neither of them exhibited a thermoneutral zone. However, they measured RMR in nonreproductive individuals and reproducing females of several species of tenrecs under the same experimental conditions at around 30 °C. On the basis of these results, they already concluded that the tenrecs do not fit into the scheme of Thompson and Nicoll (1986), since RMR was higher in reproducing females regardless of the average nonreproductive RMR of the species. Unfortunately, Stephenson and Racey (1993a) could measure only a single lactating female of the only species which exhibited at around 30 °C an RMR higher than the value expected from the Kleiber curve (*Microgale cowani*, 137%, Table 3).

The proposal that rate of metabolism is increased in reproducing female mammals mainly because of the increased size and/or activity of various tissues and organs (Hammond and Diamond, 1992; Thompson, 1992; Hammond et al., 1994; Speakman and McQueenie, 1996) receives much better support from the available data. Indeed, this proposal does not lead to the prediction of a drastically different pattern of metabolic change during reproduction in low-BMR and high-BMR species. In fact, there is evidence for the laboratory mouse that the digestive tract, liver, kidneys, heart and lungs all increase in size in reproducing females (Hammond and Diamond, 1992; Hammond et al., 1994; Speakman and McQueenie, 1996; Johnson et al., 2001a). Hammond and Diamond (1992) have also shown that the morphological changes undergone by the intestine during reproduction are linked to functional changes. Furthermore, Speakman and McQueenie (1996) found that rate of metabolism was linked to the size of the digestive tract. Similar anatomical and functional changes probably also occur in reproducing females of wild mammals. Nevertheless, the present data do not rule out a possible interspecific link between the metabolic changes occurring during lactation and the average relative BMR. A test of this hypothesis would require consideration of the potential effect of phylogenetic non-independence (Felsenstein, 1985; Garland et al., 1992; but see also McNab, 2002; Martin et al., 2005) as well as a much larger data set than presently available.

4.3. Individual variation in metabolic change during reproduction

In *C. russula* and *M. domesticus*, the change in whole-individual rate of metabolism which occurred between the NL and L states ($\log\Delta\text{MR}$) was negatively correlated with resBMR , the residual of the linear regression between $\log\text{BMR}$ and $\log m_{\text{NL}}$, when the effects of female body mass and litter mass were controlled for. Thus, within these two species and other things being equal, females exhibiting a lower than average BMR tended to exhibit a larger increase in rate of metabolism during lactation. This intraspecific pattern has not been observed previously. The few studies which reported data on both BMR and RMR_L in wild small mammals (Table 3) either did not provide measurements for both parameters in the same female, or were based on a limited sample size, such that a quantitative analysis of the pattern was out of reach. Assessing the extent and significance of the intraspecific pattern depicted here will obviously require many more data on a diverse set of small mammal species.

Individual variation in fat content and use may initially be proposed as an explanation for the larger increase in rate of metabolism exhibited at a given body mass by low-BMR females. Body fat is characterized by a very low rate of metabolism (e.g. see Nelson et al., 1992) such that changes in whole-individual rate of metabolism should indeed be observed when fat is deposited or used. Even small mammals often exhibit fat deposition and use in relation to reproduction (e.g. Randolph et al., 1977; Millar, 1987; Weiner, 1987; Liu et al., 2003) despite the fact that they usually cover the additional costs of reproduction largely by increasing food ingestion (Mattingly and McClure, 1982, 1985; McClure, 1987; Thompson, 1992). Fat content and use was not assessed in

our study, but the results demonstrate that fat utilization alone cannot account for the metabolic changes observed in the three species. Indeed, if fat use was the sole process involved, body mass should also have been reduced during lactation. A slight reduction in body mass was observed in *M. arvalis*, but in both *C. russula* and *M. domesticus* body mass was significantly larger during lactation and it is precisely in the latter two species that the negative relationship between BMR and the extent of metabolic increase was detected.

Presumably, the relationship between BMR and the change in whole-individual rate of metabolism between the NL and L states is at least partly the consequence of a relationship between the profound physiological and anatomical changes which females undergo during lactation (Hammond and Diamond, 1992; Hammond et al., 1994; Speakman and McQueenie, 1996; Johnson et al., 2001a) and the level of BMR at any given body mass. Together with these data, our results suggest that, at any body mass within at least some small mammal species, females with a lower than average BMR exhibit more extensive physiological and/or anatomical modifications in relation to reproduction, which is reflected in the larger observed increase in whole-individual rate of metabolism.

McNab (1980) has proposed that part of the variation in BMR among mammals may be linked to variation in reproductive output and that one advantage of having a higher relative BMR may be the larger reproductive output that can be achieved. This proposal has been tested at the interspecific level by several authors, with contrasting results (Hennemann, 1983; Glazier, 1985; Harvey et al., 1991), whereas at the intraspecific level not much support has been found (Derting and McClure, 1989; Earle and Lavigne, 1990; Hayes et al., 1992; Johnson et al., 2001a; Krol et al., 2003; but see Derting, 1989). As already suggested by Speakman and McQueenie (1996), McLean and Speakman (2000) and Johnson et al. (2001a) the fact that maternal rates of metabolism may be elevated above nonreproductive levels may explain why some studies have failed to obtain a correlation between BMR and reproductive output. The negative correlation that we found in *C. russula* and *M. domesticus* between the level of BMR and the increase in rate of metabolism during lactation may also explain the failure to detect a relationship between BMR and reproductive output at the intraspecific level. For example, different conspecific females of the same body mass but with a different BMR may achieve a similar reproductive output in captivity inasmuch as they make different anatomical and physiological adjustments for reproduction. However, all of these strategies might not necessarily be available under natural conditions, as the adjustments that they imply during reproduction may themselves not be without any cost. Thus, intraspecific variation in BMR may be related only indirectly to reproductive output, such that the relationship may be difficult to demonstrate in the optimal energetic conditions of the laboratory.

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