# Mammalian metabolism, longevity and parasite species richness

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Basal metabolic rate (BMR) scales allometrically with body mass in mammals, but the reasons why some species have higher or lower metabolic rates than predicted from their body mass remain unclear. We tested the idea that parasite species richness may be a contributory factor by performing a comparative analysis on 23 species of mammals for which data were available on parasite species richness, BMR, body mass and two potentially confounding variables, i.e. host density and host longevity. Parasite species richness was positively correlated with BMR and negatively correlated with host longevity independent of body mass.

**Keywords:** basal metabolic rate; mammals; comparative analysis; independent contrasts method; helminths; parasite species richness

## 1. INTRODUCTION

Parasites may be a major evolutionary force in driving the evolution of life-history traits in their hosts (Hochberg *et al*. 1992). A growing number of empirical and theoretical studies provide strong evidence for the impact of parasites on host population dynamics, host behaviour and sexual selection. Hosts should invest in immunity in order to reduce the damage and reduction in survival that parasites induce but immune function is energetically costly to the host (Sheldon & Verhulst 1996; Lochmiller & Deerenberg 2000). Life-history theory assumes that organisms face trade-offs between allocation to reproduction and survival (Roff 1992; Stearns 1992). Thus, parasites may play an important role in the allocation of energy between immunity, reproduction and survival (Zuk 1996; Nordling *et al*. 1998).

Basal metabolic rate (BMR) is an indicator of the energy expenditure of animals (Koteja 1991) and represents the minimum energetic cost of maintaining the activity of an organism. BMR has been related to a great number of variables such as body mass, dietary habits, reproductive strategies and phylogenetic relatedness. BMR scales with body mass in mammals and some possible reasons for residual variation have been discussed (McNab 1980, 1992; Harvey *et al*. 1991). Recent data have emphasized the importance of energy in maintaining the immune system (see Lochmiller & Deerenberg 2000), but there are no studies which have sought a link between BMR and parasite pressures.

Mammalian species exposed to great and diverse infections, as estimated by the number of potential parasite species, should invest in a high BMR in order to mount a costly immune response. Alternatively, as suggested by Gregory *et al*. (1996), host species with high metabolic rates for their body size may increase their exposure to parasites because a high BMR imposes a higher feeding rate and increased activity. However, if this latter exposure theory is important, we might also find positive rela-

tionships between parasite species richness and both host longevity and host population density as a consequence of the continued accumulation of parasites in long-lived hosts (Bell & Burt 1991) and the rapid accumulation of parasites in hosts living at high population density. Because BMR and immune functions decline intraspecifically with age (Piers *et al*. 1998), we tested the alternative idea that parasites have a negative influence on host longevity, that is hosts suffering from high parasite species richness should have a lower life expectancy. We tested these ideas by statistically investigating the relationships between particular traits of mammals (BMR, longevity, body mass and density) and their parasite species richness.

## 2. METHODS

### (a) *Data on parasites and hosts*

The majority of the sources for sampling effort (the number of hosts investigated), host population density and the numbers of species of parasitic helminths (cestodes, digeneans and nematodes) found in well-studied host populations were those used by Morand & Poulin (1998) (see table 1). The references contributing to the present data set on BMRs and body mass are from McNab (1988) and are given in electronic Appendix A (which can be found at the Royal Society Web site at http://www.pubs.roysoc.ac.uk). Data on maximum host longevity were obtained from various sources (Eisenberg 1981; Gittleman 1986) (see also the references in Stearns (1983) and Read & Harvey (1989)). We obtained information on body mass, BMR, host density, parasite species richness and sampling effort for 31 species of mammals and on host longevity for 23 species.

### (b) *Comparative analyses*

The phylogenetically independent contrasts method (Felsenstein 1985; Harvey & Pagel 1991; Garland *et al*. 1992; Harvey 1996) was developed in order to resolve the problem of non-independence of data (i.e. traits measured across different species) in comparative studies. We used the comparative analysis by independent contrasts (CAIC) computer application (Purvis & Rambaut 1995) for independent contrast analyses. Quantitative data were logarithmically transformed in order to

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Table 1. *List of mammalian species and data used*

(Sources are given in §2(a).)

| host species | host sampling effort | parasite species richness | host density (individuals ha$^{-1}$) | body mass (g) | BMR | longevity (months) |
|---|---|---|---|---|---|---|
| *Arvicola terrestris* | 257 | 10 | 674 | 97 | 112.5 | 18 |
| *Blarina brevicaudata* | 196 | 19 | 621 | 21 | 52.5 | 24 |
| *Clethrionomys gapperi* | 28 | 4 | 1160 | 23 | 46.2 | — |
| *Clethrionomys glaereolus* | 344 | 11 | 1890 | 25 | 58.3 | 18 |
| *Cynomys ludovicianus* | 50 | 2 | 2470 | 1112 | 422.6 | 96 |
| *Didelphis virginiana* | 46 | 12 | 69 | 3257 | 1075.0 | 84 |
| *Dipodomys deserti* | 19 | 2 | 469 | 106 | 92.2 | 66 |
| *Dipodomys merriami* | 199 | 7 | 1209 | 38 | 42.9 | 66 |
| *Dipodomys microps* | 16 | 2 | 1310 | 57 | 66.7 | — |
| *Felis concolor* | 99 | 14 | 0.02 | 41 150 | 10 288.0 | 156 |
| *Hydrochaeris hydrochaeris* | 41 | 8 | 104 | 26 385 | 6596.0 | — |
| *Lepus americanus* | 75 | 10 | 141 | 1581 | 1423.0 | 96 |
| *Lepus californicus* | 69 | 10 | 13 | 2300 | 1311.0 | — |
| *Marmota monax* | 246 | 7 | 616 | 2650 | 662.5 | 56 |
| *Meles meles* | 118 | 8 | 2.82 | 11 050 | 2984.0 | 180 |
| *Microtus longicaudatus* | 49 | 7 | 7500 | 27 | 72.1 | — |
| *Microtus pennsylvanicus* | 127 | 11 | 4040 | 38 | 73.3 | 16 |
| *Mustela erminea* | 62 | 14 | 10.5 | 210 | 310.8 | 84 |
| *Ochotona princeps* | 54 | 8 | 558 | 109 | 166.8 | — |
| *Ochrotomys nuttalli* | 54 | 2 | 351 | 20 | 27.1 | 28 |
| *Odocoileus virginianus* | 129 | 24 | 12.6 | 65 320 | 18 943.0 | 264 |
| *Peromyscus maniculatus* | 280 | 14 | 1060 | 19 | 39.0 | 12 |
| *Rattus rattus* | 116 | 16 | 3650 | 132 | 167.6 | 12 |
| *Sigmodon hispidus* | 355 | 9 | 2220 | 141 | 145.2 | 12 |
| *Sorex cinereus* | 31 | 12 | 1207 | 3 | 29.7 | 23 |

stabilize variance (Harvey 1982). All regressions between contrasts were forced through the origin (Garland *et al.* 1992). In order to verify that contrasts were properly standardized, we performed a regression of the absolute values of standardized contrasts versus their standard deviations (Garland *et al.* 1992) using CAIC. We used a working phylogeny of the mammalian species in the data set which was derived from several sources (see Cooper & Fortey 1998; Morand & Poulin 1998) (figure 1). A positive correlation between parasite species richness and sampling effort has been observed in many studies (Morand 2000). We also found a positive correlation between parasite species richness and sampling effort ($p = 0.0035$ for the 31 species of mammals). It was therefore necessary to control for sampling effort by using the residuals of a regression of species richness on host sample size as corrected estimates of species richness (Gregory 1990; Walther *et al.* 1995; Morand 2000). The phylogenetic information allowed us to compute 19 independent contrasts (the phylogeny contained some unresolved trichotomous nodes). We tested the respective importance of each factor (host density, BMR, body mass and host longevity) on controlled parasite species richness by performing a stepwise regression forced through the origin on all independent variables (Hayes & Shonkwiler 1996).

## 3. RESULTS

A significant and positive relationship was found between the BMR and body mass of mammals ($r = 0.98$ and $p < 0.0001$). A positive correlation was found between the longevity and body mass of mammals ($r = 0.53$ and $p = 0.016$) and a negative one between

density and body mass ($r = 0.57$ and $p = 0.008$). We then controlled host density, host longevity and BMR for host body mass using residuals.

We tested for partial relationships between parasite species richness (controlled for host sample size) and BMR, host density and host longevity (controlled for host body mass) using a stepwise regression on independent contrasts. Parasite species richness (controlled for host sampling size) correlated positively with the BMR (controlled for body mass) ($p = 0.0045$) and negatively with the longevity (controlled for body mass) ($p = 00093$) of mammals ($r^2 = 0.54$ and $p = 0.0014$). There was no relationship between host density and parasite species richness ($p = 0.80$).

The residuals of parasite species richness correlated negatively with host longevity (figure 2a) when controlled for BMR, host body mass and sampling size and correlated positively with BMR (figure 2b) when controlled for host longevity and host body mass.

There was no relationship between the residuals of host longevity (corrected for body mass) and the residuals of BMR (corrected for body mass) ($p = 0.94$), indicating that size-controlled increases in BMR are not incurred at the expense of host longevity. There were no significant relationships between the residuals of host density and either the residuals of host longevity ($p = 0.18$) or the residuals of BMR ($p = 0.78$).

## 4. DISCUSSION

BMR has been widely used in comparisons between mammalian species (Ricklefs *et al.* 1996), but its biological
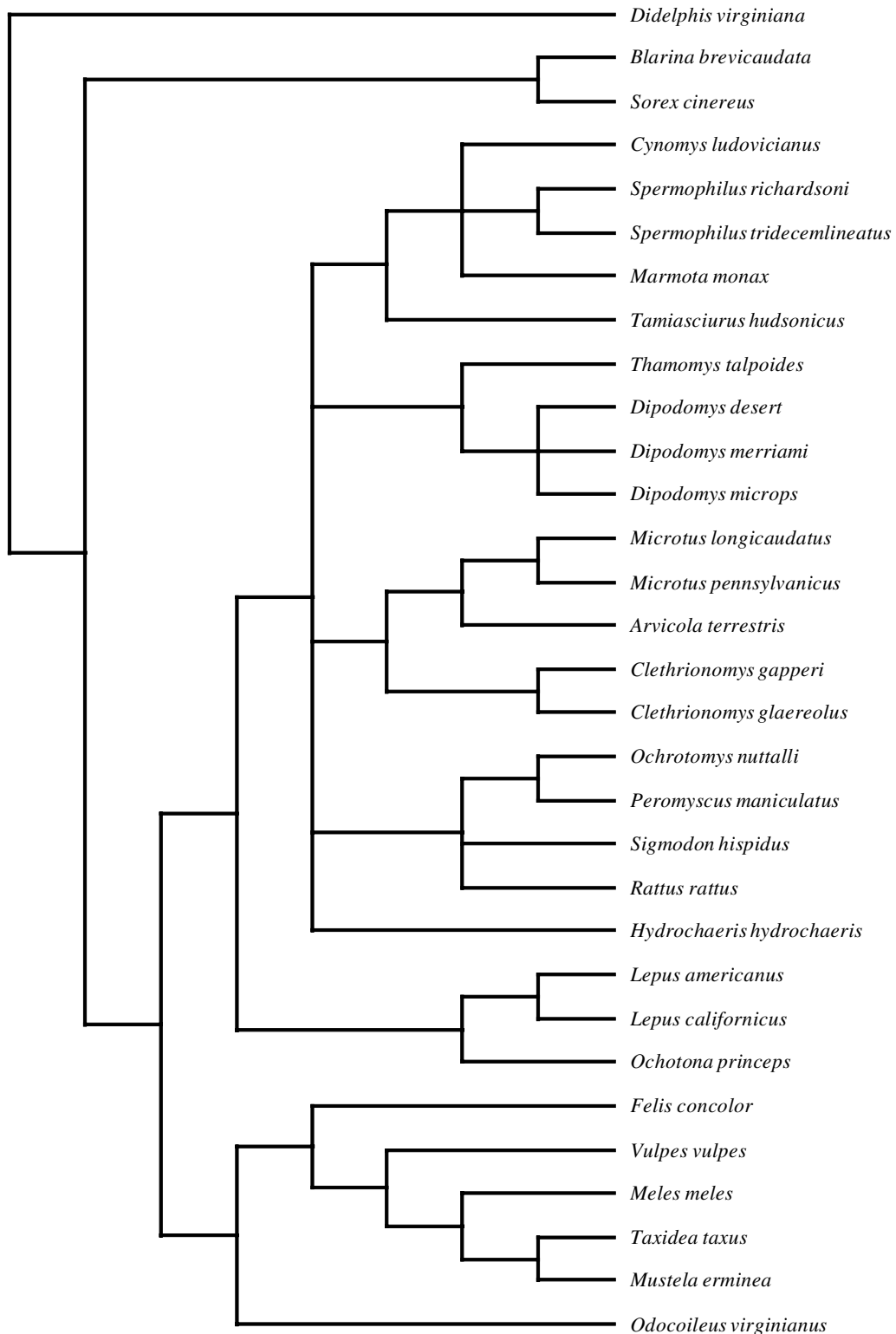
Figure 1. Phylogeny of the mammalian species.

significance is not clearly understood. Considerable attention has been given to explaining variability in BMR in relation to life-history traits in mammals (McNab 1983, 1988; Elgar & Harvey 1987; McNab & Eisenberg 1989; Harvey *et al.* 1991; Ricklefs *et al.* 1996). However, most of such studies have failed to find statistically significant relationships between life-history variation, host diet and

metabolic rates after controlling for the effects of body mass (Harvey *et al.* 1991). Our study shows a significant relationship between BMR and parasite species richness when controlling for potential confounding variables.

Recent comparative studies have attempted to explain parasite species diversity (Morand & Poulin 1998; Gregory *et al.* 1996). Of various determinants, parasite
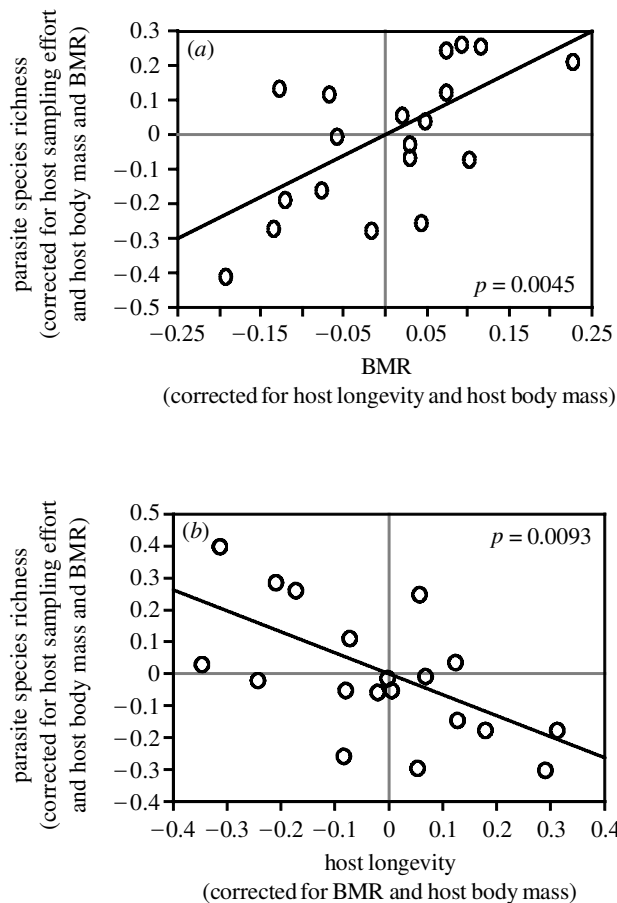
Figure 2. (*a*) Partial relationship between BMRs (controlled for host body mass and host longevity) and parasite species richness (controlled for host sampling effort, host body mass and host longevity) using independent contrasts. (*b*) Partial relationship between host longevity (controlled for host body mass and BMR) and parasite species richness (controlled for host sampling effort, host body mass and BMR) using independent contrasts.

species richness may be a function of the rate of parasite acquisition. Among others, Bell & Burt (1991) hypothesized that high host metabolic rates could increase the probability of acquisition of parasites through increased food intake. Gregory *et al.* (1996) suggested that host species with high metabolic rates for their body size might harbour a greater number of parasite species. However, if this were true, we might also expect to find a positive relationship between host longevity and parasite species richness as a consequence of accumulation of parasites in long-lived hosts (Bell & Burt 1991). In fact, we found the opposite trend. Moreover, we did not find a significant relationship between the residuals of species richness (controlled for the residuals of BMR and host longevity) and host density. This lack of relationship challenges the results of Morand & Poulin (1998) who cited epidemiological models predicting that host density and host longevity allow the maintenance of parasite populations and, thus, the accumulation of parasite species (Poulin & Morand 2000). Our results suggest, to the contrary, that such processes have little influence on the number of parasite species among mammals.

Hamilton (1966) argued that mortality and senescence are likely to be under the influence of evolutionary forces. For instance, it has been shown that ageing may alter the competence of the immune system in controlling parasitic infection (Finch 1990; Albright & Albright 1994). Indeed, our results support the hypothesis that parasites influence the evolution of life-history traits in mammals through the cost of maintaining a competent immune system, a competence that decreases with ageing. However, as suggested by our results, if BMR increases due to a higher allocation to the immune system, the costs do not appear as reduced longevity.

A similar result may be expected to arise between populations (within species) when parasite pressures vary. This could be tested in isolated populations, such as island populations, where the diversity of parasite species richness may be reduced compared to continental situations.

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