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Comparative analyses of basal rate of metabolism in mammals: data selection does matter

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ABSTRACT

Basal rate of metabolism (BMR) is a physiological parameter that should be measured under strictly defined experimental conditions. In comparative analyses among mammals BMR is widely used as an index of the intensity of the metabolic machinery or as a proxy for energy expenditure. Many databases with BMR values for mammals are available, but the criteria used to select metabolic data as BMR estimates have often varied and the potential effect of this variability has rarely been questioned. We provide a new, expanded BMR database reflecting compliance with standard criteria (resting, postabsorptive state; thermal neutrality; adult, non-reproductive status for females) and examine potential effects of differential selectivity on the results of comparative analyses. The database includes 1739 different entries for 817 species of mammals, compiled from the original sources. It provides information permitting assessment of the validity of each estimate and presents the value closest to a proper BMR for each entry. Using different selection criteria, several alternative data sets were extracted and used in comparative analyses of (*i*) the scaling of BMR to body mass and (*ii*) the relationship between brain mass and BMR. It was expected that results would be especially dependent on selection criteria with small sample sizes and with relatively weak relationships. Phylogenetically informed regression (phylogenetic generalized least squares, PGLS) was applied to the alternative data sets for several different clades (Mammalia, Eutheria, Metatheria, or individual orders). For Mammalia, a 'subsampling procedure' was also applied, in which random subsamples of different sample sizes were taken from each original data set and successively analysed. In each case, two data sets with identical sample size and species, but comprising BMR data with different degrees of reliability, were compared. Selection criteria had minor effects on scaling equations computed for large clades (Mammalia, Eutheria, Metatheria), although less-reliable estimates of BMR were generally about 12–20% larger than more-reliable ones. Larger effects were found with more-limited clades, such as sciuromorph rodents. For the relationship between BMR and brain mass the results of comparative analyses were found to depend strongly on the data set used, especially with more-limited, order-level clades. In fact, with small sample sizes (e.g. <100) results often appeared erratic. Subsampling revealed that sample size has a non-linear effect on the probability of a zero slope for a given relationship. Depending on the species included, results could differ dramatically, especially with small sample sizes. Overall, our findings indicate a need for due diligence when selecting BMR estimates and caution regarding results (even if seemingly significant) with small sample sizes.

Key words: basal rate of metabolism, BMR, brain, encephalization, allometric scaling, phylogenetic generalized least-squares regression, mammals.

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CONTENTS

I. INTRODUCTION

Rate of metabolism is highly variable in endotherms, reflecting not only body mass but also various internal states (e.g. postabsorptive *versus* postprandial, pregnant or lactating *versus* reproductively inactive), responses to environmental conditions such as ambient temperature or season, and behaviour (McNab, 1997). Confronted with this variability, biologists have long realized that meaningful comparisons of the rate of metabolism between different endotherms must be based on measurements meeting certain restrictive criteria (Benedict, 1938; Kleiber, 1961; Speakman, McDevitt & Cole, 1993; McNab, 1997). Basal rate of metabolism (BMR) is the rate of metabolism of a postabsorptive, non-reproducing adult endotherm that maintains a normal body temperature and rests at a thermoneutral temperature during a major inactive phase of its daily cycle (McNab, 1988*a*, 1997, 2012). It represents the minimal rate of energy expenditure normally compatible with temperature regulation. It is predicted to be subject to selection, notably because of its potential links to rates of energy use and allocation to various functions, including growth and reproduction (McNab, 1997, 2012; Glazier, 2015), or to the maximal or sustained maximal rates of energy expenditure (e.g. Speakman, Krol & Johnson, 2004).

BMR is regarded as a central measure in the physiological ecology of endotherms and is surely one of the most widely measured physiological parameters. As a measure of the minimal intensity of the metabolic machinery of a normothermic endotherm, or as a proxy for energy expenditure or requirements of endotherms, it has been included in a vast number of comparative analyses aimed at explaining the intra- or interspecific variance observed in diverse aspects of endotherm biology. When endotherms are considered, BMR is also given a central place in the Metabolic Theory of Ecology (MTE), which provides a formal framework explaining how metabolic rate controls various life-history attributes as well as population or ecosystem processes (Brown *et al.*, 2004). This 'metabolic pacemaker' concept has recently been evaluated by Glazier (2015), who argued that, while some biological processes may indeed be controlled by rate of metabolism, others may also be co-regulated with it or may even drive it.

Many databases have been published previously for the BMR of mammals or birds (mammals: e.g. Lovegrove, 2000; McNab, 2008*a*; Sieg *et al.*, 2009; White, Blackburn & Seymour, 2009; birds: e.g. McKechnie & Wolf, 2004; McNab, 2009), but discrepancies exist between them even after exclusion of inevitable differences due to publication date. Inclusion of a published value as a BMR estimate requires an assessment by the compiling author of the degree to which the criteria for BMR measurement had been met and of the appropriateness of many other features of the protocol (e.g. origin and handling of the animals, sample size, instruments used, calculations). Yet combining several published databases for a comparative analysis can potentially eliminate uniformity in selection criteria if the original papers are not considered in detail. The potential consequences of the required choice of criteria for BMR data selection have often remained unstated. Indeed, given the many different databases that are currently available for BMR, one might question what difference it makes to use one set rather than another. For birds, McKechnie & Wolf (2004) have shown that different scaling equations for BMR may be obtained depending on the severity of data selection. More generally, databases including descriptions and/or evaluations of the conditions under which the original data were obtained have been emphatically recommended (Borries *et al.,* 2016).

This review has two goals. First, it provides a comprehensive and fully referenced database of mammalian BMR estimates collected exclusively from primary sources, including an evaluation of the degree to which the standard criteria were met in each case. This will facilitate selection of appropriate BMR estimates for comparative purposes. It is not claimed that the database provides an evaluation of the general quality of the measurements conducted, as some of the studies cited were not originally intended to provide BMR estimates, although their results could be exploited for this purpose. For example, many authors chose to avoid the difficulty of ensuring that their animals were postabsorptive and/or were really monitored in the thermoneutral zone. They accordingly reported their measurements as resting metabolic rate (RMR).

Second, this review seeks to determine whether the process of selecting BMR data can influence results regarding relationships with various other parameters in comparative analyses. With that aim in mind, specified selection criteria were applied to extract alternative data sets from the new BMR database. These data sets either exclusively contained values judged to be acceptable BMR estimates or also included values judged to be unreliable BMR estimates. The data sets were then used for analyses in two biological contexts, both of which are the subject of ongoing studies and controversies: (*i*) the scaling of BMR to body mass, and (*ii*) the relationship between brain mass and BMR.

The scaling of BMR to body mass has been the subject of many studies (e.g. Lovegrove, 2000; Symonds & Elgar, 2002; White & Seymour, 2003, 2004, 2005; McNab, 2008*a*; Sieg *et al.,* 2009; Capellini, Venditti & Barton, 2010; Clarke, Rothery & Isaac, 2010), with particular emphasis on the effects of accounting for various confounding variables, including zoogeographical, ecological, behavioural, and physiological factors. The relationship between brain mass and BMR has also been a focus of interest for several decades (Martin, 1981; McNab & Eisenberg, 1989; Isler & van Schaik, 2006*a,b*, 2009; Barton & Capellini, 2011; Isler, 2011; Weisbecker & Goswami, 2014), particularly because the brain's rate of energy expenditure is very high, accounting for a substantial proportion of the overall energy expenditure of the organism (Niven & Laughlin, 2008). Encephalization is hence potentially associated with increased maintenance costs reflected in greater energy turnover (Isler & van Schaik, 2006*b*). Herein, these two contexts are used as case studies to examine the potential effects of applying different selection criteria for compiling BMR data.

The two examples selected for analysis differ appreciably in the strength of the relationship under consideration. Provided that a sufficiently broad range of body mass is considered in an analysed assemblage of species, body mass always explains a very large proportion of the variance in BMR (e.g. $r^2 > 0.9$ with assemblages covering all Mammalia; Lovegrove, 2000; McNab, 2015). By contrast, BMR explains at best only a small proportion of the variation in brain mass (e.g. $r^2 \leq 0.2$; Isler & van Schaik, 2006*b*; Sobrero *et al.,* 2011). We hypothesized that the results of a comparative analysis should be particularly dependent on the data-selection procedure when the strength of the studied relationship is weak and when sample size is small. We therefore performed comparative analyses with species assemblages of different sample sizes (Mammalia, the separate sub-classes Eutheria and Metatheria, as well as individual orders). This was done in order to compare results obtained with data sets that were either restricted to accepted BMR estimates or also included BMR values considered to be unreliable. Using a subsampling approach, we also illustrate the variability in results that can occur when species are gradually added to a database, both when initially compiling a data set and as data become increasingly available in the scientific literature.

II. MATERIALS AND METHODS

(1) The BMR database

A total of 1739 values for the metabolic rate of 817 species of mammals were extracted from published literature, using primary sources wherever possible, and entered into the BMR database (see online Tables S1 and S2). Among the 946 original publications involved, 95% were read and their metabolic values were evaluated. Entries for which the original publication was unavailable ($N = 57$), or those corresponding to data originally cited as 'personal communication' or as 'unpublished' ($N = 28$) were identified as such. Values were primarily entered under species names according to Wilson & Reeder (2005), although taxon names used by the original authors were also noted.

Each entry provides the mean metabolic value most closely reflecting a basal rate and the corresponding mean body mass (m) for the animals measured in each publication. When several values were given in a single paper, corresponding to different subspecies or populations, they were entered separately. However, when different seasonal values were available for the same population, a value corresponding to a season of higher resource availability was preferred (i.e. 'summer' in temperate or boreal regions, but see Section II.2*d* for issues regarding reproductive status in females; McNab, 2008*a*), unless important BMR criteria were omitted for that value. When values were given separately for males and females (e.g. due to substantial sexual dimorphism), averages between sexes were calculated for m and BMR. The following information derived from the original publications was listed or coded for each entry: (a) sample size, (b) whether or not a graphical representation of the rate of metabolism as a function of ambient temperature was available in the paper, or (b1) whether such a representation is available in some other publication for the same species, (c) whether the analysis demonstrated convincingly that the measurements were conducted in the thermoneutral zone, and whether it can be accepted that the measured animals were resting (d) and postabsorptive (e). The authors' indications regarding whether the animals were measured during a major resting phase of their daily cycle (f), were adults (g) and, for females, were non-reproductive (h) were listed. Additional potentially useful details were also noted concerning the individuals measured (i–l), the experimental set-up and protocol (m, n) and the analysis of the measurements (o–q). How these details were coded is described in detail in Table S1.

Based on an overall assessment of how well the BMR criteria (c–h) were met (E_{crit}, see Table S1), as well as of the additional problems encountered (i–q), an overall four-level evaluation (= E) was assigned to each entry (Table S1): $E = 1$ for values meeting the requirements of BMR and devoid of technical limitations reducing the reliability of the estimate; $E = 2$ for values marginally acceptable as BMR estimates due to one or more criteria being only marginally met or due to technical problems; $E = 3$ for poor estimates of BMR due to many criteria being only marginally met or to one criteria clearly not being met or due to technical problems that could have caused a significant deviation; and $E = 4$ for values which are unacceptable as BMR estimates. For use in comparative analyses, this evaluation was then translated into a two-level factor named 'reliability', distinguishing values referred to hereafter as 'accepted' ($E = 1$ or 2) and 'rejected' ($E = 3$ or 4). The frequency distribution of the reliability of entries for different clades is provided in Figure S1.

(2) Concerns regarding criteria for BMR

The evaluation (E) assigned to each entry in the database was complicated by at least three major problems, two of which directly concern the criteria for BMR. First, the difficulty of meeting all BMR criteria is variously affected by specific problems associated with each taxonomic or ecological group of species, and the methodological information required for a complete evaluation is therefore taxon-specific. Yet the methodological information provided by the authors was often insufficient for a complete evaluation of the metabolic values as BMR estimates. Second, using a protocol that does not respect or only marginally meets one particular criterion leads to deviations that are also taxon-specific. Third, methodological aspects other than the BMR criteria can also influence the reliability of a metabolic value as a BMR estimate. These include sample size, whether a graph of the rate of metabolism as a function of ambient temperature was provided or was made available for the same species in another study, respirometry techniques, precision of the results, and other aspects included in Table S1.

(*a*) *Postabsorptive state*

The requirement for a postabsorptive state is one typical example of a BMR criterion that requires taxon-specific efforts for realization. Mammals typically respond to feeding by a 25–50% increase in rate of metabolism (Secor, 2009). The time to reach a postabsorptive state varies both among and within species, depending notably on body mass and on the amount and type of food ingested (Secor, 2009). A fasting duration of more than 48 h was necessary to achieve a postabsorptive state in the 35.5 kg carnivore *Canis lupus* (Okarma & Koteja, 1987). By contrast, the specific dynamic effect of feeding lasted only about 6 h in the 9.8 g bat *Lasiurus seminolus* (Genoud, 1993), 4 h in the 64 g rodent *Phyllotis darwini* (Nespolo, Bacigalupe & Bozinovic, 2003*b*), while in shrews even small amounts of food given during measurement runs had little effect on the rate of metabolism (Lindstedt, 1980; McNab, 1991). In most species, however, no specific information is available regarding the time required to achieve a postabsorptive state, and experiments actually measuring the duration of the specific dynamic effect of feeding would be very welcome.

Of particular concern are those mammals feeding on vegetative parts of plants (e.g. Artiodactyla, Macropodidae and Lagomorpha). This feeding strategy usually involves fermentation and requires a very long gut transit time, which increases as body size increases. For example, a postabsorptive state was reached after a fast of 48 h in a 38 kg *Antilocapra americana* (Wesley, Knox & Nagy, 1973) and after more than 4 days in an *Ovibos moschatus* weighing approximately 200 kg (Nilssen, Mathiesen & Blix, 1994). Individuals of the latter species have a more than doubled rate of metabolism after eating. The question has been raised (Blaxter, 1989; McNab, 1997) whether it is even possible to measure BMR in species relying on fermentation to process plant matter (such as ruminants), because fermentation may rule out attainment of a postabsorptive state before the subjects are undergoing severe starvation. For this reason, White & Seymour (2003) discarded artiodactyls, lagomorphs and macropodid marsupials from their analyses. However, measurements done on artiodactyls fasted for variable durations have shown that the RMR tends to stabilize after an initial decrease, and a respiratory quotient compatible with a postabsorptive state (i.e. approaching 0.7) can be reached well before starvation (Silver *et al.*, 1969; Renecker & Hudson, 1986; Nilssen *et al.*, 1994; see also Williams *et al.*, 2001*a*; Ostrowski, Mésochina & Williams, 2006*a*).

We therefore accepted values as reliable BMR estimates if the authors either provided information that strongly suggested that their animals were postabsorptive, or actually estimated the length of time required to reach a postabsorptive state. For all other entries, we evaluated the reliability of the postabsorptive state criterion by establishing rough scales based on body mass and diet. To build these scales, we compiled experimentally measured fasting durations necessary to reach a postabsorptive state in different species (Table S3). For species whose diet does not consist mainly of vegetative parts of plants, the following fasting durations were considered to be necessary: <100 g, 1–2 h; 100–350 g, 2 h; 350–1000 g, 3 h; 1–10 kg, 4 h; 10–100 kg, 6 h; and >100 kg, 12 h. For species whose diet mainly consists of vegetative parts of plants, the corresponding durations were: <100 g, 2–3 h; 100–350 g, 4 h; 350–1000 g, 6 h; 1–10 kg, 12 h; 10–100 kg, 24 h; and >100 kg, 36 h.

(*b*) *Rest*

A resting state is another critical requirement for BMR measurements. Certain small mammals such as shrews are renowned for their restlessness. Yet even with shrews it is usually possible to obtain metabolic rates for resting individuals (e.g. Sparti & Genoud, 1989; McNab, 1991), if an open air-flow respirometer with continuous recording of the outlet oxygen concentration is available. A quiet state is difficult to reach with ungulates, which are also often reluctant to lie down. Yet the metabolic rate measured on a standing ungulate can represent up to 150% of the lying resting rate (Wesley *et al.,* 1973; Renecker & Hudson, 1986).

Sleep and the timing of metabolic measurements in a 24 h cycle are also fundamental issues. Benedict (1938) proposed that measurements should be done during a major resting phase of the daily cycle for the sake of comparability. Aschoff & Pohl (1970) and Kenagy & Vleck (1982) showed that the resting rate of metabolism undergoes a circadian rhythm and that the difference between minimal rates of metabolism measured during the 'normally active' and 'normally resting' phases varies markedly among species. Although a circadian rhythm may not be present in all mammals (McNab, 2008*a*), in some, such as small primates, this difference may reach 30% (Genoud, 2002). The requirement for measurements during a major inactive period of the daily cycle is therefore usually part of the definition of BMR (e.g. McNab, 1997, 2008*a*; Lovegrove, 2000; White & Seymour, 2003). In our compilation, we assumed that measurements were done during the daytime unless specific information was provided by the authors. Thus, for nocturnal species estimates were considered as fulfilling this requirement even without any specific statement concerning the timing of the measurements, whereas for diurnal species an explicit statement that measurements had been made during the night was required.

However, mammals are often asleep during their major resting phase (e.g. Lesku *et al.,* 2006), and rate of metabolism can be reduced by as much as 10–15% during sleep (Shapiro *et al.,* 1984). Accordingly, BMR measurements in man are typically done on awake subjects [e.g. Owen *et al.* (1987) and Mifflin *et al.* (1990), listed in our database]. In animals, on the other hand, sleep is not usually excluded, partly because one cannot force an animal to stay awake and partly because the sleeping patterns of the subjects measured during respirometry tests have almost never been assessed. Benedict (1938) identified this problem but suggested that measurements should be made during a major inactive phase even if the animals were asleep at that time. In any case, sleep may be an important cause of unexplained variation in the available BMR estimates, as there was insufficient information to evaluate this issue. In addition, we regarded any indication of the violation of quiescent, motionless subjects as hampering the reliability of a BMR value. In particular, we noted stressful conditions, or, for polyphasic species typically resting only for short periods (e.g. shrews, rodents), whether measurements were discontinuous or averaged over longer time periods. Estimates for ungulates were considered reliable only if the animals were lying down.

(*c*) *Thermoneutrality*

Whether a given value was obtained within thermal neutrality is also a taxon-dependent concern. A complete metabolism–temperature curve is obviously necessary to define the zone of thermoneutrality for any given species. This is absolutely required for mammals weighing less than about 1 kg, in which the lower critical temperature (or lower limit of the thermoneutral zone) usually lies well above ambient temperatures typically occurring in laboratories and in which the breadth of the thermoneutral zone is often reduced (Riek & Geiser, 2013). Comparatively, a full metabolism–temperature curve is of less concern for larger mammals. It must also be noted that in many species different thermoregulatory curves were provided by different authors, suggesting an appreciable degree of intraspecific variability in the thermoneutral zone. The determination of a thermoneutral range reported in a particular study and population can thus hardly be considered as universally applicable to the species considered, especially if its body mass is small. Furthermore, the thermoneutral zone may have to be delimited separately for each sex in species exhibiting marked sexual dimorphism, and even for each single individual in highly variable species (McNab, 2000; McNab & Armstrong, 2001).

(*d*) *Adult, non-reproductive status*

Many papers on the rate of metabolism and temperature regulation of mammals did not state whether the animals under study were adult or immature, or male or female. Sex-specific metabolic values are rarely given. In addition, the reproductive status of adult females has often been disregarded. The latter information is especially important as BMR should preferably be measured during a season of higher resource availability, which often coincides with a 'reproductive season', but a pronounced effect of pregnancy and lactation on rate of metabolism has been documented in many species (e.g. Thompson, 1992; Cretegny & Genoud, 2006; Speakman, 2008). Growing juveniles also exhibit rates of metabolism that differ from those of adults (McNab, 1983, 2002; Wieser, 1984; Hulbert & Else, 2004). For example, in small mammals rate of metabolism typically overshoots 'adult' BMR on a mass-specific scale during the postnatal growth phase. Accordingly, caution is needed with values obtained from animals clearly weighing less than normal adults. Concerns about the adult status of the individuals on which BMR was measured were noted in the database, but a systematic review of age, sex or developmental status was not possible because of a lack of information in many original publications.

(*e*) *Intraspecific variation in BMR*

A final concern is that BMR shows a large degree of intraspecific variation both within and among individuals. Even within a single population in a particular season the coefficient of variation often exceeds 10% (e.g. Labocha *et al.,* 2004; Speakman *et al.,* 2004; Cretegny & Genoud, 2006; Genoud & Christe, 2011). Hence, values obtained with a small number of individuals should always be considered as preliminary, although even measurements on a single individual can be in some cases very valuable, especially for species that are rare or difficult to handle (McNab, 1997). Different subspecies and populations of many species have also been shown to exhibit significant metabolic differences (e.g. McNab & Morrison, 1963; Bozinovic, Carter & Ebensperger, 2005*a*; Bozinovic *et al.,* 2009). Furthermore, BMR shows appreciable phenotypic flexibility, as illustrated by numerous populations that exhibit seasonal variation in BMR (Genoud, 1990; Lovegrove, 2005). It is beyond the scope of the present paper to analyse intraspecific variation, despite its importance. But our database does provide mean BMR values for different conspecific populations wherever possible.

(3) Data sets

Three different BMR data sets were extracted from the BMR database. In each only a single entry from the BMR database was used for any species included, which mimics the procedure generally adopted in interspecific comparative analyses.

Data set 1: ALL. All species entered in the BMR database were included in this data set ($N = 817$ Mammalia), whether an acceptable BMR estimate was available or not. In each case, the most reliable metabolic value was selected, i.e. the one with the smallest integer for the evaluation criterion E. This is equivalent to the standpoint that a poor estimate of BMR for a species is better than none. When several values with identical E were available for a particular species, the value with a smaller E_{crit} was chosen, or, all else being equal, preference was given to larger sample size, rates graphed as a function of ambient temperature to define the thermoneutral zone, open-flow respirometry permitting continuous recording of oxygen consumption, and metabolic results stated numerically (rather than requiring recalculation from graphs). When two or more entries for the same species were identical in all aspects of their evaluation, which sometimes was the case for populations or subspecies studied by the same author, one of them was chosen randomly.

Data set 2: SELECT. Only accepted BMR estimates ($E = 1$ or 2) were selected for this data set ($N = 549$ Mammalia). SELECT is a subset of ALL.

Data set 3: SPOILED. This data set has the same sample size as SELECT ($N = 549$) and contains the same species. However for those species having more than one entry in the database (256 out of 549), the SELECT BMR estimate was replaced by the least-reliable estimate. This least-reliable BMR estimate was determined by calculating the absolute differences from the SELECT value for all entries (accounting for body mass and phylogeny, see Section II.4) and by taking the entry that was most divergent from the corresponding SELECT value.

(4) Statistical analyses

Humans and domestic animals were excluded from consideration. All three complete data sets were used for analyses of the scaling of BMR to body mass. For analyses of the brain mass/BMR relationship, the data sets were reduced to those species for which corresponding data for brain mass were available. Brain-size data were compiled from various sources listed in Isler *et al.* (2008) and Isler & van Schaik (2009, 2012). For most carnivores, rodents, and primates, brain mass was estimated from endocranial volume, while the mass of fresh brains was available for bats, artiodactyls, and smaller orders. Only adult specimens were included and, if available, sex-specific values were averaged to obtain a species mean. Both the scaling of BMR to body mass and the relationship between brain mass and BMR were analysed first among 'large clades', i.e. Mammalia, Eutheria and Metatheria. These analyses were then repeated for order-level clades represented in the SELECT data set by more than 10 species [orders *sensu* Wilson & Reeder (2005): Dasyuromorpha, Diprotodontia, Carnivora, Chiroptera, Primates; rodents belonging to the Hystricomorpha, Myomorpha, Castorimorpha and Sciuromorpha were considered separately; Soricomorpha and Erinaceomorpha were pooled in Eulipotyphla]. Only illustrative results of the latter analyses are reported.

Among mammals, variation in BMR, as well as in body mass and brain mass, contains a significant phylogenetic signal (Symonds & Elgar, 2002; Capellini *et al.,* 2010; Kamilar & Cooper, 2013; Rojas *et al.,* 2013). Phylogenetically informed analyses were therefore performed using phylogenetic generalized least squares models (PGLS) with the package *Caper* (function pgls; Orme *et al.,* 2012) in R (R Development Core Team, 2012). The mammalian phylogenetic tree used in all analyses (see online Nexus File S1) was based on the phylogeny ('best estimate' tree) of Bininda-Emonds *et al.* (2007). Until 2015, we updated and expanded this tree following more recent sources on the phylogeny of mammalian clades, especially if they provided a better resolution of polytomies, contained more species for which BMR is available, or were based on new molecular studies (e.g. the molecular phylogeny for rodents of Fabre *et al.,* 2012). Remaining polytomies were resolved randomly. Note that for our purpose of comparing the effect of data reliability, tree accuracy is not crucial as long as one specific tree is used throughout all analyses. Lambda (a parameter indicative of the phylogenetic signal in the data) was estimated by maximum likelihood in the modelling process. Critical assumptions of PGLS were checked as follows: with PGLS, normality of the residuals was examined visually with a Q–Q plot, and homoscedasticity of the residuals was checked by plotting model residuals as a function of fitted values. Deviations from normality revealed by appropriate tests (e.g. Shapiro's test) depend heavily on sample size (Mundry, 2014). This is not necessarily a problem, except when outliers are present. Outliers corresponding to a studentized residual >3 were identified and the analyses were repeated after discarding them. As the results were always similar in these repeat analyses, they are not reported here.

Absolute rather than mass-specific values of BMR were used in all analyses. Because both BMR and brain mass scale with body mass allometrically, body mass, BMR and brain mass values were $\log_{10}$-transformed before analysis in order to correct for non-linearity and heteroscedasticity. To control for the influence of body mass in analyses of the relationship between brain mass and BMR, ideally all variables should be measured on the same individuals. However, available brain mass values were all collected independently of BMR estimates. In our analyses, we used the body mass corresponding to the BMR measurements as a covariate. Although individuals whose brain mass was estimated could differ both in body mass and BMR from those which had their BMR measured, this would not be remedied by using another, independently gathered estimate of body mass for each species. Using two different body masses when studying the relationship between two variables depending on body mass, equivalent to a residual–residual approach, would also be problematic due to an acute collinearity problem (Sobrero *et al.,* 2011). Our analyses of the relationship among brain mass, body mass and BMR rest on the assumption that, for each species, the reported brain mass is sufficiently close to that of the conspecifics whose BMR was estimated. At least, we see no *a priori* reason to expect a consistent difference. Collinearity is still an issue in the analyses of the relationship between brain mass and BMR, as the covariates body mass and BMR are strongly correlated. We therefore report variance inflation factors for these models, although the necessity to control for the effect of body mass precludes the omission of this covariate from the models.

We tested the effect of reliability on statistical analyses including BMR using four different approaches. First, we tested whether unreliable BMR estimates differ significantly from reliable BMR estimates within the data sets ALL and SPOILED, which contain both accepted ($E = 1$ or 2) and rejected ($E = 3$ or 4) values. Phylogenetic ANCOVA was used for this purpose, whereby body mass was included as a covariate and reliability as a two-level factor. Second, we tested whether including unreliable BMR estimates in a data set increased the variance of the model's residuals. We compared the variances of the SELECT data set with either the ALL or the SPOILED data set using Bartlett's test. These tests were applied both to the scaling of BMR and to the relationship between brain mass and BMR. Third, we would expect that including unreliable values in a data set decreases the phylogenetic signal in the residuals of a model. Maximum likelihood estimates of lambda were therefore compared between the SELECT and the SPOILED data sets for all examined clades.

Finally, to explore consequences of the interaction between sample size and reliability of the BMR data set for results of comparative analyses, we used a subsampling approach, henceforth referred to as the 'repeated subsampling procedure'. This procedure was applied to compare the results from SELECT and SPOILED data sets across all mammals. In the context of the scaling of BMR ($N = 549$ for each data set), subsets of species were sampled randomly in each of the two data sets compared, and the probability of a zero slope for the influence of body mass on BMR was calculated with PGLS. The latter analysis was repeated 100 times with the same subsample size but each time with a new random selection of species, thus ensuring that in the subsamples from the SPOILED set, the mean proportion of unreliable values in the 100 subsamples would be similar to that of the entire set (47%, or 256 out of 549). This was done for different subsample sizes ($N = 5$, 10, 20; and $N = 30{-}390$ in steps of 30). The same procedure was applied in the context of the relationship between brain mass and BMR ($N = 369$, including 200 unreliable values in the SPOILED set), each of the analyses being done as described above (PGLS, brain mass being the dependent variable; body mass and BMR being independent variables). The probability of a zero slope for the effect of BMR on brain mass was calculated using a simple model without the body mass × BMR interaction, the latter effect being non-significant (see Section III.2). For each data set and context, the relationship between the calculated probability and subsample size was analysed using a generalized additive model (gam) with the package *mgcv* in R (Wood, 2015). Note that in context of this subsampling procedure, P values are regarded as a measure of the observed power of an effect, but not as probabilities of Type-I error in the strict sense of hypothesis testing. Therefore, a correction for repeated testing is not applied.

III. RESULTS

(1) Scaling of BMR with body mass

As expected, the influence of body mass on BMR was highly significant in all clades studied, while the scaling coefficient and exponent varied within narrow limits (Table 1 for the large clades). In Mammalia and Eutheria, the scaling exponent was found to be close to 0.73 for the SELECT set, with 95% confidence intervals excluding both 3/4 and 2/3. The estimated lambda value was close to 1 in both cases, confirming strong phylogenetic structure in the data. In Metatheria, the confidence intervals of the scaling exponent of 0.74 included 3/4, there was no phylogenetic signal in the model residuals (maximum likelihood estimate of lambda = 0), and the scaling coefficient was lower than in Eutheria.

Table 1. Scaling of basal metabolic rate (BMR) to body mass among all mammals, and among Metatheria and Eutheria, using different data sets for BMR

Clade	Parameter	ALL	SELECT	SPOILED
	α	0.366 ± 0.127	0.377 ± 0.114	0.487 ± 0.122
Mammalia	β	0.737 ± 0.009	0.729 ± 0.010	0.711 ± 0.013
	t_{n-1}, P	80.6, $<10^{-15}$	73.4, $<10^{-15}$	56.7, $<10^{-15}$
	r^2	0.888	0.908	0.855
	lambda	0.867	0.906	0.801
	N	817	549	549
	Outliers	15	12	6
	α	0.379 ± 0.039	0.382 ± 0.026	0.453 ± 0.037
Metatheria	β	0.746 ± 0.013	0.743 ± 0.010	0.725 ± 0.014
	t_{n-1}, P	58.7, $<10^{-15}$	76.3, $<10^{-15}$	52.5, $<10^{-15}$
	r^2	0.977	0.989	0.976
	lambda	0.230	0	0
	N	84	70	70
	Outliers	1	1	0
	α	0.456 ± 0.057	0.455 ± 0.060	0.526 ± 0.067
Eutheria	β	0.735 ± 0.010	0.726 ± 0.012	0.714 ± 0.015
	t_{n-1}, P	70.9, $<10^{-15}$	62.4, $<10^{-15}$	48.8, $<10^{-15}$
	r^2	0.874	0.892	0.834
	lambda	0.798	0.866	0.731
	N	730	476	476
	Outliers	8	6	5

N is sample size (number of species). $\log_{10}\mathrm{BMR} = \beta \cdot \log_{10}\mathrm{mass} + \alpha$, α and β are the allometric coefficient and exponent (±S.E.), respectively. BMR is expressed in $\mathrm{mlO_2/h}$ and mass is in g. Results of a t-test for $\beta = 0$ are given (t-value and corresponding probability, P) as well as r^2 and the number of outliers. Lambda is a parameter indicative of the phylogenetic signal in the data. Data sets: ALL = best (although not necessarily accepted) estimate available for each species in the database. SELECT = best estimate available for those species of the database which have at least one accepted (evaluation criterion $E = 1$ or 2) BMR estimate. SPOILED = SELECT data set 'spoiled' by less-appropriate values, whenever available (see Section II.3 for further details).

The phylogenetically informed scaling relationships obtained with the ALL data set were similar to those obtained with the SELECT set for all three large clades (Table 1). However, in Mammalia the variance of the residuals found with the ALL data set was significantly greater than with the SELECT set (Table 2). A similar tendency was observed in the Eutheria and in the Metatheria taken separately, although Bartlett's chi-squared was not quite significant in these cases (Table 2). Within the ALL data set, reliability ('accepted' *versus* 'rejected') affected BMR among Mammalia and Eutheria: in these clades the PGLS ANCOVA including both body mass and reliability yielded a highly significant effect of reliability if the non-significant interaction term body mass × reliability was omitted (Table 3). On average, rejected BMR values exceeded accepted ones at all body masses by approximately 12% (Fig. 1). In Metatheria, the interaction term body mass × reliability was significant, with rejected BMR values tending to be higher than accepted ones, especially at large body masses.

The SPOILED data set also yielded results broadly similar to those of the SELECT set (Table 1). Nevertheless, consistent differences were found between these two data sets for all three large clades. The variance of the residuals obtained with the SPOILED set was significantly larger than that with the SELECT set (Table 2). In addition, the scaling relationships obtained with the SPOILED data set typically yielded a slightly smaller allometric exponent in combination with a larger allometric coefficient than those obtained with the SELECT set (Table 1). Finally, the PGLS ANCOVA performed within the SPOILED data set, and including body mass as a covariate and reliability as a factor, led to a significant effect of reliability in Mammalia and Eutheria, once the non-significant interaction term body mass × reliability was removed from the analysis (Table 3). Rejected BMR values again tended to be higher than accepted ones (by around 20% in Mammalia). For Metatheria, the effect of reliability was non-significant (Table 3).

When considering the relationship betwen BMR and body mass, the SPOILED data set mostly led to a weaker phylogenetic signal in the residuals than the SELECT data set (Table S4). This was the case for the Mammalia and Eutheria, as well as for most of the order-level clades examined, except for Primates. When only BMR was considered without taking body mass differences into account, the difference between lambda values obtained with the SELECT and the SPOILED sets was much less consistent (Table S4).

Including rejected data occasionally had a larger effect when more restricted clades were considered. Sciuromorph rodents provided a straightforward and extreme example of

Table 2. Test of equality of the variances of the residuals obtained with different data set pairs for the scaling of basal metabolic rate (BMR) to body mass and for the relationship between brain mass and BMR

Analysis	Clade	Parameter	ALL (1)*vs* SELECT (2)	SPOILED (1)*vs* SELECT (2)
Scaling of BMR	Mammalia	N_1, N_2	817, 549	549, 549
		Var_1, Var_2	0.0321, 0.0268	0.0407, 0.0268
		P	0.021	1×10^{-6}
	Metatheria	N_1, N_2	84, 70	70, 70
		Var_1, Var_2	0.0092, 0.0062	0.0122, 0.0062
		P	0.082	0.005
	Eutheria	N_1, N_2	730, 476	476, 476
		Var_1, Var_2	0.0328, 0.0279	0.0431, 0.0279
		P	0.053	2×10^{-6}
Brain *vs* BMR	Mammalia	N_1, N_2	526, 369	369, 369
		Var_1, Var_2	0.0604, 0.0441	0.0456, 0.0441
		P	0.001	0.750
	Metatheria	N_1, N_2	71, 59	59, 59
		Var_1, Var_2	0.0221, 0.0205	0.0183, 0.0205
		P	0.772	0.665
	Eutheria	N_1, N_2	453, 308	308, 308
		Var_1, Var_2	0.0639, 0.0460	0.0532, 0.0460
		P	0.002	0.204

Data sets are as described in Table 1. Bartlett's test was applied to test for equality of the variances in the residuals of the models BMR ∼ body mass ('scaling of BMR') and brain mass ∼ body mass + BMR ('Brain vs BMR') using phylogenetic generalized least squares (PGLS). The residuals were obtained separately with each of the two data sets compared. N_1, N_2, Var_1 and Var_2 are the sample sizes and variances for each data set.

this. Fifty-four species of sciuromorphs had entries in the BMR database and were therefore included in the ALL data set. Of these, 24 could also be included in the SELECT set ($E = 1$ or 2). Some of the remaining 30 species were discarded from the SELECT set, notably because of concerns that metabolic measurements had been conducted during the day with fully diurnal animals. On a traditional allometric scaling plot of the ALL data, the SELECT data clearly tended to lie in the lower region of the data cloud (Fig. 2). The 54 species of the ALL set led to a phylogenetically informed scaling relationship of:

$$\log_{10} \mathrm{BMR} = 0.69\ [0.11] + 0.67\ [0.04]\ \log_{10} m, \quad (1)$$

where BMR is in ml O_2 h^{-1}, m in g and values in brackets are S.E. However, the factor reliability had a highly significant effect on BMR ($P = 4 \times 10^{-6}$), when the non-significant ($P = 0.57$) interaction body mass × reliability was discarded from the analysis. Incorporating this factor led to the scaling equation

$$\log_{10} \mathrm{BMR} = 0.88\ [0.07] + 0.60\ [0.03] \log_{10} m$$
$$-0.15\ [0.03]\ \text{reliability}, \quad (2)$$

with reliability taking the value of 0 for rejected values (Fig. 2, dashed red line) and 1 for accepted values (Fig. 2, continuous blue line). This direct comparison between sciuromorph accepted and rejected values of the ALL data set is complicated by the fact that they represent different species. However, the effect of reliability could be assessed directly for the 19 species that had both accepted ($E = 1$ or 2) and rejected ($E = 3$ or 4) BMR values. For each of these species, we calculated the average of all accepted, and of all rejected values, respectively, as deviations from the BMR predicted by a phylogenetically informed scaling equation based on the 19 SELECT values ($\log_{10}\mathrm{BMR} = 0.63$ [0.12] + 0.66 [0.05] $\log_{10} m$). Then, we applied a PGLS analysis to the difference between these average deviations (accepted *versus* rejected). This difference was found to differ significantly from 0 (difference $= -0.11 \pm 0.02$; $N = 19$; estimated lambda = 0; $t_{18} = -4.72$, $P = 0.0002$). On average, rejected values exceeded accepted ones by about 28% in this restricted assemblage.

Sample size had only a weak influence on the significance of the relationship between body mass and BMR obtained with different data sets. This was revealed by the repeated subsampling procedure applied to the SELECT and SPOILED data sets across all mammals, a procedure which further illustrated the strength of the BMR/body mass relationship (Fig. 3A1 and A2). Indeed, with both of these data sets, the effect of body mass on BMR remained highly significant at all subsample sizes, except for the very smallest ($N = 5$), where the associated probability became highly erratic.

(2) Relationship between brain mass and BMR

All analyses conducted with the SELECT data set in the context of the relationship among brain mass, body mass

Table 3. Effect of data reliability on basal metabolic rate (BMR) in data sets containing both accepted (evaluation criterion $E = 1$ or 2) and rejected ($E = 3$ or 4) metabolic values

Clade	Parameter	ALL	SPOILED
Mammalia	$P_{reliability}$ (t)	$\underline{3 \times 10^{-7}}$ (−5.19)	$\underline{1 \times 10^{-9}}$ (−6.21)
	$\beta_{reliability}$	−0.050	−0.082
	P_m (t)	$<2 \times 10^{-16}$ (81.8)	$<2 \times 10^{-16}$ (58.4)
	β_m	0.736	0.714
	N (accepted, rejected)	817 (549, 268)	549 (293, 256)
Metatheria	$P_{reliability}$ (t)	$\underline{0.092}$ (1.70)	$\underline{0.206}$ (−1.28)
	$\beta_{reliability}$	0.113	−0.034
	P_m (t)	$<2 \times 10^{-16}$ (30.7)	$<2 \times 10^{-16}$ (52.6)
	β_m	0.801	0.724
	$P_{interaction}$ (t)	$\underline{0.018}$ (−2.41)	—
	$\beta_{interaction}$	−0.064	—
	N (accepted, rejected)	84 (70, 14)	70 (28, 42)
Eutheria	$P_{reliability}$ (t)	$\underline{1 \times 10^{-6}}$ (−4.94)	$\underline{5 \times 10^{-9}}$ (−5.97)
	$\beta_{reliability}$	−0.050	−0.086
	P_m (t)	$<2 \times 10^{-16}$ (71.9)	$<2 \times 10^{-16}$ (50.6)
	β_m	0.734	0.720
	N (accepted, rejected)	730 (476, 254)	476 (265, 211)

Data sets are as described in Table 1. The effect of reliability on BMR was tested with ANCOVA [using phylogenetic generalized least squares (PGLS)] including body mass (m) as a covariate and reliability as a two-level factor ('accepted' for $E = 1$ or 2 and 'rejected' for $E = 3$ or 4; 'rejected' is taken as the reference level). Results are given for the full model including the interaction body mass × reliability and, when the latter was non-significant, for the simplified model without interaction. For each effect, the probability (P, underlined for reliability and for the interaction) and the associated t value, as well the estimate (β) are given. A negative $\beta_{reliability}$ means that reliable BMR values tend to be lower than rejected ones. The effect of body mass was always highly significant (see Table 1). N is sample size, the sample sizes given in parentheses are those of the accepted and rejected data, respectively.

and BMR led to equally high r^2 (with PGLS, all $r^2 \geq 0.865$). This was primarily due to the tight relationship between brain mass and body mass, the effect of BMR on brain mass always being much weaker. Among the large clades, the interaction body mass × BMR never had a significant effect on brain mass. When this effect was discarded from the model, the relationship between BMR and brain mass was significant among Mammalia or Eutheria, but not among Metatheria (Table 4). Among the order-level clades examined, the SELECT data set led to a significant body mass × BMR interaction only for Primates and Dasyuromorpha. Removal of the non-significant interaction led to a non-significant effect of BMR on brain mass in all remaining clades, except in Carnivora (Fig. 4). The estimated lambda was variable in these analyses (Table S4), although generally high (median 0.8, range 0−1), except for Diprotodontia and Dasyuromorpha, reflecting an appreciable phylogenetic signal in the data.

With the ALL data set, the interaction body mass × BMR again had a non-significant effect on brain mass, and when this interaction was removed from the analyses the relationship between brain mass and BMR was significant in Mammalia and Eutheria (Table 4). However, this relationship was now also significant in Metatheria (Table 4, Fig. 4), as well as in Carnivora and Diprotodontia (Fig. 4). The ALL data set also differed from the SELECT set in that it led to a significantly larger variance in the residuals in Mammalia and Eutheria (Table 2), reflecting the added noise caused by the rejected values of the ALL set. The variances of these residuals were nevertheless not significantly different in Metatheria (Table 2).

The effect of BMR on brain mass was no longer significant among Mammalia and Eutheria in the SPOILED data set, and the effect sizes were considerably smaller than in the SELECT or ALL data sets (Table 4). In Metatheria, the non-significant effect of BMR on brain mass was further from significance with the SPOILED than with the SELECT data set. In this clade, the effect size of BMR was smaller, but the effect size of body mass was larger in the SPOILED data set than in the SELECT or ALL data sets. Variance inflation factors (VIF) were generally high (Table 4), around 10 in Mammalia and Eutheria, and up to 95 in Metatheria, as expected due to the strong correlation between brain mass and body mass on the one hand, and BMR and body mass on the other. In the SPOILED data set, VIFs were slightly lower, indicating reduced collinearity of the predictor variables due to increased error variation in BMR. However, the variances of the residuals obtained with the SPOILED and SELECT data sets never differed significantly, including in Metatheria (Table 2). The lambda estimated with the SPOILED data set was also often lower than with the SELECT data set (seven out of 13 clades, Table S4), reflecting a lower phylogenetic structure in the residuals. However, the reverse was found in four clades out of 13.

When applied in the context of the mammalian brain mass/BMR relationship, the repeated subsampling approach emphasized three major aspects of comparative

Table 4. Effect of basal metabolic rate (BMR) and body mass on brain mass in several clades using different data sets for BMR

Clade	Parameter	ALL	SELECT	SPOILED
Mammalia	P_{BMR} (t)	$\underline{1 \times 10^{-4}}$ (3.89)	$\underline{4 \times 10^{-4}}$ (3.61)	$\underline{0.082}$ (1.75)
	β_{BMR}	0.159 ± 0.041	0.183 ± 0.051	0.068 ± 0.039
	VIF_{BMR}	12.2	13.6	8.5
	P_m (t)	$<2 \times 10^{-16}$ (15.7)	$<2 \times 10^{-16}$ (12.7)	$<2 \times 10^{-16}$ (19.5)
	β_m	0.503 ± 0.032	0.490 ± 0.039	0.578 ± 0.030
	VIF_m	11.6	13.3	8.2
	lambda	0.929	0.952	0.926
	r^2 (model)	0.883	0.900	0.890
	N	526	369	369
Metatheria	P_{BMR} (t)	$\underline{0.025}$ (2.29)	$\underline{0.110}$ (1.62)	$\underline{0.356}$ (0.93)
	β_{BMR}	0.372 ± 0.162	0.332 ± 0.205	0.150 ± 0.161
	VIF_{BMR}	75.2	94.3	42.6
	P_m (t)	8.6×10^{-3} (2.71)	0.018 (2.45)	$<1 \times 10^{-5}$ (4.85)
	β_m	0.335 ± 0.124	0.376 ± 0.154	0.571 ± 0.118
	VIF_m	75.2	94.3	42.6
	lambda	0.805	0.759	0
	r^2 (model)	0.924	0.929	0.962
	N	71	59	59
Eutheria	P_{BMR} (t)	$\underline{6 \times 10^{-4}}$ (3.47)	$\underline{7 \times 10^{-4}}$ (3.43)	$\underline{0.075}$ (1.79)
	β_{BMR}	0.147 ± 0.042	0.179 ± 0.052	0.069 ± 0.039
	VIF_{BMR}	10.7	11.4	7.3
	P_m (t)	$<2 \times 10^{-16}$ (15.4)	$<2 \times 10^{-16}$ (12.4)	$<2 \times 10^{-16}$ (18.8)
	β_m	0.513 ± 0.033	0.496 ± 0.040	0.564 ± 0.030
	VIF_m	10.2	11.2	7.1
	lambda	0.890	0.930	0.934
	r^2 (model)	0.876	0.896	0.881
	N	453	308	308

Data sets are as described in Table 1. Results are given for the simplified model including body mass and BMR, without interaction. For both predictors BMR and body mass (subscripts BMR and m), the probability (P, underlined for BMR) of the t value (t-test of 0 slope, t reported in parentheses) is provided, along with the estimate of the slope (β) and its S.E., and the variance inflation factor (*VIF*). The maximum likelihood estimate for lambda, sample size (N) as well as the associated r^2 are also given. In the complete model the interaction body mass × BMR was never significant.

analyses including BMR. First, the probability of the brain mass/BMR relationship was highly dependent on the particular assemblage of species entered in a data set. For example, different subsets of $N = 90$ randomly sampled within the SELECT data set could lead to a probability of the BMR effect ranging anywhere between 10^{-4} (highly significant) and 0.99 (Fig. 3), with a median of 0.09. Second, this approach also demonstrated the importance of sample size. With both the SELECT and the SPOILED data sets, a progressive increase in subsample size affected the probability of the BMR effect on brain mass in a non-linear manner (Fig. 3), whereby this probability gradually converged towards the value obtained with the entire data set (i.e. $P = 4 \times 10^{-4}$ for the SELECT data set and 0.082 for the SPOILED data set; Table 4). Third, the importance of the data-selection process was also confirmed. At all sample sizes, P tended to remain consistently higher with the SPOILED set when compared to the SELECT set. As a consequence, significance tended to be achieved with smaller samples when only SELECT values were used. For example, the effect of BMR on brain mass was significant with the entire SELECT data set ($N = 369$, $P = 4 \times 10^{-4}$; Table 4), but tended to be non-significant with subsamples of less than about 180 species (Fig. 3). When this same data set was spoiled by 200 unreliable BMR estimates, this effect tended to be non-significant at all sample sizes up to 369 (Fig. 3).

IV. DISCUSSION

(1) Effect of the reliability of the BMR data

We have shown that the results of comparative analyses including BMR can be influenced appreciably by the selection criteria applied while compiling the data. Both the coefficients and the significance of a tested model may be affected and, in some analyses, relaxing the BMR selection criteria may result in crossing the significance limit for a particular effect. Although there have been occasional discussions in the literature about the appropriateness of particular measurements as BMR estimates (McNab, 1987, 1992*a*, 1997, 2006; Speakman *et al.*, 1993; White & Seymour, 2003, 2004, 2005), the extent to which different BMR data-selection procedures affect the results of comparative analyses has never been examined in mammals. In a re-analysis of a previous comparative study on birds

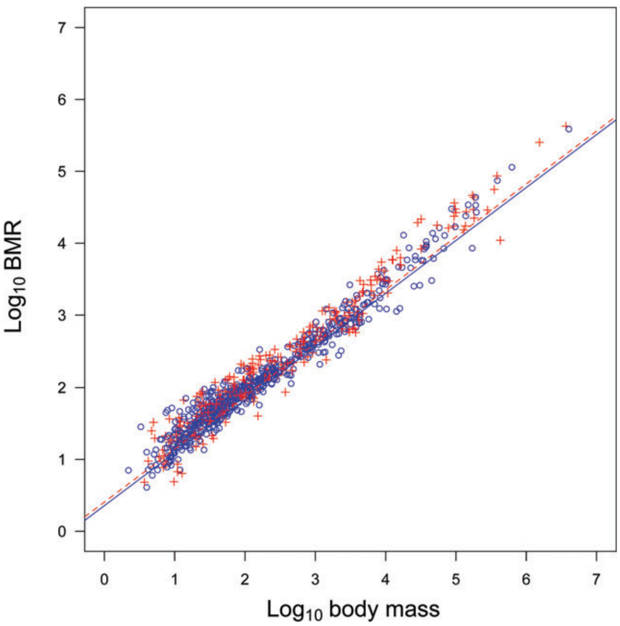

Fig. 1. Scaling of basal metabolic rate (BMR) in Mammalia as depicted by the ALL data set ($N = 817$, best BMR estimate for each species in the database). Blue circles depict 'accepted' BMR values (SELECT data set; evaluation criterion $E = 1$ or 2, $N = 549$) and red crosses depict the remaining, 'rejected' values included in the ALL data set ($E = 3$ or 4, $N = 268$). Solid blue and dashed red lines are the phylogenetically informed (PGLS) best-fit lines for the 'accepted' and 'rejected' values, respectively. The effect of reliability ('accepted' *versus* 'rejected') was highly significant once the non-significant interaction body mass × reliability was discarded from the model (Table 3).

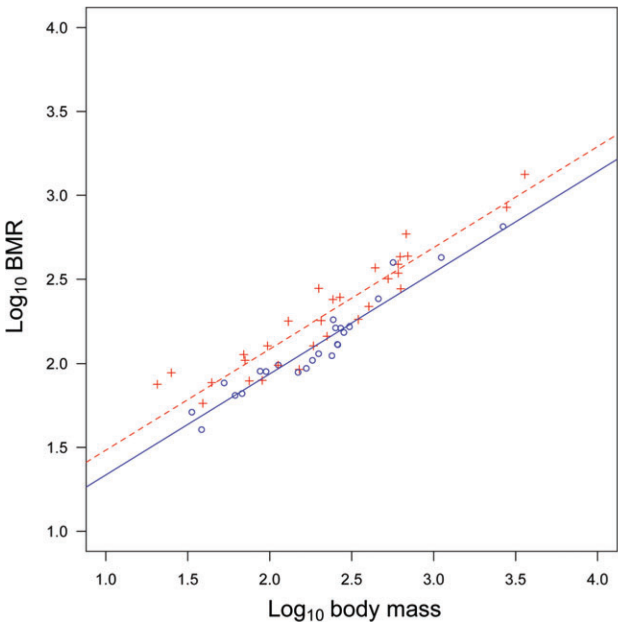

Fig. 2. Scaling of basal metabolic rate (BMR) to body mass in sciuromorph rodents. Each sciuromorph species in the ALL data set is represented by a single value corresponding to the 'best' estimate available for that species. Blue circles are species for which this best estimate was considered 'accepted' ($E = 1$ or 2; SELECT data set) and red crosses are species for which the estimate was considered 'rejected' ($E = 3$ or 4). Solid blue and dashed red lines are the phylogenetically informed (PGLS) best-fit lines for the 'accepted' and 'rejected' values, respectively. The non-significant interaction body mass × reliability in the complete model was discarded and the scaling coefficients of the two lines differed significantly.

(Reynolds & Lee, 1996), McKechnie & Wolf (2004) observed that many of the rejected metabolic data failed to meet one or more of the BMR criteria, thus overestimating the BMR value. Ultimately, the inclusion of such data led to a scaling equation with a significantly different scaling coefficient. In our BMR database, such overestimations are also common (e.g. animals not postabsorptive, not resting, and/or not measured during a major resting phase of their daily cycle) and in some cases the authors intentionally did not fulfill all BMR criteria (e.g. in studies aimed at measuring RMR). We corroborate the McKechnie & Wolf (2004) finding in birds by demonstrating that, within both the SPOILED and ALL data sets, rejected BMR estimates are generally about 12–20% larger than accepted ones for both Mammalia and Eutheria (Table 3, Fig. 1). Hence increasing the number of unreliable BMR estimates in a data set will potentially increase the bias in the resulting model. Due to insufficient information, it is currently impossible to assess the extent to which this difference between reliable and unreliable data is attributable to sleep. Finally, at least in the context of scaling of BMR to body mass, the SPOILED data set consistently led to a weaker phylogenetic signal in the model's residuals than the SELECT data set, which included the same species (Table S4). This was expected since unreliable estimates should introduce additional noise into a data set.

Apart from the failure to fulfill one or more BMR criteria, many other reasons were found for rejecting a value as a BMR estimate in the mammalian database. As was pointed out by McKechnie & Wolf (2004), lack of information provided by the authors often precluded a sound assessment as to whether the metabolic values provided could be considered to be reliable BMR estimates. For example, adult status and non-reproductive condition were often not explicitly stated. In some cases, the body mass of the measured subjects was not given. Still other entries were associated with dubious interpretations (e.g. concerning the range of the thermoneutral zone), miscalculations, or other technical problems, and some of these presumably even underestimated the BMR. Thus, rather than leading to a systematic overestimation of the BMR, the use of relaxed criteria for the BMR data-selection process mainly adds noise to a data set. Indeed, significantly different variances were obtained in the model residuals with the SELECT and SPOILED data sets in the analyses of the scaling of BMR (Table 2). A similar tendency was also found when the SELECT and ALL sets were compared (Table 2). However, presumably due to their greater similarity, these data sets led to variances of the residuals that differed significantly only for Mammalia. Let it be noted that, apart from the

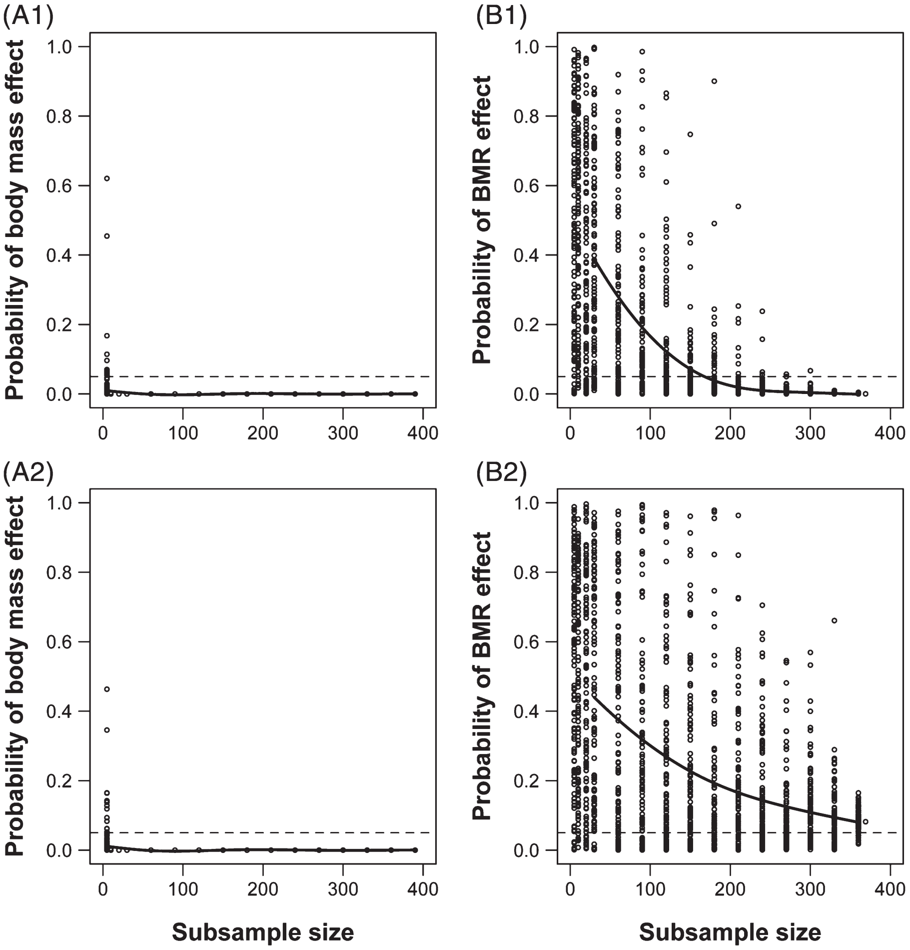

Fig. 3. Comparison between results of the repeated subsampling procedure, for SELECT and SPOILED data sets, and for a strong and a weak relationship: (A) the effect of body mass on basal metabolic rate (BMR) (strong) and (B) the effect of BMR on brain mass, controlled for body mass (weak). In A1 and B1, random subsamples are drawn from the SELECT data sets, and in A2 and B2 from the SPOILED data sets, respectively. The *x*-axis shows the sample size of the random subsample, while the *y*-axis gives the *P* value of the effect of the explanatory variable (A: body mass; B: BMR). Each dot represents the result of a phylogenetic generalized least-squares (PGLS) analysis based on a random subsample of the original data set (data set A: $N = 549$; data set B: $N = 369$). The final dot at the right of the B graphs corresponds to the *P* value obtained with the complete data set (Table 4). Continuous curves are best-fit curves obtained with a generalized additive model (gam). Horizontal dashed line depicts $P = 0.05$.

inclusion of inappropriate BMR estimates in a database, added noise may also result from the combination of different previously published data sets, each based on different data-selection criteria. Yet this appears to be common practice for time-saving convenience.

(2) Interaction among data reliability, sample size and strength of a relationship

Our results only partly confirm the expectation that differences in the BMR data selection criteria will have a larger effect in the case of relatively weaker relationships. Indeed, very similar curves were obtained with the subsampling procedure applied to the SELECT and SPOILED data sets in the context of the scaling of BMR to body mass. As expected, the relationship between BMR and body mass was highly significant at all subsample sizes for the two data sets, down to subsample sizes of 10, confirming the strength of this scaling effect. However, consistent differences did arise in this context (variances of the residuals, model coefficients), and with smaller species assemblages the deviations could be fairly large. The example of the sciuromorph rodents, for which many metabolic values obtained during the alpha ('normally active') phase of the daily cycle are available, was an extreme and illustrative case. Interestingly, Hayssen & Lacy (1985) obtained an equation for Sciuridae ($\log_{10}\text{BMR} = 0.816 + 0.615 \log_{10}m$; BMR in ml O_2 h^{-1} and *m* in g) in which the scaling coefficient was roughly intermediate between ours for accepted and rejected values of the ALL set (0.73 *versus* 0.88, scaling exponents similar). This can be understood when one realizes that these authors included several values corresponding to an alpha phase resting metabolic rate, thus grossly overestimating the BMR values.

Larger effects of the data-selection process were observed in the context of the weaker brain mass/BMR relationship, even affecting the significance of the relationship. Using PGLS, this relationship was significant for all three large clades with the ALL data set, in none of them with the SPOILED set, and only in Mammalia and Eutheria with the SELECT set (Table 4). In this context, reliability of the data set clearly interacted with sample size in affecting the results of the analyses. First, the results obtained with the different data sets tended to differ more with small than with large sample sizes (e.g. Fig. 4). They even appeared erratic at small sample sizes, the brain mass/BMR relationship being significant for only a few orders, and the more reliable data sets not necessarily leading to a lower probability. Second, the interaction between sample size and data reliability was illustrated by the subsampling procedure (Fig. 3), a process that sheds light on the results obtained with clades having different sample sizes (Fig. 4). Indeed, discarding at random even a limited number of species in a large data set led to a rapid increase in the scatter around an average probability, which itself departed in a non-linear way from the probability obtained with the entire corresponding data set. At the same time, the probability of a null effect of BMR on brain mass was consistently higher at all subsample sizes for a SPOILED-derived subsample than for a SELECT-derived subsample, which was clearly due to the added noise in the BMR data of the SPOILED data set. One conclusion would be that, even when a significant relationship is observed, comparative tests of a relationship between BMR and brain mass (or any other weak relationship) should always be treated with caution when based on small samples. This may, for example, occur when restricting an analysis to a particular order of mammals, except for those with the largest species richness. The subsampling procedure might even be an interesting way to test the reliability of a demonstrated relationship as it might help to assess the sensitivity of a significant result to the omission of a small number of species from a data set. Furthermore, while increasing sample size is obviously desirable, it should also be approached with caution, especially when it involves inclusion of more unreliable data.

(3) Scaling of BMR to body mass

The biological relationships analysed herein were used primarily to illustrate the potential effects of BMR data-selection procedures on the results of comparative analyses. Nevertheless, these results still merit attention in their own right. Our analyses of the scaling of BMR to body mass broadly confirm results from many previous studies (e.g. McNab, 1988*a*; Lovegrove, 2000; Symonds & Elgar, 2002; White & Seymour, 2003, 2004, 2005; Sieg *et al.*, 2009; Capellini *et al.*, 2010; Clarke *et al.*, 2010). The phylogenetic signal obtained among eutherians (or mammals in general) was close to unity (lambda, Tables 1 and S4, SELECT data set), confirming the strong phylogenetic structure of the residuals already reported by others (Isler & van Schaik, 2009; Sieg *et al.*, 2009; Capellini *et al.*, 2010). By contrast, the optimized value of lambda was 0 for the marsupials, reflecting an absence of phylogenetic structure in the residuals. Capellini *et al.* (2010) also found a low phylogenetic signal (lambda = 0.4) for marsupials.

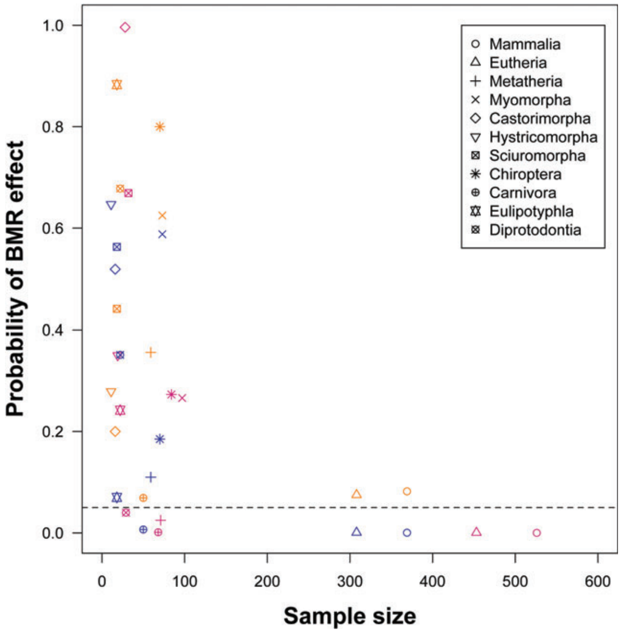

Fig. 4. Probability of $\log_{10}$ basal metabolic rate (BMR) effect on $\log_{10}$ brain mass as a function of sample size in different clades, using three different data sets. The graphed probability refers to the model including only the direct effects of $\log_{10}$ body mass and $\log_{10}$ BMR, without their (non-significant) interaction. Displayed are the larger clades (Mammalia, Eutheria and Metatheria) and orders for which sample size in the SELECT data set was larger than 10. Primates and Dasyuromorpha are not represented as the interaction body mass × BMR was significant in these orders. Colour indicates the data set considered: pink symbols: ALL; blue symbols: SELECT; orange symbols: SPOILED. Dashed line depicts significance level of $P = 0.05$.

The allometric coefficients found for Metatheria and for Eutheria broadly corroborate earlier findings. The coefficient found for the marsupials was lower than that found for eutherian mammals (0.382 ± 0.026 *versus* 0.455 ± 0.060, Table 1, SELECT data set), although 95% confidence intervals for these coefficients overlap in this case and scaling exponents also differed slightly, with BMR values for the marsupials tending to be lower especially at low body masses. That marsupials collectively tend to exhibit lower basal rates of metabolism than eutherians has been recognized previously (McNab, 2005, 2008*a*; Capellini *et al.*, 2010). White & Seymour (2003, 2004) argued that this difference is linked to differences in body temperature and proposed that BMR should be corrected for these differences. Sieg *et al.* (2009) then demonstrated that body temperature explains only a very small part of the variation in BMR in addition to body mass. But even if BMR and body temperature were strongly correlated, a correction of BMR for differences in body temperature would seem inappropriate as it is unlikely that body temperature determines BMR (McNab, 2006).

McNab (2005) proposed that the low scaling coefficient observed in the marsupials is due to the absence of high-BMR species in this clade. He argues that only a placental mode of reproduction allows species to profit from high-energy ecological niches by increasing their reproductive output concomitantly with the rate of biosynthesis. However, it is unclear why marsupials would not also be able to do so during lactation. Further work is still needed to understand the BMR differences observed between Metatheria and Eutheria.

The scaling exponent obtained for the eutherians with a phylogenetically informed analysis (0.726 ± 0.012, Table 1, SELECT data set) is similar to many previously published values [e.g. 0.716–0.724 (McNab, 1988*a*, 2008*a;* Capellini *et al.,* 2010)]. For the metatherians, this exponent (0.743 ± 0.010, Table 1, SELECT data set) is also close to that (0.724 ± 0.015) obtained by Capellini *et al.* (2010) and its confidence intervals include 3/4. However, as found by White *et al.* (2009) and Capellini *et al.* (2010), the confidence intervals of the exponent obtained for eutherians included neither 2/3 nor 3/4, values which have been 'predicted' by mechanistic models (e.g. West, Brown & Enquist, 1997; Roberts, Lightfoot & Porter, 2010). Despite many attempts to derive mechanistically a 'theoretical' allometric exponent for the scaling of BMR (e.g. Beuchat *et al.,* 1997; West *et al.,* 1997; Roberts *et al.,* 2010), no single value is universally accepted and, as Sieg *et al.* (2009) and Capellini *et al.* (2010) have argued, it is even presently unclear whether BMR should be expected to scale with body mass in a uniform fashion in different lineages. McNab (2008*a*) also showed that the allometric exponent depends on the confounding variables included in the analysis besides body mass. A key point is that despite selecting only the most reliable BMR estimates we could not find any support for the predicted 'theoretical' scaling exponents of either 3/4 or 2/3.

(4) Relationship among brain mass, body mass and BMR

The relationship between brain mass and BMR was significant and positive in Eutheria as well as in Mammalia (Table 4, SELECT data set). In Metatheria, it was non-significant, as within the individual orders examined, except for Carnivora (Fig. 4). Again, the latter results must clearly be interpreted with caution, given the small sample sizes concerned [$N = 59$ for Metatheria (Table 4); $N \leq 97$ for individual orders (Fig. 4)] and the demonstrated effect of sample size on the probability of a BMR effect on brain mass (Fig. 3B1). Martin (1981) argued that a link between brain size and BMR was reflected in the (~0.75 power) scaling of brain size to body mass. Attempts to demonstrate such a link statistically failed initially (Pagel & Harvey, 1988; McNab & Eisenberg, 1989), but later studies consistently found a weak, although significant, positive relationship (Martin, 1996, 1998; Martin, Genoud & Hemelrijk, 2005; Isler & van Schaik, 2006*b*, 2009; Sobrero *et al.,* 2011). Our results are similar to those of Isler & van Schaik (2006*b*). Martin *et al.* (2005) included gestation length in their analyses of the brain size/BMR relationship, in an attempt to examine the maternal energy hypothesis (Martin, 1981, 1996). The latter hypothesis, which states that encephalization is limited by the amount of energy that a mother is able to allocate to her growing offspring, was supported by their conclusion that the relationship between brain mass and body mass among placentals was primarily due to a direct link between BMR and brain size. Recent examinations of the brain size/BMR link often include life-history variables reflecting the rate of offspring production (e.g. litter size or maximum reproductive rate), because encephalization may be traded off against reproductive rate, and because this trade-off might then obscure the relationship between brain size and BMR (Isler & van Schaik, 2009; Barrickman & Lin, 2010).

Taking body mass and gestation length into account, Barton & Capellini (2011) obtained a significant correlation between neonate brain size and BMR, providing support for the maternal energy hypothesis. They argued that the weakness of the adult brain size/BMR relationship is due both to the effect of other life-history variables and to the fact that BMR constrains brain growth rate only during the prenatal period. As for the Metatheria, recent examinations of the brain size/BMR link led to contradictory results. Isler (2011) found the relationship to be significant when the maximum reproductive rate was accounted for, but Weisbecker & Goswami (2010, 2014) did not find a significant effect of BMR on brain size and argued that weaning age and litter size were the best-supported correlates of relative brain size in marsupials. But in this case, too, these results must be viewed in light of the smaller sample sizes involved. Moreover, collinearity problems are most striking in Metatheria. While the effect of the covariate body mass is consistently very strong in these models, and sample size is large, the observed collinearity effect does not impair the results regarding the BMR effect in Mammalia or Eutheria. In Metatheria, however, VIFs are strikingly high (between 40 and 95, Table 4) and the effect size of body mass varies considerably among data sets. A brain mass–body mass slope of about 0.35 in the ALL and SELECT data sets is relatively low compared to the interspecific slope of 0.5–0.8 commonly observed in most mammalian clades, while in the SPOILED data set a more reasonable estimate of 0.57 is observed. This indicates an extremly tight correlation between brain mass, BMR and body mass in Metatheria, which, however, is therefore not very robust. The inclusion or exclusion of single data points may determine the outcome of the analyses, which may also explain why the relationship between BMR and brain size in Metatheria is disputed (Weisbecker & Goswami, 2010, 2014; Isler, 2011). We conclude that, in cases of unavoidable collinearity issues, strict monitoring of data quality is of even greater importance.

In any case, the weakness of a possible link between BMR and brain mass must be recognized even for placental mammals. Low r^2 values have been reported earlier for the effect of BMR on brain mass in placentals or more restricted clades of eutherians (Isler & van Schaik, 2006*b*; Weisbecker & Goswami, 2010, 2014; Sobrero *et al.,* 2011). Any conclusion about such a relationship rests on the hypothesis that no important confounding factor has been neglected. The major confounding variable is always body mass and this variable was taken into account in all cited examples as well as in our analyses. However, a wealth of other factors could potentially affect the brain mass/BMR relationship (e.g. diet, climate, life history, geographic distribution, patterns of parental care) through an effect on brain size, on BMR, or on both.

(5) On the use and usefulness of the BMR database

We have acknowledged the difficulties in estimating the BMR in many mammals and have argued that these difficulties are often taxon-specific. Resting rate of metabolism, or RMR, is a rate measured under much less restrictive conditions than BMR, the only specific requirement being that the animal is resting during the measurements. RMR is typically referred to when minimal rates of metabolism of resting normothermic endotherms are measured in conditions incompatible with BMR. For example, the term has been applied to rates measured in pregnant or lactating females (e.g. Stephenson & Racey, 1993*b*; Zenuto, Antinuchi & Busch, 2002; Krol, Johnson & Speakman, 2003; Cretegny & Genoud, 2006), in individuals exposed to temperatures below the thermoneutral zone (e.g. Ron & Haim, 2001; Konarzewski, Ksiazek & Lapo, 2005; Oelkrug *et al.,* 2012) or in postprandial (i.e. not postabsorptive) individuals (e.g. Zenuto *et al.*, 2002; Speakman *et al.*, 2004; Larivée *et al.*, 2010; Careau, 2013). While the use of RMR can be justified in an experimental context, its inclusion in comparative studies poses problems due to its lack of comparability (e.g. see discussion in McNab, 2012). Indeed, RMR exceeds BMR by a variable amount depending on the additional activity in which the organism is engaged and on its intensity. By contrast, BMR is much more standardized (McNab, 1997; McKechnie & Swanson, 2010), precisely because the criteria by which it is defined eliminate various factors that can affect it, such as activity, reproduction, growth or digestion (Speakman *et al.,* 2004). BMR can be estimated in the vast majority of endotherms, except for very few species such as some tenrecs or bats that might not exhibit a basal rate at all (McNab, 1997). It expresses the minimum rate of metabolism of individuals maintaining their normal body temperature (i.e. not undergoing daily torpor or hibernation), the comparison of which is justified even if many mammals (e.g. small mammals living in cold or temperate regions) only rarely express their basal rate in nature. BMR is also useful to estimate the incremental energetic costs related to particular activities (Brody, 1945; Hulbert & Else, 2004).

Despite its comparability, BMR might not always be the most relevant energetic variable to be included in a comparative analysis. The summit metabolic rate (maximum cold-induced metabolic rate) and VO_2max (maximum metabolic rate during exercise) are other standardized rates that have sometimes been included in comparative analyses (e.g. McKechnie & Swanson, 2010). These rates are not necessarily expressed more frequently in the field and are best considered as complementary to BMR. Furthermore, BMR is often used as a proxy for overall energy expenditure or requirements. In such cases, field metabolic rates (FMR) or estimates of field energy requirements might be more appropriate. While FMR directly expresses the energy expenditure of free-living animals, its intra- and interspecific variation is always difficult to interpret as it reflects not only physiological variation, but also behavioural differences and ecological (especially thermal) variation within and among species (McNab, 1997).

Interspecific comparative analyses typically select one single value for each species, a procedure that was also adopted in our analyses. This entirely discards intraspecific variation in BMR and assumes that a single value entered for a species is representative of the individuals of that species (Konarzewski & Ksiazek, 2013). Firstly, BMR exhibits appreciable phenotypic flexibility, notably across the seasons (Genoud, 1990; Lovegrove, 2005; McKechnie, 2008). The latter factor can be included explicitly among the BMR criteria in order to enhance comparability of BMR (McNab, 2008*a*). In our database, values obtained during a season of higher resource availability were usually preferred. Secondly, even after accounting for body-mass variation, season or other potentially influential factors, considerable individual variation in BMR was often observed (e.g. Speakman & McQueenie, 1996; Cruz-Neto & Bozinovic, 2004; Speakman *et al.,* 2004; Cretegny & Genoud, 2006; Burton *et al.,* 2011; Genoud & Christe, 2011). Its causes are multiple, including intrinsic factors (local adaptation, maternal effects, anatomical or behavioural differences) as well as extrinsic factors (reviewed in Burton *et al.,* 2011). Consequences for fitness have also been demonstrated, even if the link between BMR and fitness has sometimes been described as context-specific, with no single rate being optimal in any given population (Jackson, Trayhurn & Speakman, 2001; Boratynski & Koteja, 2009, 2010; Boratynski *et al.,* 2010; Larivée *et al.,* 2010). In view of the diversity of causes and components of intraspecific variation in BMR, taking account of intraspecific variability in BMR in interspecific comparative analyses is certainly a complicated task. Sieg *et al.* (2009) demonstrated that varying the ratio of the intraspecific variances of body mass and BMR can affect the model coefficients obtained for the interspecific scaling of BMR to body mass in different clades of mammals. In general, results of interspecific comparative analyses are expected to be more strongly affected by intraspecific variation when species averages are based on small samples, or when intraspecific variation is substantial relative to the expected variance among species (Felsenstein, 2008). The latter is most likely to occur in analyses of relatively small clades such as genera or subfamilies. Then, it becomes relevant to apply either a technique to include intraspecific variation in interspecific comparative analyses (Ives, Midford & Garland, 2007; Felsenstein, 2008) or a Bayesian mixed-model approach which models within-species variation as repeated measures with a random effect (Hadfield & Nakagawa, 2010; Revell & Reynolds, 2012). Our database already provides BMR estimates for different conspecific populations whenever available. Such differences should be considered cautiously if they rely on estimates associated with a low reliability and/or measured by different authors with different methods. On the other hand, the database can help in selecting those entries that could be relevant for assessment of populational differences.

The BMR database is primarily intended to facilitate the difficult task of data selection. Yet we emphasize that this selection process requires personal choices as to how BMR values are to be selected. The database should also be useful in various other ways. It may, for example, help identify species of particular interest that are currently absent from the database, or species for which additional measurements are particularly welcome (e.g. due to small sample size or doubts about the reliability of available estimates). It could also be used to improve an experimental protocol with the aim of obtaining more-reliable estimates of BMR. Whatever its usefulness, this database is, however, far from exhaustive and could be enhanced in various ways. Apart from the obvious improvement brought about by additional entries, new variables could also be added, as more data are gradually published. In this context, much work still remains to be done to obtain comparable data on the minimum energy requirements of normothermic endotherms. For example, additional information on the duration of the postprandial metabolic response in various species or the patterns of sleep and their metabolic consequences for the BMR would be especially interesting.

V. CONCLUSIONS

(1) We have demonstrated that the criteria applied during the BMR data-selection process can influence the results of comparative analyses including BMR among mammals. Depending on the particular clade and relationship examined and depending on the sample size available, the reliability of a data set can affect the model parameters, the variance of the model's residuals and even the significance of the tested model. A large proportion of previously published studies used metabolic data gathered by others without considering the actual conditions under which they were obtained. Our analyses substantiate the arguments marshalled by Borries *et al.* (2016), who emphasized the need for more careful reliability control with data used in comparative analyses. These authors strongly recommended more transparency in comparative databases, including a better description of the methods applied in the original papers. The comprehensive BMR database provided herein represents a significant step in this direction in that it should facilitate the challenging procedure of data selection.

(2) Even with strong relationships such as the BMR/body mass relationship, the data-selection process can significantly affect the results of a comparative analysis. We demonstrated that unreliable estimates of the BMR mostly tend to overestimate basal rate of metabolism and lead to slightly larger scaling coefficients. The finding of McKechnie & Wolf (2004) that the addition of unreliable BMR estimates leads to a larger scaling coefficient in birds was accordingly corroborated for mammals.

(3) The results of comparative analyses including BMR are especially sensitive to the BMR data-selection process when weak relationships are examined. In such cases, the inclusion of unreliable BMR estimates in a data set may even result in different conclusions. By sequentially removing one or a few species from a data set, the repeated subsampling procedure showed that our brain mass/BMR results are highly sensitive to the particular species that are included in the analyses, to the reliability of the selected data as well as to the sample size. Even when considering only reliable BMR estimates, sample sizes of more than 180 species were required to find a significant relationship consistently between brain mass and BMR among the Mammalia. We conclude that, when weak relationships such as the brain mass/BMR relationship are examined, and when large sample sizes are unavailable (e.g. when restricting an analysis to a particular order), the interpretation of results from comparative analyses demands great caution, even with seemingly significant results.

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VII. REFERENCES

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VIII. SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article.

Figure S1. Reliability distribution among entries in the database.

Table S1. Legend information for the basal metabolic rate (BMR) database provided in Table S2.

Table S2. Basal metabolic rate (BMR) database.

Table S3. Duration required to reach a postabsorptive state in various species feeding mostly on vegetative parts of plants or mostly on other items.

Table S4. Phylogenetic signal in the residuals as depicted by the maximum likelihood (ML) lambda estimated with the SPOILED and SELECT data sets for different clades.

File S1. Mammalian phylogeny used in comparative analyses.

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