Effects of body mass, climate, geography, and census area on population density of terrestrial mammals

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ABSTRACT

Aim The aim of this study was to investigate the effects of climate, geography, census area and the distribution of body mass on the mass : density relationship in terrestrial mammal populations.

Location The areas covered include most major terrestrial biomes including the tropics, savannas, and temperate forests.

Method Data on population density and body mass from 827 populations belonging to 330 different terrestrial mammal species were derived from a review of the literature.

Results LOWESS and polynomial regression analysis indicated that the overall mass : density relationship on log-log scales was not linear and that the slope of this relationship behaves differently across the range of body mass. Body mass explained between 37 and 67% of the variability in population density depending upon the dietary category or the biome group. We also developed two multivariate models that can explain up to 65% of the variability in population density in terrestrial mammals. We also tested for a confounding effect of census area on the mass : density relationship on log-log scales in terrestrial mammals.

Conclusions Our findings support previous studies suggesting that body mass is a major predictor of the variance in population density in terrestrial mammals. We suggest that the non-linearity of the mass : density relationship may result from the fact that the overall distribution of body mass is a mixture of distributions across dietary groups and biomes. In contrast to body mass, our results indicate that climatic and geographical factors have a minor effect on population density. Although census area was closely correlated with body mass, body mass was generally a better predictor of population density than was census area.

Key words Body mass distribution, census area, climate, latitude, macroecology, mass density relationship, precipitation, temperature, terrestrial mammals.

INTRODUCTION

During the past two decades, a number of studies have examined the relationship between body mass (M) and population density (D) across a wide variety of habitats and in various animal groups (e.g. Damuth, 1981, 1987; Blackburn et al., 1990, 1993; Blackburn et al., 1993; Currie, 1993; Silva & Downing, 1995; Blackburn & Gaston, 1997; Silva et al., 1997). However, despite the large number of studies, no consensus has yet been reached regarding various issues associated with the mass : density (M : D) relationship.
Several authors (Damuth, 1981, 1987; Peters & Wassenberg, 1983; Peters & Raelson, 1984; Robinson & Redford, 1986; Macpherson, 1989; Marquet et al., 1990) have found the slope of the M : D relationship on log-log scales to be approximately –0.75. This was taken as evidence that processes associated with energy use are important in generating M : D relationships (Damuth, 1981). Total energy used by a population can be estimated by multiplying D by average individual metabolic rate (e.g. Damuth, 1981, 1987; Brown & Maurer, 1986; Silva & Downing, 1995). The allometric relationship between M and metabolic rate (R) typically has an exponent of 0.75 on log-log scales, suggesting that if the exponent of the M : D relationship is approximately –0.75, then the total energy used (E) by a population would be independent of M (or E = R × D = M^{0.75} × M = M^0) (Damuth, 1981, 1987). This conclusion is now known as the energetic equivalence rule (Damuth, 1981). However, other studies have provided evidence suggesting that mammalian species do not always conform to this rule (e.g. Peters & Raelson, 1984; Marquet et al., 1995; Silva & Downing, 1995).

For instance, Silva & Downing (1995) found a non-linear relationship between log D and log M where the slope value varies across the range of M covered by terrestrial mammals, implying that a single slope value may be inappropriate. However, Griffiths (1995) pointed out the possibility that Silva & Downing’s (1995) trend may partially be an artefact of the smoothing procedure.

Another issue that is intensively debated is the necessity of standardizing D or M by actual census area (Blackburn & Gaston, 1996a, 1999a,b; Smallwood et al., 1996; Johnson, 1999). The census area mechanism suggests that small-bodied species are generally censused across smaller areas than large-bodied size species. Consequently, M : D relationships may result partially from differences in survey area among studies from which density estimates are gathered (Blackburn & Gaston, 1996a, 1999a, 1999b; Smallwood et al., 1996). When examining the M : D relationship in mammalian carnivores, Smallwood et al. (1996) found a strong relationship ($r^2 = 0.46$) between M and D with an exponent of –0.76. However, the effect of M on D became insignificant after the effect of census area on D was removed from the analysis. Similarly, Blackburn & Gaston (1996a) found a strong M : D relationship ($r^2 = 0.70$) with an exponent of –0.74 in mammalian herbivores, but only a weak relationship between M and D ($r^2 = 0.07$) with a shallower exponent (–0.27) after the effects of census area on D were considered in the analysis. Johnson (1999) argued that a solution to solve this problem may be to adjust the study area to the density of the population being surveyed. However, he also pointed out that this may also produce correlations between census area and the residual variation of density around the M : D relationship.

It is also possible that much of the disagreement between previous studies regarding the slope value may be associated with differences in body sizes of community members and/or underlying M distributions across trophic levels, spatial scale or biomes (e.g. Brown & Nicoletto, 1991; Loder et al., 1997; Griffiths, 1998; Marquet & Cofré, 1999). Griffiths (1998) pointed out that overall M : D relationships may result from a mixture of component relations with exponents that differ from the overall exponent as distributions of M are rarely uniform. Furthermore, the distributions of body masses of terrestrial mammals can also vary depending upon the spatial scale of the study. Brown & Nicoletto (1991) found that the distribution for the entire North American continent was highly modal and right-skewed, those for local habitats were uniform, and those for the biomes were intermediate between the one for the continent and those for the local habitats. Marquet & Cofré (1999) showed that, in general, these patterns also hold for the body size distribution of terrestrial mammals in South America. In addition, it has also been suggested that M : D relationships can vary depending on body sizes of community members and the range of sizes (Currie, 1993; Silva & Downing, 1995). This suggests that M : D relationships may be quite different for mammals belonging to different trophic groups, found in different biomes, or showing different M distributions.

Although controversy surrounds various issues associated with the M : D relationship, most studies agree that there is a considerable amount of variability in D left unexplained by variations in M. In terrestrial mammals, D varies between 3 and 4 orders of magnitude at any given M and generally accounts for about 40–70% of the logarithm of this variance (e.g. Damuth, 1981, 1987; Peters & Raelson, 1984; Robinson & Redford,
This suggests that a large amount of the variability in mammalian density may be related to variations between populations resulting from the influence of other factors. In addition to M, other biotic factors have also been found to account for some of the variability in mammalian densities (Clutton-Brock & Harvey, 1977; Peters & Raelson, 1984; Robinson & Redford, 1986; Damuth, 1987, 1993; Silva & Downing, 1995). In virtually all of these studies, trophic level has been reported to be the most important factor beyond M affecting mammalian abundance (e.g. Robinson & Redford, 1986; Silva & Downing, 1995; Silva et al., 1997). It has also been suggested that phylogenetic relatedness between the species may also influence population density and the M : D relationship (e.g. Harvey & Pagel, 1991; Nee et al., 1991; Cotgreave & Harvey, 1992, 1994). However, the consideration of phylogenetic relatedness between species in macroecological studies is still a controversial issue. For British birds, Nee et al. (1991) showed that although across species the relationship between M and D was negative, no significant relationship between these two variables occurred when the taxonomic groups were examined separately. However, it has been argued that phylogenetic methods favour explanations based on phylogeny at the expense of explanations based on ecology (Westoby et al., 1995a, 1995b, 1995c). Phylogenetic relationships provide information on what happened millions of years ago while population abundance is controlled by events that happen on a much shorter time scale (Cotgreave, 1995). Ricklefs & Starck (1996) also argued that phylogenetic methods tend to result in weak correlations and broad confidence limits around parameter estimates obtained in macroecological studies.

In contrast to M or trophic level, the influence of local environmental conditions such as energy availability or climate on the relationship between M and D has received little attention even though field studies have shown their effect on average population abundance to be important (e.g. Caughley, 1964; Churchill, 1991; Roberts & Dunbar, 1991). An explanation may be that most prior studies have investigated the M : D relationship at the species level rather than population level, thus local environmental conditions could not be examined. Another reason is that measures of energy availability (e.g. productivity, food production) are rare in the mammalian literature and even rarer when coupled with detailed studies of mammalian abundance. However, several studies have shown that primary productivity and habitat vegetation are strongly correlated with climatic factors such as precipitation and temperature (e.g. Rosenzweig, 1968; Phillipson, 1973; Whittaker, 1975; Coe et al., 1976; Fritz & Duncan, 1994). This suggests that climatic factors can be used as surrogates for energy availability to mammals and may account for some of the variability in D. Currie & Fritz (1993) investigated the effect of various climatic factors on D in 135 mammalian populations and found this to be negligible after accounting for M. They also found that D declines with increasing evapotranspiration, suggesting that habitats of low primary productivity may support greater mammal densities than those of high productivity. However, theoretical arguments suggest that available energy may limit the carrying capacity of habitats (e.g. Hutchinson, 1959; Brown, 1981), suggesting the possibility that in energy-rich habitats mammalian populations would reach higher densities. Support for this hypothesis comes from studies that have reported differences in densities at the species level between temperate and tropical mammals of similar M (Peters & Raelson, 1984; Damuth, 1987).

Geographic descriptors such as latitude, longitude or altitude often combine both geographical and climatological information regarding environmental conditions surrounding animal populations. Although the effects of both longitude and altitude on D have rarely been investigated in macroecological studies, several studies have provided some controversial information regarding the effects of latitude on mammalian abundance. On one hand, some studies have shown that mammalian diversity is high at low latitudes (e.g. Baker, 1967; Fleming, 1973; Wilson, 1974; Rapoport, 1982; Stevens, 1989), suggesting that niche space may be small for populations inhabiting the tropics. On the other hand, the combined effect on population density of high levels of both primary productivity and species diversity may result in no latitudinal variations in D (Blackburn & Gaston, 1996b,c; Johnson, 1998). If niche space is limited in the tropics, one possible trend for the effect of latitude on D is that mammal populations inhabiting the tropics maintain lower densities than those occurring at higher latitudes.
where competition for niche space may be less important. Recently, Johnson (1998) examined distribution and abundance in Australian mammals and found a significantly positive correlation between D and latitude. In addition, Cot greave & Stockley (1994) found that communities of insectivores near the equator show less strongly negative relationships between population abundance and M than those occurring at high latitudes, suggesting that the strength of the correlation between M and D may also be subject to latitudinal variations. Support for the idea of no latitudinal variations in D comes from Currie & Fritz (1993), who found that latitude had a minor effect on D after accounting for variations in M, suggesting that latitudinal variations in animal abundance are weak. In the light of these studies, it is presently not clear whether latitude has an effect on D.

The goal of this study is to examine the general relationship between M and D at the population level in terrestrial nonvolant mammalian species. We will investigate the effects of climate and geography on mammalian population density as reflected in dietary categories and terrestrial biomes. In particular, we predict that differences in M : D relationships would reflect differences in M distributions between trophic categories and terrestrial biomes. We will also test for a confounding effect of census area on the M : D relationship in terrestrial nonvolant mammalian species.

METHODS

Data

Data on D (individuals/km²) and M (kg) were obtained from a database derived from a systematic review of the literature described in detail elsewhere (Silva & Downing, 1995). Based on their food habits, populations were classified into three dietary categories: herbivores, insectivores and carnivores. Information on food habits was obtained from individual population studies or from related works (Eisenberg, 1981; Nowak, 1991). Census area estimates (A; km²) were also obtained from individual population studies. The entire dataset and reference list used in this study are available on request from M. Silva.

Global biomes (taiga, desert, savanna, grassland, tropical dry forest, temperate dry forest, tropical rain forest and temperate rain forest) of studied populations were determined using Whittaker’s (1975) protocol. This classification is based on zones of temperature and precipitation. For example, taiga and desert are differentiated on the basis of temperature while grassland and temperate dry forest are primarily differentiated on the basis of precipitation. Average annual temperature (°C) and total annual precipitation (mm) data were taken directly from population studies when published or from a world climatic database (Wernstedt, 1972). Geographic information such as latitude (°), longitude (°) and altitude (m) of study sites were obtained from population studies, or were estimated from geographical site descriptors. As a major purpose of this study was the investigation of the effects of both climate and geography, we excluded from our dataset populations for which we could not ascertain geographical location (latitude and longitude) and at least one climatic variable.

Analysis

D, M and A values were transformed logarithmically to reduce heteroscedasticity (Gujarati, 1978). The data were analysed using various graphical and statistical procedures. Graphical analyses included non-parametric techniques such as kernel density-based histograms (Wand & Jones, 1995) and locally weighted sequential smoothing (LOWESS; Cleveland, 1979). LOWESS is a non-parametric local least squares graphical procedure that was developed to be a robust means of finding patterns in refractory data (Cleveland & McGill, 1985). In this study, LOWESS is used to help determine the unbiased form of the relationship between M and D both overall and across biomes and trophic groups. Polynomial regression analysis was used to assess the statistical significance of non-linearities detected by LOWESS. M distributions were examined for log-normality using the Wilk-Shapiro test, the Kolmogorov–Smirnov test and the chi-square test (Sokal & Rohlf, 1981; Zar, 1996).

Multivariate cluster analysis employing a centroid-based selection procedure was used to examine correlations and clusters between variables. The centroid approach is a common measure of nearness that uses distances based on Pearson correlation values to group the variables by degree of similarity (Johnson & Wichern, 1992). Clusters apparent
in the Pearson correlation matrix itself will for
the most part be apparent in the dendrogram plot
which reflects a broad multiple-correlation setting.
In addition, multiple regression models were also
developed to examine the relationship between D
and explanatory variables. Since census area values
were available for approximately 46% of the studies
comprising the database, we present the results of
these analyses separately.

It is important to underline that phylogenetic
methods focus on the variation found among
species rather than among populations. However,
for a given species both body mass and popu-
lation density can vary depending on various
factors including climatic conditions and food
availability. In particular, population density of a
given species can vary by more than three orders
of magnitude across its range of distribution.
For example, the impala (Aepyceros melampus)
average population densities vary from 0.02/km²
in Kafue National Park (Dowsett, 1966) to 49.7/km²
in Akagera National Park (Montfort, 1972). Since
one of the main objectives of this study was to
investigate the effects of climatic conditions and
geographical location, the use of data on mam-
malian populations rather than species averages
was fundamental. In this study, therefore, we have
not attempted to use any phylogenetic method
because accurate information to reconstruct phylo-
genetic relatedness among populations within
mammalian species does not yet exist.

RESULTS

The collected data were for 827 distinct populations
belonging to 330 different terrestrial mammal
species covering the range of M from 0.0026 to
3000 kg. The database included species from 16
different mammalian orders (Wilson & Reeder,
1992) and eight different terrestrial biomes. D varied
from 0.004 to 12 500 ind/km² and followed an
overall log-normal distribution (Wilk–Shapiro;
Kolmogorov–Smirnov; χ², P > 0.05).

Effects of body mass

Overall, the distribution of M did not differ
significantly from a log-normal distribution (Wilk–
Shapiro, Kolmogorov–Smirnov, χ², P > 0.05) (Fig. 1).
However, when populations were separated on
the basis of dietary categories, the shape of M
distributions differed significantly from each
other as well as from the log-normal distribution
(Fig. 1). For herbivores, the M distribution dif-
fered significantly from the log-normal distribution
(Wilk–Shapiro and χ², P < 0.01). Moreover,
Kernel density plots showed some evidence that
the M distribution of herbivores may be bimodal
with one mode at about 0.01–0.1 kg and another
at 10–100 kg (Fig. 2). For insectivores, the ana-
lyses were inconclusive. While the Wilk–Shapiro
test supported the log-normal distribution (P > 0.05),
the chi-square test indicated that the M distribu-
tion of insectivores differed significantly from the
log-normal distribution (P < 0.05). Our analyses
also indicated that the M distribution of carnivores
was not statistically distinguishable from the log-
normal distribution (Wilk–Shapiro and χ², P >
0.05). M distributions for biomes for which the
sample size was sufficiently large (n = 30) were also
examined. With the exception of the temperate
rain forest, none of these distributions were log-
normal (Fig. 3). Although some of these differ-
ences may reflect differences in sample size, they
may also reflect differences in species composition.

Log M was a useful predictor of Log D in
terrestrial mammals, explaining about 59% of the
variability in Log D when all mammals were
pooled together (Table 1). However, LOWESS
and polynomial regression analysis indicated that
the overall Log M : Log D relationship is non-linear,
suggesting that the slope of this relationship
behaves differently across the range of M-values
(Fig. 4, Table 1). With the exception of insect-
ivores, the coefficient of Log M (Table 1) differed
significantly from –1 (95% confidence intervals)
for all mammals and across dietary groups.
LOWESS and polynomial regression analyses also
showed significantly non-linear relationships for
both herbivores and insectivores, suggesting that
both the slope and the correlation value of the
Log M : Log D relationship varies among dietary
groups. For instance, the correlation between
Log M and Log D appeared to be stronger in carni-
vores than in any other dietary group. Analysis
of the Log M : Log D relationship across biomes
(n = 30) also resulted in various non-linear rela-
tionships and different correlation values (see
LOWESS lines in Fig. 5). Log M alone explained
between 37 and 62% of the variability in Log D
across biomes. Furthermore, the slopes of these
relationships were all significantly different from
–1 (95% confidence limits of the slopes; Fig. 5). However, no significant differences in slope value were found between tropical and temperate biomes (test for homogeneity of slopes; $P > 0.05$).

**Effects of climate and geography**

Log D was significantly correlated with various explanatory variables (Table 2). Log M was also strongly correlated with most of the other explanatory variables, with the exceptions of precipitation and altitude. Cluster analysis showed that Log D is more strongly correlated with both latitude and altitude than it is with Log M, although underlying latent variables may be relevant here (Fig. 6a). In fact, it takes the inclusion of diet in the analysis to bring Log M and Log D closer together (Fig. 6b).

Using multiple regression, we developed two models that fit the overall data (Table 3). Although the effect of Log M was included in both models, the Log M : Log D relationship was linear in Model I, while in Model II the variable Log M was non-linearly related to Log D. Besides M, only the effects of diet and biome were found to be significant in Model I. While the non-linear component was statistically significant, Model II explained only approximately 1% more of the variation in Log D than Model I (Table 3), and approximately 3% more than the model including exclusively Log M (see Table 1).

**Effects of census area**

Census area values ($A$) were available for 377 populations (approximately 46%) comprising the database. The distribution of log $A$ values followed an overall log-normal distribution (Wilk–Shapiro and $\chi^2$, $P > 0.05$). Lack of inclusion of census values seems a random but pervasive phenomenon.

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**Fig. 1** Frequency distributions of $\log_{10}$ transformed body masses (kg) for all mammals ($n = 827$), herbivores ($n = 675$), insectivores ($n = 91$), and carnivores ($n = 61$).
across the studies included in the database, suggesting that no undue selection bias was induced by incorporating census values. Log M explained between 52% and 62% of the variation in Log D (Table 4). Although LOWESS indicated some non-linearities (Fig. 7), the polynomial regression analysis did not detect any significant ($P > 0.05$) curvilinearity in the Log M : Log D relationship either for all mammals or across dietary groups. Therefore, it is difficult to affirm that the non-linearities in the Log M : Log D relationships may be a consequence of census area for this particular dataset. Our analyses also showed that the residuals of the Log M : Log D relationships were still significantly correlated with log A (except for insectivores) even though the correlations were weak (Table 4). The relationship between log A and Log D were also statistically significant, but log A was generally a weaker predictor of Log D than was Log M. Furthermore, the residuals of the log A : Log D relationships were significantly correlated with Log M, although the slope was significantly shallower than −0.75 both for all mammals and herbivores, but not for insectivores and carnivores (95% confidence intervals). The best multivariate model including census area and other explanatory variables ($Log D = -0.008 – 0.608 \cdot Log M - 0.160 \cdot \log A + 0.003 \cdot Longitude + 1.715 \cdot 10^{-4} \cdot \text{Altitude} + 0.144 \cdot \text{Biome} + 0.036 \cdot \text{Temperature} - 0.367 \cdot \text{Diet}; n = 275; r^2 = 0.66; all P-values < 0.02$) explained approximately 13% more of the overall variation in Log D than the model including exclusively Log M (see Table 5).

**DISCUSSION**

Our findings showed that Log M alone can predict between 37% and 67% of the variability in Log D depending upon the dietary category or biome group. Although other factors not examined in
this study may also explain a high proportion of the variance in mammalian population density, our findings support previous studies suggesting that $M$ is a major predictor of the variance in $D$ in terrestrial mammals (e.g. Peters & Raelson, 1984; Damuth, 1987; Currie & Fritz, 1993). This may suggest that the size of a mammal’s body puts a more determining limit on mammalian

Fig. 3 Frequency distributions of $\log_{10}$ transformed body masses (kg) of terrestrial mammals occurring in various biomes. Biomes included are only those for which $n = 30$. $D_W$ is the Kolmogorov–Smirnov statistic and ‘$p$’ is the probability associated with $D_W$. 

population abundance than any other environmental factor examined in this study.

This study also provides evidence supporting the idea that the slope of the Log M : Log D relationship varies across the range of M (Brown & Maurer, 1989; Silva & Downing, 1995), suggesting that the Log M : Log D relationship is not linear. Although we did not examine E in

Table 1 Relationship between the logarithm of population density (Log D; ind/km$^2$) and the logarithm of body mass (Log M; kg) in mammals of various dietary categories. Models were developed using polynomial regression analysis. Only coefficients significantly different (P < 0.05) from zero are shown. $r^2$ is the coefficient of determination of the models and n is the sample size.

<table>
<thead>
<tr>
<th>Group</th>
<th>Model</th>
</tr>
</thead>
<tbody>
<tr>
<td>All mammals</td>
<td>$\log D = 1.36 - 0.83(\log M) - 0.05(\log M^2) + 0.04(\log M^3)$</td>
</tr>
<tr>
<td></td>
<td>$\text{SE}_{\log M} = 0.039 \quad r^2 = 0.5868 \quad n = 827$</td>
</tr>
<tr>
<td>Herbivores</td>
<td>$\log D = 1.43 - 0.68(\log M)$</td>
</tr>
<tr>
<td></td>
<td>$\text{SE}_{\log M} = 0.021 \quad r^2 = 0.6113 \quad n = 675$</td>
</tr>
<tr>
<td>Insectivores</td>
<td>$\log D = 0.90 - 0.89(\log M) - 0.14(\log M^2)$</td>
</tr>
<tr>
<td></td>
<td>$\text{SE}_{\log M} = 0.116 \quad r^2 = 0.4971 \quad n = 91$</td>
</tr>
<tr>
<td>Carnivores</td>
<td>$\log D = 1.41 - 1.83(\log M) - 0.34(\log M^2) + 0.28(\log M^3)$</td>
</tr>
<tr>
<td></td>
<td>$\text{SE}_{\log M} = 0.297 \quad r^2 = 0.6742 \quad n = 61$</td>
</tr>
</tbody>
</table>
this study, the systematic changes observed in the slopes of the Log M : Log D relationships can be seen as evidence that small and large mammals differ in terms of energy used. Silva & Downing (1995) suggested various explanations for the significant differences in energy use within terrestrial mammals including that population densities of very small mammals may be limited by the...
energetic costs associated with living near to the ultimate body size constraints imposed by the energetics of homeothermy. At the other end of the body size spectrum, it is possible that large mammals may make more efficient use of resources or, perhaps, that populations of extremely large mammals that have persisted at extremely low densities may simply have been driven to extinction. Support for the non-linearity of the Log M : Log D relationship found in this study also comes from empirical and theoretical analysis that have reported allometric scaling of various ecological traits (e.g. continental population extinction of species) that are not monotonically related to M (Pimm, 1992; Marquet et al., 1995; Marquet & Taper, 1998).

Our analyses also showed that the non-linearity of the Log M : Log D relationship may be more than an artefact of the smoothing (LOWESS) procedure. Differences in M distribution may affect the slope value of Log M : Log D relationships because it has been shown previously that body sizes of community members as well as the range of sizes can affect M : D relationships (Currie, 1993; Silva & Downing, 1995). These results also provide support for Griffiths’s (1998)
idea that some of the disagreement between previous studies may result from differences among M distributions (e.g. Damuth, 1981, 1987; Peters & Raelson, 1984; Robinson & Redford, 1986; Silva & Downing, 1995). Although in most macroecological studies the range of body mass of non-volant terrestrial mammals is covered adequately, the datasets generally differed in terms of both species composition and the fraction of the world’s terrestrial mammals that are included. Many of these studies are based on compiled data from different communities and therefore may be subject to large sampling and selection biases. In addition, studies of mammalian communities are often limited to taxonomically related species (e.g. Chew & Chew, 1970; Freese et al., 1982; Brown, 1984) or may reflect the interests of the investigator (e.g. Bourlière, 1961; Peres, 1990).

Table 3 Models describing the statistical effect of body mass (Log M; kg), climate and geography on population density (Log D; ind/km²) in terrestrial mammals. Models were developed using Stepwise multiple regression. Only coefficients significantly different ($P < 0.05$) from zero are shown. Latitude (Lat) is absolute latitude ($\circ$) and (P) is total annual precipitation (mm). $n$ is the sample size and $r^2$ is the multiple coefficient of determination.

<table>
<thead>
<tr>
<th>Model</th>
<th>Log D =</th>
<th>Coefficients</th>
<th>$R^2$</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>1.15 - 0.668 Log M - 0.42 Diet + 0.061 Biome</td>
<td>$n = 666$</td>
<td>0.61</td>
<td>$P &lt; 0.001$</td>
</tr>
<tr>
<td>II</td>
<td>1.33 - 0.802 Log M - 0.055 Log M² + 0.039 Log M³ - 0.402 Diet + 0.004 Lat + 4 x 10⁻⁴ P</td>
<td>$n = 666$</td>
<td>0.62</td>
<td>$P &lt; 0.001$</td>
</tr>
</tbody>
</table>

1 All coefficients are significant at $P < 0.001$ except Log M² ($P = 0.018$), Lat ($P = 0.026$), and P ($P = 0.021$).

Table 4 Ordinary least squares regressions (OLS) of Log M (kg) on Log D (ind/km²) and log A (km²) on Log D for populations for which census area values were available ($n = 377$). We also present the results of OLS for the relationship between the residuals of Log M : Log D relationships (relationship 1) and log A, as well as the relationship between the residuals of log A : Log D (relationship 2) and Log M for all mammals and across dietary groups.

<table>
<thead>
<tr>
<th>Group</th>
<th>Log M : Log D</th>
<th>log A : Log D</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>a ± SE</td>
<td>$r^2$</td>
</tr>
<tr>
<td>All mammals ($n = 377$)</td>
<td>1.271 ± 0.685 ± 0.034</td>
<td>0.52</td>
</tr>
<tr>
<td>Herbivores ($n = 313$)</td>
<td>1.420 ± 0.713 ± 0.036</td>
<td>0.55</td>
</tr>
<tr>
<td>Insectivores ($n = 27$)</td>
<td>0.735 ± 0.836 ± 0.153</td>
<td>0.55</td>
</tr>
<tr>
<td>Carnivores ($n = 37$)</td>
<td>1.060 ± 1.309 ± 0.175</td>
<td>0.62</td>
</tr>
</tbody>
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<table>
<thead>
<tr>
<th>Group</th>
<th>Residuals of Log M : Log D and log A</th>
<th>Residuals of log A : Log D and Log M</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>a ± SE</td>
<td>$r^2$</td>
</tr>
<tr>
<td>All mammals ($n = 377$)</td>
<td>0.186 ± 0.113 ± 0.033</td>
<td>0.03</td>
</tr>
<tr>
<td>Herbivores ($n = 313$)</td>
<td>0.171 ± 0.097 ± 0.033</td>
<td>0.03</td>
</tr>
<tr>
<td>Insectivores ($n = 27$)</td>
<td>0.097 ± 0.129 ± 0.138</td>
<td>0.03</td>
</tr>
<tr>
<td>Carnivores ($n = 37$)</td>
<td>0.457 ± 0.343 ± 0.163</td>
<td>0.16</td>
</tr>
</tbody>
</table>

a, Intercept; b, slope; SE, standard error of the slope; $r^2$, coefficient of determination; $P$, probability that the correlation could occur by chance alone; $n$, sample size.
**Fig. 7** Relationship between the log_{10} of body mass (Log M) and the log_{10} of population density (Log D) for terrestrial mammal populations for which census area values were available (n = 377). The curves represent LOWESS fits (tension 0.5) to the data.

**Table 5** Models describing the statistical effect of Log M (kg), census area, climate and geography on Log D (km²) in terrestrial mammal populations for which census area values were available (n = 377). Models were developed using Stepwise multiple regression. Only coefficients significantly different (P < 0.05) from zero are shown. Latitude (Lat) is absolute latitude (°) and precipitation (P) is total annual precipitation (mm). n is the sample size and $r^2$ is the multiple coefficient of determination.

<table>
<thead>
<tr>
<th>Group</th>
<th>Model</th>
<th>$r^2$</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>All Mammals</td>
<td>Log D = −0.608 Log M − 0.160 log A + 0.003 Long + 1.715 × 10⁻⁴ Alt + 0.144 Biome − 0.367 Diet + 0.036T</td>
<td>0.66</td>
<td>275</td>
</tr>
<tr>
<td>Herbivores</td>
<td>Log D = 0.638 − 0.186 log A − 0.601 Log M + 0.006 Long + 2.596 × 10⁻⁴ P</td>
<td>0.66</td>
<td>227</td>
</tr>
<tr>
<td>Insectivores</td>
<td>Log D = 1.004 − 0.037 Lat − 0.525 log A − 0.935 Log M</td>
<td>0.78</td>
<td>22</td>
</tr>
<tr>
<td>Carnivores</td>
<td>Log D = −0.781 − 0.834 Log M + 0.265 Biome + 8.198 × 10⁻⁴ Alt</td>
<td>0.74</td>
<td>26</td>
</tr>
</tbody>
</table>

and not the species that are really present in the study area. This finding may also explain why slope values can vary when individual mammalian communities are analysed separately (for example see Table 3 in Silva & Downing, 1995). Mammalian communities generally differ in species composition, thus we can expect that they would also differ in M distribution. Although this does not necessarily mean that they would differ in Log M : Log D relationships, our findings suggest that communities may show differences in M : D relationships depending on the trophic groups and body sizes of community members, the M distribution, as well as the terrestrial biome where they occur.

In contrast to M, climatic and geographical factors have a negligible effect on D, suggesting that environmental conditions may be poor predictors of abundance in mammalian populations. Similar results were found by Currie & Fritz (1993) who also investigated the joint effects of climate and geography on mammalian population density and energy use. Since many ecological variables and processes are scale-dependent, with patterns and processes at one scale not applying to other scales, it is possible that although field studies have shown that variables such as altitude and climatic conditions affect population density (e.g. Caughley, 1964; Churchill, 1991), this cannot be extrapolated to a larger spatial scale. Another explanation may be that since M is significantly correlated with most of the geographical and climatic factors examined here, some of the variability in D explained by M may result from climatic and/or geographical differences among habitats occupied by populations. Currie & Fritz (1993) also reported significant correlations between M and some of the explanatory variables examined in their study.

The significant positive relationship between D and latitude reported in our analyses indicates that D increases with increasing latitude. This result concurs with Johnson’s (1998) findings on the effects of latitude on the abundance of Australian mammals. As Johnson (1998) suggested, the simplest explanation for this trend is that since at low latitudes species diversity is high and niche space is possibly restricted, the spatial density of mammal populations in tropical areas may be limited by the interaction between these two factors. It is also possible that higher climatic stability in the tropics may allow mammal populations to sustain themselves at minimal densities that are lower than minimal densities sustainable in temperate climates (Silva & Downing, 1994). Our findings also showed a negative relationship between Log M and latitude, as reported by Currie & Fritz (1993). This may reflect the fact that tropical studies in our dataset focused on large-bodied species (Blackburn & Gaston, 1999a). It is interesting to mention, however, that the mean Log M did not differ significantly between the biomes for which \( n \geq 30 \); the only exception was the savanna biome for which the mean Log M was significantly greater than that of other biomes (ANOVA and Tukey’s multiple comparison test; \( P > 0.05 \)). It is also possible that our findings reflect the current patterns of geographical distribution of mammalian species. A substantial fraction of the large mammalian fauna of various regions of the world including northern Eurasia, North America and southern South America have disappeared since humans started to expand their geographical range (e.g. Brown, 1995; Brown & Lomolino, 1998). Not only is the global species diversity in mammals the highest at low latitudes, partially explaining why more species are found at these latitudes including large-bodied ones, but it is also where large-bodied mammals are currently the most abundant and diverse.

Considerable attention has recently been focused on the effects of census area on the M : D relationship (e.g. Blackburn & Gaston, 1996a, 1999a, 1999b; Johnson, 1999). It was felt that undue bias had not been induced by this restriction as the inclusion of census area in reported studies seemed a random phenomena. Although the models incorporating census area gave a much improved overall fit of the M : D relationship, especially for secondary consumers such as insectivores and carnivores, our findings do not confirm previous studies (e.g. Blackburn & Gaston, 1996a; Smallwood et al., 1996) suggesting that census area is a better predictor of the density of a mammalian species than is its body size. It is difficult to explain why our results would differ from these studies, but one possibility is that our study is based on population abundances rather than species averages. The close correlation of census area and body mass values both overall and across all dietary levels raises a serious difficulty in the interpretation that can
be offered for such results. Type of species and therefore expected body mass are often predetermined aspects of abundance studies reflecting investigator interest (Johnson, 1999). This would seem to imply that census area would often be a predetermined component and most probably a component expected to be highly correlated with body mass. This was observed in this database, obscuring the use of census area as a clearly interpretable element of species-abundance models. Here, the inclusion of both density and census area as distinct variables in the regression analysis explaining body mass leads to this difficulty. Previous studies on the patterns of variation in population density have been dominated by the effects of M and to a lesser extent diet, because these two variables explain a large portion of the variation in density of mammals both at the population and the species level. Our findings show that variables such as temperature, precipitation, and latitude only have a minor and often non-significant effect on D. On the other hand, it seems clear that an issue which needs more careful consideration is the relationship between the distribution of M and the slope value of the Log M : Log D relationship. Although other factors not yet examined may explain the differences in slope values between or within studies, a rigorous analysis of the implications that M distributions may have on allometric studies appears to be needed.

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Patterns of population density


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