Diet and body temperature in mammals and birds

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Keywords: **Energetics, macroecology, macrophysiology, metabolism, mammal, reptile, bird, fish, endothermy**

ABSTRACT

Aim We test the hypothesis that endotherm body temperature varies with diet.

Location Global terrestrial ecosystems

Methods We compile data from the literature on diet and body temperature in mammals and birds. We analyse these and demonstrate global macrophysiological patterns.

Results In mammals, carnivores overall have a lower mean body temperature (T_b) than either herbivores or omnivores. However within carnivores, those taking vertebrate prey have a higher mean T_b than predators of invertebrates. Among herbivores, species eating grass, leaves or seeds have the highest mean T_b, those taking fruit an intermediate mean T_b and those taking flowers or nectar the lowest mean T_b. These patterns are robust to the influence of body mass and phylogenetic non-independence. In birds the relationship between T_b and diet is complicated by a significant inverse relationship between body mass and T_b and strong dietary niche conservation within lineages. After allowing for body mass, herbivores show an identical qualitative pattern to mammals, whereas carnivores show the opposite trend to mammals: those taking invertebrate prey have a higher mean T_b than those taking vertebrates.

Main conclusions There is a relationship between diet and T_b in mammals that is statistically and phylogenetically robust. Published studies show that in reptiles and fish herbivory is largely confined to species that can maintain a relatively high T_b either through living in warm environments or through behavioural thermoregulation. We therefore propose a general relationship for all vertebrates: herbivory requires a warmer body than carnivory. Basal metabolic rate (BMR) will then be higher in herbivores because of the universal relationship between BMR and T_b, together with the higher maintenance costs of their longer guts. We suggest that the evolution of endothermy was a key factor in the widespread incidence of herbivory in mammals.

INTRODUCTION

It has been known for a long time that the basal metabolic rate (BMR) of mammals is correlated with their diet (McNab 1992, 2008), and similar patterns have also been detected in field metabolic rate (Speakman 2000).

Recently Clarke et al. (2010) re-examined the relationship between BMR and body mass, incorporating body temperature, T_b, in the statistical model. This confirmed previous suggestions of a curvilinear relationship between body mass and BMR (Heusener 1985; Lovegrove 2003; Glazier 2005) and also the marked dependence of BMR on body temperature (White & Seymour 2003, 2004, 2005). Interestingly, the well established relationship between BMR and diet (McNab 1992, 2008) vanished when body temperature was included in the model (Clarke et al. 2010). The cause was a strong covariance between body temperature and diet, and this suggested the possibility that the underlying relationship was between diet and body temperature, with BMR responding through its dependence on T_b.

Here we explore the relationship between diet and body temperature in mammals in more detail. Specifically we test the hypothesis that herbivory requires a higher body temperature than carnivory. We extend the analysis to include birds, compare the results with published studies of reptiles, amphibians and fish, and propose a general macrophysiological relationship for all vertebrates.

METHODS

The data sets comprised body mass, body temperature and diet. The data for body temperature (T_b) came from previous studies of the scaling of body temperature (Clarke & Rothery 2008) and BMR (Clarke et al. 2010).

Data for diet and the mean environmental temperature within the range for each mammalian species in our data set were downloaded from the PanTheria database (Jones et al. 2009). The dietary information for birds was taken from del Hoyo et al. (1992-2011). In many cases a given species feeds on more than one class of item; where this was the case then the diet class assigned was based on the most frequent item(s), as determined from quantitative dietary analyses.

The differing chemical composition of plant leaves, fruits and animal tissue led Chivers & Hladik (1980) to propose an alternative dietary classification for primates: faunivory (carnivory), frugivory and foliovory. This classification was based on the adaptations of the gut necessary to digest and absorb the different diets (see also Karasov et al. 2011). We extended this classification to all endotherms, adding an extra category (granivory) for those species eating seeds. We also split the carnivore category to distinguish species taking invertebrates from those preying principally on vertebrates.

Because of the potential errors introduced by the assignment of taxa with a broad dietary niche to a single food category, an alternative classification based on broader trophic levels was also used. For mammals the classification of trophic levels in the PanTheria database was used without modification. For birds, species were classified as omnivores when their diet contained more than 30% of both animal and vegetable matter. Where dietary analysis was non-quantitative (presence/absence data only) then the assignment was based on

subjective judgement. To check the robustness of ecological conclusions following from statistical analysis based on this initial classification (*Trophic Level 1*), a stricter trophic level classification was used, whereby some taxa classified as carnivores or herbivores, because a majority of their food was animal or plant material, were reclassified as omnivores (*Trophic Level 2*). As an example of the differences between these two classifications, thrushes and finches were classified as carnivores or herbivores respectively in the first, but as omnivores in the second.

There were data for 426 species of mammal and 414 species of bird (with less detailed dietary information available for a further 71 bird taxa). The species-level taxonomy and assignment of taxa to families and orders used here followed Wilson & Reeder (2005) for mammals and Gill & Donsker (2011) for birds.

To test for relationships at the family level we classified a family as carnivorous or herbivorous only if every species in that family for which we have T_b data was a carnivore or herbivore. Families that contained omnivores, or included both carnivorous and herbivorous species, we classified as 'mixed'. The frequency distribution of T_b values within each family was typically skewed, and so we used median T_b values to characterise each family; the patterns and statistical conclusions were identical if mean values were used.

Data were analysed with one-way ANOVA and a General Linear Model (GLM) with diet as fixed factor. All statistical analyses were performed using Minitab. To allow for phylogenetic non-independence, we used Phylogenetic Generalised Least Squares Regression (PGLS), assuming trait evolution under Brownian motion ($\kappa = 1$). For mammals we used the species-level supertree updated by Fritz *et al.* (2009) and for birds we used a set of 100 phylogenies randomly selected from the distribution provided by Jetz et al. (2012) based on the Hackett tree. We used Pagel's λ (Pagel 1999) to account for phylogenetic covariance between T_b, diet class and body size. PGLS analyses were performed in R 2.13.2 using the package CAPER.

Details of the T_b and body mass data, dietary classification and all statistical analyses are given in Appendix S1.

RESULTS

Correlation of diet with body temperature

The mean body temperature of mammals varied significantly between trophic levels: carnivores had the lowest mean T_b, with herbivores and omnivores showing higher, and similar, mean T_b values (Table 1). Although the mean values differ by only ~1 K, the differences between trophic levels were highly significant statistically ($F_{2,425} = 14.9$, p < 0.001 for Trophic Level 1, $F_{2,425} = 17.2$, p < 0.001 for Trophic Level 2).

In birds there was a marginally significant variation in mean T_b across trophic levels ($F_{2,482} = 3.41$, p = 0.034), driven principally by a high value for omnivores (Table 1). When the analysis was repeated with the stricter trophic level classification (Trophic Level 2), the pattern of variation in mean T_b across trophic levels was similar but statistically much stronger ($F_{2,482} = 19.8$, p < 0.001).

The mean body temperature of mammals varied significantly with Pantheria diet class ($F_{7,425}$ = 12.0, p < 0.001). This conclusion was strengthened when the analysis was confined to those six diet classes with data for more than 20 species ($F_{5,401}$ = 15.2, p < 0.001). Of the eight diet classes examined, carnivores consuming invertebrate prey had the lowest mean T_b, and herbivores eating seeds or grass had the highest mean T_b; intriguingly, carnivores taking vertebrate prey also had a high mean T_b. The body temperature of birds also varies with Pantheria diet category ($F_{7,411}$ = 9.08, p < 0.001), with the highest mean T_b in herbivores eating grass or seeds, and (in contrast to mammals) carnivores taking invertebrates.

We repeated the analysis using the modified dietary classification of Chivers & Hladik (1980). In mammals there was a highly significant difference in mean T_b between the modified Chivers diet classes ($F_{5,318}$ = 15.8, p < 0.001), with foliovores and granivores having the highest mean T_b and frugivores and carnivores taking invertebrates the lowest (Table 2). In birds there was also a significant variation in mean T_b across the modified Chivers diet categories ($F_{5,391}$ = 14.5, p < 0.001), with granivores having the highest mean T_b and species taking flowers or nectar the lowest (Table 2).

Allowing for the effects of body mass

In both birds and mammals T_b varies with body mass, M_b, with larger mammals tending to be warmer and larger birds cooler (McNab 1966; White & Seymour 2003; Clarke & Rothery 2008). We therefore repeated the analysis using a General Linear Model (GLM) to control for M_b, with trophic level or diet category as a fixed factor.

For mammals there was no indication that the scaling relationship of T_b with M_b differed between carnivores, herbivores and omnivores (Trophic Level 2: $F_{2, 371}$ = 0.87, p = 0.42). After fitting a common slope there were significant differences in elevation ($F_{2,371}$ = 19.5, p < 0.001): herbivores were warmest, carnivores coolest and omnivores intermediate. For the modified Chivers diet classification, the hypothesis of common slope again could not be rejected ($F_{5,274}$ = 2.18, p = 0.056), and after fitting a common slope there were significant differences in elevation between diet classes ($F_{5,274}$ = 13.8, p < 0.001). The pattern matched the initial analysis, with the lowest mean T_b in carnivores taking invertebrates and herbivores taking flowers or nectar, and the highest mean T_b in herbivores eating foliage or seeds and carnivores taking vertebrate prey (See Appendix S1). Correction for the effects of body mass thus does not change either the pattern or the significance of the variation in mean T_b with diet class in mammals.

In birds the GLM indicated that there was significant heterogeneity in the scaling of T_b on body mass for different trophic levels ($F_{2,452}$ = 14.0, p < 0.001), and also across the modified Chivers diet categories ($F_{5,361}$ = 4.33, p < 0.001). The GLM analysis suggested that the pattern of variation of T_b across trophic levels and modified Chivers diet categories was strikingly similar to that of mammals, but the heterogeneity of slopes makes further interpretation difficult.

Allowing for phylogenetic non-independence

Because species within families or orders are likely to be similar in physiology and ecology as a result of a shared evolutionary ancestry, the relationship between T_b and diet was examined with data pooled at family and order level (see Methods).

A plot of median T_b as a function of median M_b for mammal families (Figure 1a) showed that in families with median body mass > 50g, there was a clear tendency for herbivores to exhibit a higher median T_b than carnivores. For these larger taxa there was only one herbivore family with median $T_b < 35^oC$ (Xenarthra, where T_b is highly labile; n = 2) and only one carnivore family with a median $T_b > 35^oC$ (Felidae, n = 8). For mammals as a whole carnivorous families have a significantly lower T_b than herbivores, or families with mixed diets (ANOVA, $F_{3,100} = 8.22$, p < 0.001). There is also significant variation in T_b across mammalian orders ($F_{24,425} = 15.5$, p < 0.001). For those mammalian orders for which we have diet data on ten or more species, the two orders with the highest mean T_b (Lagomorpha, Artiodactyla) are both purely herbivorous (for details see Appendix S1).

In bird families there was no significant difference in mean family T_b between the three diet groups ($F_{2,81} = 1.87$, p = 0.161). There was no visual discernible tendency for herbivorous families to have a higher median T_b (Figure 1b) but most bird orders are dominated by consumers of invertebrates and very few have any herbivorous taxa.

In mammals the phylogenetic signal (λ) in the data was strong, but analysis with PGLS indicated a significant relationship between trophic level and T_b, with herbivores warmer than carnivores, after allowing for the effects of both body mass and phylogenetic non-independence (Table 3). For the analysis based on modified Chivers diet categories, the pattern of mean T_b across diet categories was similar to that of the GLM analysis though the estimated mean T_b values were lower than those estimated from the GLM (Table 4). For birds the phylogenetic signal was again strong, but here the distribution of T_b across trophic levels and diet categories was non-significant after allowing for the effects of body mass and phylogenetic non-independence (Table 3).

Relationship between environmental temperature, diet and body temperature

At the species level, carnivores with relatively low T_b are only found in warmer habitats, and only herbivores are found in the very coldest habitats (Figure 3a). The relationship between diet type and mean ambient temperature within the range is significant (one-way ANOVA with modified Chivers diet category as factor, $F_{5,288} = 7.15$, p < 0.001), with foliovores and granivores being associated with the lowest mean environmental temperature, and frugivores the highest (see Appendix S1). The pattern is fairly similar at family level (Figure 3b), and the ten families extending into the coldest habitats are either herbivorous or omnivorous. Whilst there are striking examples of carnivores such as Polar Bears, *Ursus maritimus*, and Wolves, *Canis lupus*, extending into the high Arctic, our analyses concern mean values for dietary categories or families.

DISCUSSION

We have demonstrated a significant tendency for herbivory in mammals to be associated with a high T_b, and in particular for mean T_b to be highest in foliovores. This pattern is robust to

correction for the effects of body mass and phylogenetic non-independence. There was, however, considerable overlap in the range of T_b values for each diet category. This means that a particular species, or a comparison based on a small number of selected taxa, may not fit the broad general pattern we have established. In birds the highest T_b was found in herbivorous diet categories (foliovores, granivores and frugivores), but the pattern was not significant after allowing for phylogenetic non-independence.

Is there a common pattern across endotherms?

If we are seeking a general relationship between diet and T_b in endotherms, we should expect the pattern to be similar in mammals and birds. Direct comparison is however complicated by the difference in T_b between the two groups: birds exhibit a higher T_b than mammals, and the range of individual T_b values is narrower than in mammals (birds: range 35.0 −41.7 ^{o}C, interquartile range 1.8 K; mammals: range 30.2 −40.7 ^{o}C, interquartile range 2.2 K).

Fitting ordinary least-squares (OLS) regressions to allow for the effects of body mass indicates a striking commonality in the relation between mean residual T_b and diet for herbivorous mammals and birds (Figure 2). In both classes, mean T_b is highest in foliovores and granivores, and lowest in species taking flowers or nectar. This pattern is intriguing, as the mean T_b for the different diet categories increases in parallel with the fraction of cellulose in the diet (low in fruit, intermediate in seeds, high in foliage). Although the distribution of residuals across diet classes is highly suggestive of a common pattern across endotherm herbivores, the relationship in birds could not be resolved with a GLM because of the heterogeneity of slopes across diet classes. The residual for carnivores overall is lower than that of foliovores and granivores.

In mammals the residuals show excellent agreement with the mean T_b values estimated by both GLM and PGLS analyses (see Appendix S1 for details). A comparison was not possible for birds because the diet/T_b relationship PGLS was not significant in a PGLS analysis.

Is there a general relationship between temperature and herbivory?

If there is a fundamental physiological link between high T_b and a herbivorous diet, as suggested by our analyses, then we would expect this to be observed in other vertebrate groups. In reptiles an association between high T_b and herbivory has long been known (Cooper & Vitt 2002), in both large (Pough 1973) and in small (Espinoza *et al*. 2004) taxa. Most lizards are carnivorous but comparative studies have shown clearly that whilst carnivorous species can exhibit a wide range of T_b values, herbivorous lizards generally maintain a narrower range of higher body temperatures (Espinoza *et al*. 2004).

With the possible exception of some small fruit-eating tropical frogs (for example *Xenohyla truncata*: da Silva & de Britto-Pereira 2006), all adult amphibians take invertebrate prey, principally insects (Hillman *et al.* 2009). Interestingly, herbivory is widespread among larval amphibians (Altig & Kelly 1974), whose aquatic habitat means that T_b is likely to be highly variable and difficult to control. Herbivory is also uncommon among fishes, and is most frequent in warmer waters. In temperate marine habitats between 5 and 15% of species are herbivorous, whereas in coral reef assemblages up to 50% of the species may be herbivorous (Horn 1989).

In both reptiles and fish, digestion of plant material appears to be reliant on fermentation by gut microbes (Mountfort *et al.* 2002; Rimmer & Weibe 2006). Gaines & Lubchenco (1982) suggested that the low frequency of herbivory in fishes living at higher latitudes might be caused by temperature constraints on the activity of the gut microflora, and Floeter *et al.* (2005) concluded that herbivory in marine fishes was only possible above a threshold of ~15°C. Whilst there is clearly room for more work (Clements *et al.* 2009), there remains a general consensus that low body temperatures make herbivory energetically unfavourable, in that they constrain the rate at which energy can be extracted from the diet.

The link between herbivory and a high T_b in reptiles and fish suggests a fundamental ecophysiological relationship evident over broad spatial scales: herbivory becomes common only above a threshold T_b of ~15°C. All mammals and birds have a T_b that exceeds this threshold (except when torpid or hibernating), but the data we report here indicates that even within endotherms there may be subtle energetic advantages for some classes of herbivores from quite small increases in T_b. In mammals the difference in mean T_b between carnivores taking invertebrate prey and herbivores consuming grass or leaves is ~ 2.6 K (Table 2). In birds the signal is complicated by the strong association between T_b and body mass, but correction for body mass suggests a similar pattern of difference among dietary groups (Figure 2). These differences are small, but they suggest that the energetic advantages to be gained from having a warmer body when utilising some herbivorous diets outweighs the metabolic costs of maintaining a slightly warmer body.

Whilst the association between some herbivorous diets and a warmer body is clear, the precise physiological mechanism is not. It has long been argued that herbivores require a warmer body to support fermentation by gut microbes, but all digestive processes will proceed faster in warmer bodies (Wang *et al.* 2002) and many ectotherms select a warmer microenvironment when digesting food (Lang 1979; Petersen *et al.* 2011). The intriguing question is why the trade-off between enhanced rates of energy acquisition and the associated increased metabolic costs should be at different temperatures for different diets.

Do other factors influence the relationship between diet and body temperature?

Whilst mammals and birds show a significant difference in the mean T_b of herbivores and carnivores, there is considerable overlap in the range of T_b values for each trophic level. Some of this variability is correlated strongly with phylogeny. For example the high mean T_b for mammalian herbivores is driven principally by artiodactyls and lagomorphs, and cats exhibit a high mean T_b compared with other carnivorous mammals (Clarke & Rothery 2008). This suggests that other factors, additional to diet, are involved in determining T_b. One of these may be activity level; Lovegrove (2000, 2004) found that in larger mammals (> 500 g), a high residual BMR was correlated with cursoriality. Since BMR and T_b are correlated in mammals (Clarke *et al.* 2010), this would suggest that more cursorial mammals will also have a higher T_b, all other things being equal. Lovegrove (2012) showed that all mammalian lineages with a mean $T_b > 37.9$°C were highly cursorial. These cursorial lineages included Lagomorpha, Artiodactyla and Carnivora, the three orders with the highest mean T_b in our analysis (see Appendix S1). This suggests strongly that whilst T_b is clearly associated with diet in mammals, the picture is complicated by covariation with activity level.

The influence of phylogeny

It has long been recognised that within a data set comprising many different species, the degree of phylogenetic relatedness between the species may be reflected in the degree of similarity in the ecological traits of interest. The influence of phylogeny on ecology means that it is important to frame hypotheses carefully, and then use an appropriate statistical analysis (Harvey &Pagel 1991; Freckleton 2009; White *et al.* 2012).

The hypothesis we have tested is explicitly physiological: a herbivorous diet requires a warmer body than carnivory. In testing this hypothesis with conventional analyses (ANOVA, GLM), we are assuming implicitly that phylogeny has a minimal influence on T_b, and that the primary driver for the pattern of T_b across species is physiological. This is unlikely to be the case, and so we have also tested a subtly different hypothesis, which is that the distribution of T_b across species is influenced by both diet and phylogenetic descent. The relationship between diet and body temperature was significant in mammals in a PGLS analysis, but not in birds (Table 3).

In both mammals and birds there is strong niche conservation of diet within lineages (orders: see Appendix S1): all artiodactyls and lagomorphs are herbivores, all cats are carnivores, and so on. This strong covariation between diet and phylogeny must be considered in the interpretation of possible causes of the relationship we observe (or not) between diet and body temperature. Do artiodactyls have a high T_b because they are artiodactyls, or because they are herbivores? For mammals, T_b explained variation in diet in addition to variation explained by phylogenetic descent, lending support to a potential physiological explanation. In birds, the result was less clear, because the effect of T_b was no longer significant after phylogenetic variation was modelled.

An alternate approach to this question is to look for evolutionary reversals, that is an isolated carnivore in a lineage of herbivores, or *vice versa*. Unfortunately such examples are infrequent in our data set. In mammals only for Rodentia and Chiroptera were there enough taxa with a sufficient range of diets to undertake a test. In Rodentia, the mean T_b of foliovores ($37.1 \pm 1.1^{\circ}$C, n = 50), frugivores ($37.4 \pm 1.3^{\circ}$C, n = 5) and granivores ($36.4 \pm 1.8^{\circ}$C, n = 33) exceeded that of the few predominantly carnivorous taxa taking invertebrate prey ($35.8 \pm 1.5^{\circ}$C, n = 3), but the ANOVA is not quite significant ($F_{3,87} = 2.54$, p = 0.06). Among bats (Chiroptera) the ANOVA was significant ($F_{3,53} = 4.54$, p = 0.031), driven principally by a high mean T_b for frugivores ($36.4 \pm 1.0^{\circ}$C, n = 22) in comparison with invertebrate carnivores ($34.6 \pm 2.8^{\circ}$C, n = 25).

In birds only two non-passerine orders show sufficient dietary variation to allow a test, and within neither Anseriformes nor Apodiformes is there significant variation in T_b across diet categories (all p > 0.05). The bird data set is dominated by Passeriformes (238 of 485 species). When the analysis is confined to passerines, a GLM indicates that whilst herbivores eating foliage had the highest mean T_b for any diet class, variation across trophic levels and diet categories remains non-significant after controlling for body mass (all p > 0.05).

The strong phylogenetic signal evident in all the PGLS analyses (Table 3) suggests that in both mammals and birds the distribution of T_b across species has a significant historical element. Lovegrove (2012) has suggested that an increase in mammalian T_b was associated with global cooling and the change in vegetation following the Palaeocene/Eocene thermal maximum, and specifically the evolution of cursoriality. This hypothesis is independent of

diet, and may explain why strongly cursorial carnivores exploiting vertebrate prey have a T_b approaching that of herbivores such as artiodactyls and lagomorphs, whereas other carnivores have a lower T_b. Whilst diet does appear to play an important role in influencing T_b (Figure 2), there are clearly other factors involved.

Is diet related to body temperature or to BMR?

The pattern of T_b and herbivory across vertebrates in general suggests strongly that utilisation of plant material is associated with a warm body. There is, however, an interesting dichotomy in that ecologists working with reptiles and fish have interpreted diet in terms of T_b (Pough 1973; Gaines & Lubchenco 1982; Zimmerman & Tracy 1989; Cooper & Vitt 2002; Espinoza et al. 2004), whereas those interested in mammals have generally emphasised the relationship between diet and metabolic rate (McNab 1992, 2008). The resolution of this dichotomy comes through the interdependence of metabolic rate and temperature. In endotherms the main source of heat for maintaining a high T_b comes from metabolism; at the same time the level of T_b influences basal metabolic rate (BMR), because it is energetically more expensive to maintain a warm body than a cool one (Clarke et al.2010).

For endotherms although the mean increase in T_b in herbivores compared with carnivores is small, this higher T_b comes at an energetic cost: a higher T_b necessarily leads to a higher BMR (Clarke et al. 2010). The energy required to fuel a higher BMR must be met by a higher energy intake, and the difference is not trivial. For example, based on the mean T_b values observed in this study and the temperature sensitivity of BMR in endotherms (Clarke et al. 2010), a 150g foliovore has a predicted BMR higher by ~29% compared with an invertebrate carnivore of similar size.

The extent to which herbivores are warmer must thus reflect a trade-off between the enhanced energy intake from food at a higher T_b and the higher metabolic costs following from that T_b. Additional to the effect of T_b on BMR will be a contribution from the energetic costs of differences in gut length, activity level (for example cursoriality), brain size and so on (see for example Williams et al. 2001). Together these lead to a significantly higher BMR in mammalian herbivores than mammalian carnivores, on average. This increased BMR is not of itself an energetic advantage; it represents the cost of maintaining a body adapted to eating a diet containing cellulose. The benefit comes from the greater energy available from plant food at the higher T_b.

Concluding remarks

We can therefore propose a general picture for all vertebrates, which is that herbivores consuming plant tissues high in cellulose tend to maintain a higher T_b than carnivores. This higher T_b may be generated either through endothermy (mammals, birds), by behavioural thermoregulation (small reptiles) or by living in a warm environment (tropical reptiles and fish). Whilst a high T_b is a widespread feature of herbivores, it is not universal. For example sloths (Xenarthra) and some temperate fishes are herbivorous despite a lower T_b.

Overall, the association between herbivory and a high T_b in vertebrates is highly persuasive, and can be regarded as a useful macrophysiological generalisation (Gaston et al. 2009). This association might suggest that amongst ectotherms, herbivory would exhibit a relationship

with climate, with herbivory commoner in warmer habitats. This does appear to be the case: the diversity of modern herbivorous insects and the pressure they exert on their plant hosts generally increases towards the tropics (Wilf & Labandeira 1999; but see also Salazar & Marquis 2012). Furthermore increases in the extent of insect herbivory can be detected during early Cenozoic warming (Wilf *et al.* 2001) and during the Palaeocene/Eocene thermal maximum (Currano *et al.* 2008, 2010). Terrestrial reptiles were important herbivores during the Mesozoic, and many of these achieved a high and stable T_b through their large size (O'Connor & Dodson 1999; Eagle *et al.* 2011; Head *et al.* 2013).

Despite the associated metabolic costs, herbivory is widespread in mammals, and the incidence of herbivory at class level exceeds that in reptiles, amphibians and fish by a wide margin. Whilst a broadening of the diet cannot of itself have been the initial driving force behind the evolution of endothermy (Clarke & Pörtner 2010), it may well be one of its most important ecological consequences. The evolution of a permanently warm body allowed an increasing diversity of mammals to utilise a widespread and abundant food resource that was previously the preserve of insects and the large herbivorous dinosaurs, until the latter's demise at the K/Pg extinction event.

Acknowledgements

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Biosketches

Andrew Clarke is interested in the relationship between temperature, physiology and ecology.

Mary O'Connor studies how temperature affects trophic interactions and community structure.

Table 1. Mean body temperature, T_b (^{o}C), for mammals and birds in different trophic levels. The two trophic level classifications differ in the strictness of definition of carnivore and herbivore in taxa which switch diet seasonally. Data are uncorrected for body mass.

Trophic level	Mammal T_b			Bird T_b		
	Mean	SD	n	Mean	SD	n
Trophic level classification 1						
Carnivore	35.7	2.39	156	41.3	1.32	345
Herbivore	36.8	1.59	197	41.3	1.54	96
Omnivore	36.8	1.23	73	41.9	1.25	44
Trophic level classification 2						
Carnivore	35.5	2.54	109	41.2	1.32	295
Herbivore	36.8	1.53	156	41.0	1.84	55
Omnivore	36.6	1.61	161	42.0	1.00	135

Table 2. Mean body temperature, T_b (^{o}C), for mammals and birds in different diet categories, using a modified version of the diet classification of Chivers & Hladik (1980). Data are shown in italics where there were data for fewer than 10 species in that diet class. Data are uncorrected for body mass.

Diet class	Mammal T_b			Bird T_b		
	Mean	SD	n	Mean	SD	n
Carnivores						
Vertebrate prey	37.1	2.70	22	40.4	1.02	62
Invertebrate prey	35.0	2.01	94	41.4	1.31	247
Herbivores						
Fruit	36.4	1.11	43	*41.3*	*1.85*	*3*
Foliage (grass or leaves)	37.3	1.38	81	41.3	0.65	15
Seeds	36.4	1.84	31	42.0	1.00	48
Flowers or nectar	*34.7*	*0.54*	*5*	39.8	2.12	22

Table 3. Phylogenetic generalised least-squares (PGLS) regression analysis of relationship between diet and T_b in mammals, with significance of variation across trophic levels or modified Chivers & Hladik (1980) diet categories. TroL2: trophic level 2 diet classes, λ: phylogenetic signal (maximum likelihood estimate), F: variance ratio, df: degrees of freedom, p: probability. For birds the data for λ and F are given as mean with 95% confidence intervals in parentheses for 100 phylogenies randomly selected from the distribution provided by Jetz et al. 2012.

Diet classification	λ	F	df	p
Mammals				
TroL2	0.85	4.78	4, 366	< 0.001
Modified Chivers	0.770	3.60	7, 266	0.001
Birds				
TroL2	0.87 (0.83, 0.91)	1.00 (0.54, 1.47)	4, 454	(al lp > 0.21)
Modified Chivers	0.83 (0.78, 0.88)	0.87 (0.68, 1.01)	7, 366	(all p > 0.42)

Table 4. Body temperature estimated for a representative mammal (body mass 150g) and a representative bird (body mass 50g) utilising different diets. T_b values estimated both from a GLM (allowing for body mass) and PGLS (allowing for both body mass and phylogeny). For birds the estimates were based on mean data from 100 phylogenies analysed. Representative body mass values were rounded values for the median body mass of all mammals or all birds in our data set. Note that in birds the PGLS analysis was non-significant and hence a single T_b is estimated for all diet categories.

|	Diet category (modified Chivers)	T_b (°C)	
		GLM	PGLS
Mammal (150g body mass)			
	Foliovore	37.2	35.4
	Granivore	36.4	35.1
	Frugivore	36.4	34.9
	Flowers/nectar	34.8	34.0
	Carnivore (vertebrate prey)	36.5	34.5
	Carnivore (invertebrate prey	35.0	33.8
Bird (50g body mass)			
	Foliovore	42.3	(41.3)
	Granivore	42.1	(41.3)
	Frugivore	42.2	(41.3)
	Flowers/nectar	39.6	(41.3)
	Carnivore (vertebrate prey)	41.2	(41.3)
	Carnivore (invertebrate prey)	41.5	(41.3)

Figures
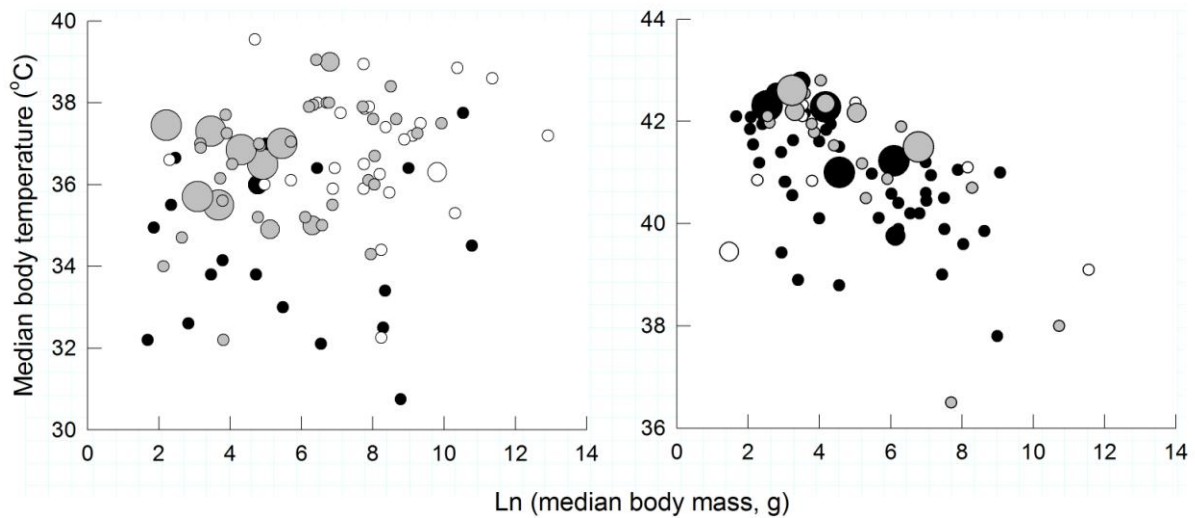
Figure 1. Relationship between median body temperature, T_b (°C), and median body mass (g, natural log transformed) of endotherm families. Families classified into carnivores (black symbols), herbivores (white symbols) and mixed or omnivorous families (grey symbols), with size indicating the number of species within each family for which we have both dietary and T_b data: <10 taxa (small symbols), 10-19 taxa (medium symbols) and 20+ taxa (large symbols). A (left panel): Mammals. B (right panel): Birds.
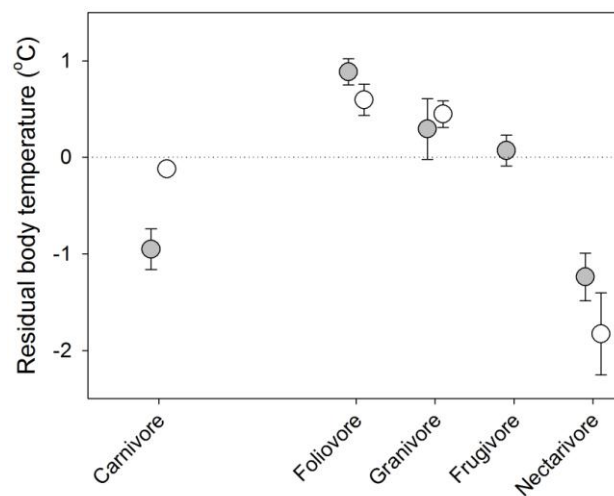

Figure 2. Mean residual body temperature in mammals (grey symbols) and birds (white symbols) for different diet types. Residuals are for OLS regression of T_b on body mass (g, natural log transformed). Data are mean ± SE. Data plotted only for diet categories with data for 5 or more species (range 5 to 237).
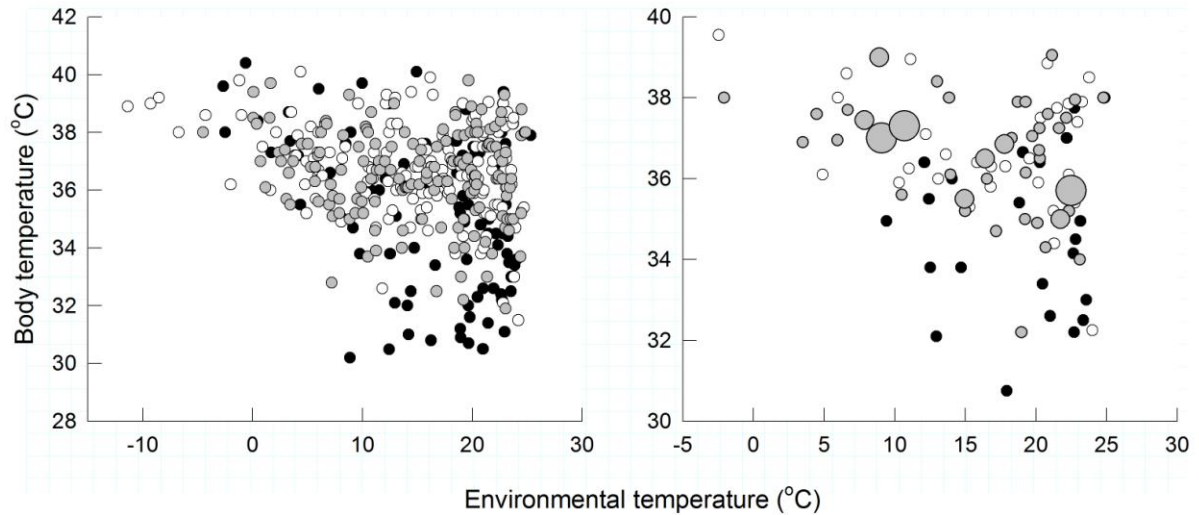
Figure 3. Body temperature and ambient temperature in mammals. A (left panel): Data for individual species, classified by trophic level (herbivores: white symbols, Omnivores: grey symbols, carnivores: black symbols). B (right panel): Data pooled by family. Environmental temperature is the mean temperature over the geographical range of a given species (left panel), or median value for those species of a family represented in the data (right panel). Families classified into carnivores (black symbols), herbivores (white symbols) and mixed or omnivorous families (grey symbols), with size indicating the number of species within each family for which have both dietary and T_b data: <10 taxa (small symbols), 10-19 taxa (medium symbols) and 20+ taxa (large symbols).