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Effects of Contingency versus Constraints on the Body-Mass Scaling of Metabolic Rate

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Received: 16 December 2017; Accepted: 17 January 2018; Published: 29 January 2018



Abstract: I illustrate the effects of both contingency and constraints on the body-mass scaling of metabolic rate by analyzing the significantly different influences of ambient temperature (T_a) on metabolic scaling in ectothermic versus endothermic animals. Interspecific comparisons show that increasing T_a results in decreasing metabolic scaling slopes in ectotherms, but increasing slopes in endotherms, a pattern uniquely predicted by the metabolic-level boundaries hypothesis, as amended to include effects of the scaling of thermal conductance in endotherms outside their thermoneutral zone. No other published theoretical model explicitly predicts this striking variation in metabolic scaling, which I explain in terms of contingent effects of T_a and thermoregulatory strategy in the context of physical and geometric constraints related to the scaling of surface area, volume, and heat flow across surfaces. My analysis shows that theoretical models focused on an ideal 3/4-power law, as explained by a single universally applicable mechanism, are clearly inadequate for explaining the diversity and environmental sensitivity of metabolic scaling. An important challenge is to develop a theory of metabolic scaling that recognizes the contingent effects of multiple mechanisms that are modulated by several extrinsic and intrinsic factors within specified constraints.

Keywords: allometry; body size; contextual multimodal theory; ectothermic vs. endothermic animals; metabolism; metabolic-level boundaries hypothesis; scaling; thermal conductance; thermoregulation

1. Introduction

The sizes of living things vary enormously, which has major consequences for how they look, act, and function. How biological traits vary with body size is the subject of an exciting and controversial field called “allometry” or “biological scaling” [1–8]. This field of study is important because it has great potential for contributing to a unifying theory of biological systems [9,10]. All living systems have size and most of their structural and functional features scale to size. Moreover, these scaling relationships are often not simple proportional (1:1 or isometric) relationships, but may involve diverse kinds of disproportionate (allometric) relationships. Although these various kinds of scaling relationships have been the subject of decades of research, they remain little understood.

A classic example is the scaling of the rate of metabolism (i.e., the transformation of energy and materials in support of various biological processes). Early theoretical and empirical studies in the 1800s suggested that the scaling of metabolic rate in endothermic (warm-blooded) birds and mammals obeys a 2/3-power law [11,12]. Maintenance of a constant, high body temperature requires metabolic heat production to balance exactly the loss of heat through the body surface, which scales to the 2/3 power in relation to body mass or volume (assuming isomorphic body shapes). Therefore, metabolic rate should also scale to the 2/3 power, as observed within many species of birds and mammals ([3,12–15], but see [16]). However, in the 1930s, animal scientists such as Kleiber and Brody discovered that the interspecific scaling of basal (resting) metabolic rate in mammals more closely matched a 3/4-power relationship than a 2/3-power relationship [17,18]. In 1960, Hemmingsen [19]

reported 3/4-power metabolic scaling relationships for not only endothermic birds and mammals, but also various ectothermic (cold-blooded) animals and even unicellular organisms. This finding led to the proclamation of a universal 3/4-power scaling law for metabolic rate (also called Kleiber's Law) that most biologists accepted [4–6,20,21] until quite recently [10,16,22]. A belief in the 3/4-power law also spurred a continuing search for intrinsic physical causes of metabolic scaling. If such a universal law existed, contingent biological and ecological factors would not be important in explaining it. As a universal law, it by definition must operate in all organisms and in all environments. Taxonomic and ecological variation should be irrelevant, or at most secondary in importance. In addition, the physical explanation could not be a simple function of heat loss through body surfaces because the power of the scaling relationship is allegedly 3/4 and not 2/3. Moreover, this law reputedly applied to organisms that did not maintain constant body temperatures, and thus need not balance their metabolic heat production with heat loss. In short, the once conventional thermoregulatory model of metabolic scaling appeared to be inadequate, at least as a general explanation, though it may still be applicable to endotherms, at least in part, as argued here and in [23–28].

Many investigators have attempted to provide a universal, intrinsic, physical explanation of 3/4-power metabolic scaling, which has been called the “Holy Grail in comparative biology” (Carol Beuchat cited in [29]), but none of these explanations enjoy wide acceptance (reviewed in [10,16,22,30,31]). The lack of a consensus view results from two major problems. First, recent work has made it clear that no universal 3/4-power scaling law for metabolic rate actually exists. The scaling slopes of metabolic rate vary from ~ 0 to >1 (but mostly between 2/3 and 1) in various kinds of organisms under various kinds of conditions [10,16,22]. Second, all of the proposed models are limited in scope, and thus not universally applicable, and (or) have other problems with their assumptions, internal logic and (or) predictions [10,16,22,30–32].

Consider, for example, the most influential of the metabolic scaling explanations based on intrinsic physical constraints published to date. According to this resource-transport-network (RTN) model [33], and others like it [34–37], the classical 3/4- or 2/3-power scaling of metabolic rate results from increased physical and geometric constraints on the supply of resources to cells in large organisms with longer transport distances, on average, than those of smaller organisms. However, RTN models have received extensive criticism [10,16,22,30,31,38]. First, they are not universally applicable because they do not apply to organisms without closed resource-transport (e.g., circulatory) systems. Second, several lines of evidence contradict the fundamental assumption of RTN models that resource supply limits resting metabolic rates in organisms [16,27,30,38]. For example, in various kinds of animals, cells of large species are not more oxygen limited than are cells of smaller species [38]. In addition, avian and mammalian cells grown in nutrient- and oxygen rich culture media often exhibit lower rather than higher metabolic rates compared to cells in vivo, contrary to predictions of RTN models [27]. Third, scaling slopes of metabolic rate in pelagic invertebrates that grow mainly in two dimensions more closely match those predicted by surface-area models (slope ~ 1) than those predicted by RTN models (slopes $\sim 1/2$, $5/8$ or $2/3$, depending on the type of network) [39,40]. Fourth, intrinsic physical explanations, such as those of RTN models, cannot explain the extensive variation of metabolic scaling systematically associated with various biological and ecological factors.

Several recent studies have shown that many kinds of extrinsic environmental factors affect the scaling of metabolic rate [10,16,22,32]. These include abiotic factors, such as temperature, pH and oxygen availability [10,16,26,41], and biotic factors, such as predation, parasitism and food quantity and quality [10,16,42–45]. Metabolic scaling relationships also vary with lifestyle, developmental stage and physiological status [10,16,23,26,46–48]. As a result, it has become increasingly clear that biological and ecological contingency plays an important role in metabolic scaling. A major challenge now is to determine the relative influences that contingency versus constraints have on metabolic scaling. Some investigators still promote the view that internal constraints predominate, especially the proponents of RTN models [8,9,21,33–37] and the influential metabolic theory of ecology [49]. Others

claim that heterogeneous contingent factors are importantly involved in determining both the slopes and elevations of metabolic scaling relationships [10,16,23,32,50–52].

As a point of departure for my discussion about the contingency versus constraints debate, I focus on published data showing that an extrinsic factor, namely ambient temperature, not only significantly affects the scaling of metabolic rate, but also does so in fundamentally different ways in ectothermic and endothermic animals. This comparison allows for not only a fresh assessment of the relative roles of contingency and constraints in metabolic scaling, but also a useful comparative evaluation of several prominent theoretical models. I conclude with a brief discussion about what future research is required to advance our understanding of metabolic scaling.

2. Results

Ectothermic crustaceans and teleost fishes show negative relationships between the body-mass scaling slope for metabolic rate and ambient temperature (Figures 1 and 2), whereas endothermic birds and mammals show positive relationships (Figures 3 and 4).

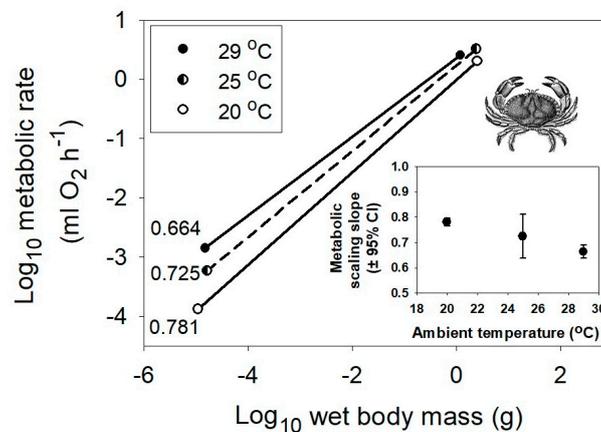


Figure 1. Interspecific scaling of metabolic rate in relation to body mass of marine crustaceans at three different habitat temperatures, 29, 25 and 20 °C (data from [53]). The correlation coefficients (r) and sample sizes (n) are 0.963 and 212, 0.727 and 249, and 0.977 and 247, respectively. All probability values are <0.001 . The inset graph shows the negative relationship between the metabolic scaling slope ($\pm 95\%$ confidence intervals) and habitat temperature. The crab picture is from [54].

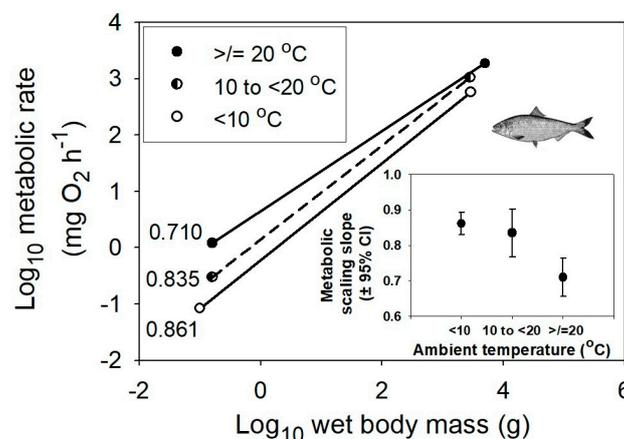


Figure 2. Ontogenetic scaling of metabolic rate in relation to body mass averaged for multiple species of marine teleost fishes at three different habitat temperature ranges, ≥ 20 , 10 to <20 , and <10 °C (data from [48]). The sample sizes (n) are 30, 19 and 40, respectively. The inset graph shows the negative relationship between the mean metabolic scaling slope ($\pm 95\%$ confidence intervals) and habitat temperature. The fish picture is from [55].

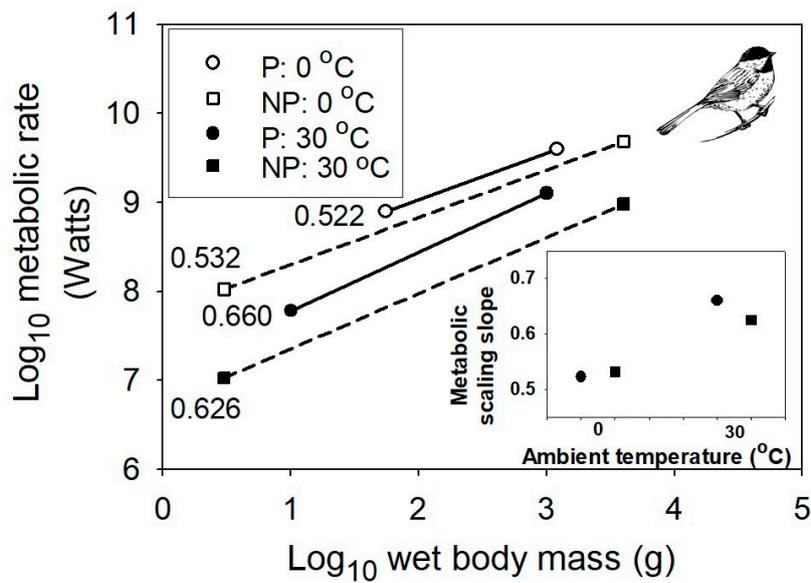


Figure 3. Interspecific scaling of existence metabolism in relation to body mass for multiple species of passerine and non-passerine birds at two different air temperatures, 0 and 30 °C (data from [56]). The sample sizes (*n*) are 71 for passerine birds, and 40 for non-passerine birds. The inset graph shows the positive relationships between the metabolic scaling slopes and temperature for both passerine and non-passerine birds. The bird picture is from [57].

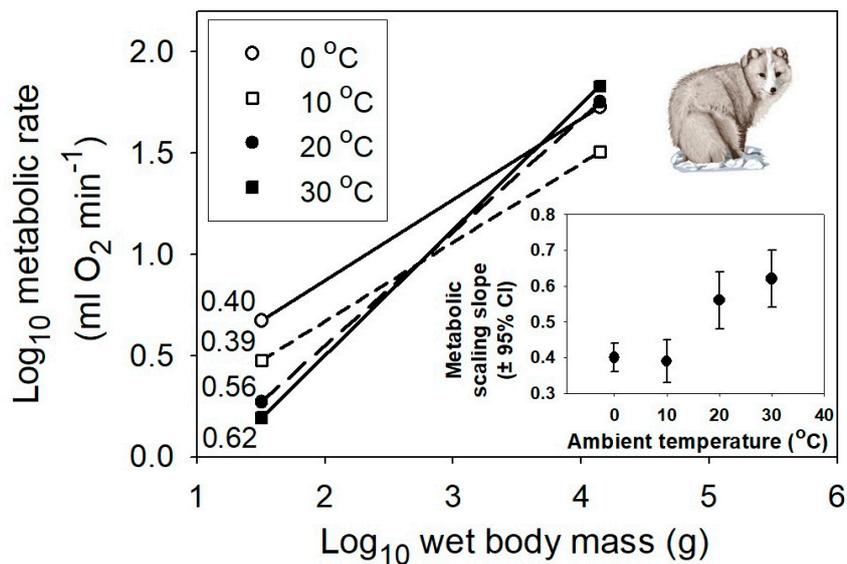


Figure 4. Interspecific scaling of metabolic rate in relation to body mass for multiple species of eutherian mammals at four different air temperatures, 0, 10, 20 and 30 °C (data from [58]). The correlation coefficients (*r*) and sample sizes (*n*) are 0.91 and 61, 0.84 and 69, 0.88 and 73, and 0.89 and 81, respectively. All probability values are <0.001. The inset graph shows the positive relationship between the metabolic scaling slope ($\pm 95\%$ confidence intervals) and temperature. The mammal picture is from [59].

3. Discussion

3.1. Implications of Results for Theory

The results just presented are important and challenging, because they cannot be explained completely by any published model of metabolic scaling. RTN models are clearly inadequate.

These models either ignore the possibility of temperature effects [33–37], or assume that body size and temperature act independently on metabolic rate [49,60]. According to the metabolic theory of ecology (MTE) [8,49], which includes the RTN model of [33], temperature should affect the elevation, but not the slope (exponent) of metabolic scaling relationships. The present results clearly contradict this prediction.

Increasing temperature tends to be associated with smaller cell sizes in a variety of organisms (reviewed in [61,62]; also see [63–68]). Small cells (and organisms containing them) tend to have higher mass-specific metabolic rates than large cells (and organisms containing them) [26,69–77]. Therefore, like the MTE, cell-size theory predicts that changing temperature should affect the elevation of metabolic scaling relationships, but not their slopes (but see Section 3.2.2), which again is contradicted by the results described in this study. Most other models focused on the differential scaling of various resource-demanding processes and tissues or organs with different metabolic rates (see e.g., [10,38,52]) have yet to consider how ambient temperature may affect metabolic scaling slopes (but see discussion of dynamic energy budget theory below). Furthermore, a recent study has shown that temperature acclimation does not affect the size and metabolic rate of various organs of the prawn *Macrobrachium tolmerum* [78].

The model that best explains the observed results is the metabolic-level boundaries hypothesis (MLBH) [23,26]. It predicts that changes in temperature should affect both the elevation and slope of metabolic scaling relationships [26], as observed in this study and several other studies (e.g., [16,26,48,53]; also see Section 3.2.2). Moreover, it uniquely predicts that increasing temperature should result in decreases in the metabolic scaling exponent in ectotherms (Figures 1 and 2), but increases in the exponent in endotherms (Figures 3 and 4), again as observed. This is because it predicts inverse relationships between the slopes and elevations of scaling relationships for resting metabolic rate. Therefore, since decreasing temperature decreases metabolic level (scaling elevation) in ectotherms, but increases it in endotherms because of increased metabolic heat production required to maintain a constant body temperature, the opposite responses of scaling slope to temperature in ectotherms and endotherms are as expected. According to the MLBH, at low metabolic levels, volume-related tissue maintenance chiefly influences metabolic scaling (scaling slope approaching 1 in organisms with uniform scaling of metabolic rate in different tissues), whereas at high metabolic levels, surface-area-related processes (such as resource uptake, metabolic waste removal, and heat dissipation) predominate (scaling slope approaching 2/3 in isomorphic organisms). In short, the scaling exponent for resting metabolic rate should vary between 2/3 and 1, depending on metabolic level [23,26].

However, even the MLBH, as currently formulated, falls short of completely explaining the effects of temperature on the metabolic scaling of endotherms. In both birds and mammals, as temperature decreases, the metabolic scaling exponent falls below the lower limit of 2/3 predicted by the MLBH (see Figures 3 and 4). Why? A likely answer involves an increasing influence of the body-mass scaling of thermal conductance on the scaling of metabolic rate, as ambient temperature (T_a) declines, and thus becomes increasingly different from the relatively high body temperature (T_b) maintained by endotherms. Following Fourier's Law (which is related to Newton's law of cooling), rate of heat flow across an organism's surface is a function of four major factors: surface area, thickness and thermal conductivity of the surface layer of insulation, and the temperature differential ($T_b - T_a$) between the inside and outside of an organism [25,56]. At thermoneutrality, which is near 30 °C in most endothermic vertebrates, the temperature differential is relatively small, and the cost of thermoregulation is minimal, thus causing the metabolic scaling exponent to approximate 2/3, which follows the classic surface law [11,12], as pointed out by [56]. Within the thermoneutral zone, metabolic heat production exactly balances the heat dissipated, which is chiefly a function of surface area. However, as the cross-surface temperature differential increases, the metabolic scaling slope should approach ~0.45–0.55, as typically observed for the scaling of thermal conductance in birds and mammals [6,79–86]. As predicted, when T_a equals 0 °C (which is greater than 30 °C below T_b), the metabolic scaling exponents for

mammals (0.40), passerine birds (0.52) and nonpasserine birds (0.53) ([56,58]; Figures 3 and 4) all approach that observed for the scaling exponent of thermal conductance.

Therefore, the MLBH requires amendment to explain the scaling of resting metabolic rate of endotherms outside their thermoneutral zone. Heat dissipation importantly affects the metabolic scaling of endotherms at all ambient temperatures (also see [23–26,28,56,58,87]), but in the thermoneutral zone, surface area is chiefly important, whereas at increasingly lower ambient temperatures outside the thermoneutral zone, insulation and the cross-surface temperature differential become increasingly important, as well. As Kendeigh and colleagues argued [56], metabolic heat production that exactly compensates for heat dissipation in the cold should scale approximately to the 0.5 power, or as $(M^{0.167})(M^{0.667})/(W^{0.333})$, which are the hypothesized power relations for the thermal conductivity of the surface layer of insulation (h), surface area (A), and insulation thickness (I), respectively, for endotherms. This dimensional analysis uses a formula for the rate of heat flow across a surface (k) that is based on Fourier's Law: i.e., $k = hA/I(T_b - T_a)$ (cf. [6,25,28,58]). It also assumes that T_b and body shape are constant and pelage mass increases isometrically with body mass (scaling slope = 1), and ignores the effects of other factors such as radiation and air convection [6,25]. Notably, the hypothesized power relations for h , A and I approximate empirical estimates quite closely [56,83]. Similarly, Schmidt-Nielsen [6] noted that the insulation of mammals scales as $M^{0.17}$, and thus thermal conductance should scale as $(M^{0.67})/(W^{0.17})$ or as $M^{0.50}$, as approximately observed (cf. [88]). Therefore, the greater insulation of larger mammals causes the scaling slope for heat dissipation at low T_a to approximate 0.5, which in turn requires the scaling slope for metabolic heat production to approximate 0.5, in order to maintain a constant body temperature (cf. [25,89]). In support, maximal non-shivering thermogenesis (induced by noradrenaline injection) scales similarly in mammals (exponent = 0.546 [90]). In addition, if one minimizes the size-related effect of insulation by exposing birds or mammals of different size to low temperatures in a He-O₂ atmosphere with high thermal conductivity, surface-area related heat dissipation chiefly influences metabolic scaling, which thus has a scaling slope approximating 2/3 (see [91–93]).

I know of only two other theoretical models that predict that the metabolic scaling slope should vary with T_a . According to dynamic energy budget theory, as recently modified by [94,95], negative associations between T_a and the metabolic scaling exponent should occur in some, but not all colonial animals. However, the ability of this model to explain T_a effects on the metabolic scaling of unitary organisms is problematic. It invokes effects of T_a on growth rate, which cannot explain negative associations between T_a and the metabolic scaling exponent commonly observed in ectothermic organisms. Decreasing T_a inhibits growth rate, and decreased growth rates are associated with lower, not higher metabolic scaling exponents (see [10,32,44,96]).

According to the viscosity hypothesis [97], small aquatic animals have greater difficulty engaging in respiratory ventilation and thus oxygen uptake in colder, more viscous water than do larger animals. Consequently, as water temperature decreases, and viscosity increases, smaller animals should exhibit a greater depression of metabolic rate than that of larger animals, thus resulting in a negative association between temperature and the metabolic scaling slope. However, this model is not general, as it applies only to aquatic, actively ventilating, ectothermic animals, and not to plants, terrestrial ectothermic animals, or endothermic animals. Nevertheless, inverse relationships between the metabolic scaling slope and temperature also occur in plants [26,98] and various terrestrial ectothermic animals (e.g., [99–101]), as predicted by the MLBH [26]. In addition, the viscosity hypothesis cannot explain why the metabolic scaling exponent decreases with decreasing temperature in endotherms (Figures 3 and 4). Nor can it explain responses of the metabolic scaling exponent to metabolic level related to other factors besides temperature (e.g., taxonomic variation [23,102], lifestyle [23,26,48], and activity state [16,23,26,103,104]), as predicted by the MLBH. Therefore, the MLBH has broader predictive power than the viscosity hypothesis.

3.2. Challenges for Future Research

3.2.1. General Perspective

The results of this study clearly show that both contingency and constraints affect metabolic scaling. The contingencies considered here include T_a and thermoregulatory lifestyle (ectothermy versus endothermy). The metabolic scaling slope varies with T_a , and the nature of this variation differs markedly between ectotherms and endotherms (Figures 1–4). One cannot understand this variation in metabolic scaling without recognizing these and other contingencies. In birds and mammals, photoperiod and time of day of metabolic measurements may also affect thermal conductance and its scaling with body mass [6,82], and by association, metabolic rate and its scaling with body mass in the cold [56]. These contingent effects operate within the boundaries of geometric and physical constraints, including surface-area-to-volume relationships, and physical laws of heat flow.

However, one might argue that fish and crustaceans show different effects of T_a on metabolic scaling than do birds and mammals, because of differences in ecological habitat (aquatic vs. terrestrial), rather than thermoregulatory strategy (ectothermy vs. endothermy). Increasing temperature not only increases metabolic demand for oxygen both in water and on land, but in water, it also decreases oxygen concentration and thus its availability. The double jeopardy of higher oxygen demand and lower oxygen supply at high T_a in water, especially as body size increases, may therefore cause inverse relationships between T_a and the metabolic scaling exponent to be more prevalent in aquatic vs. terrestrial animals. However, as pointed out in Section 3.1, negative associations between T_a and the metabolic scaling exponent also occur in many terrestrial ectotherms. In addition, the habitat hypothesis cannot explain why associations between T_a and the metabolic scaling exponent are positive in endotherms. Therefore, I believe that it is more likely that the taxonomic differences in how T_a affects metabolic scaling observed in this study relate more to differences in thermoregulatory strategy than to habitat.

The MLBH succeeds in explaining temperature effects on metabolic scaling because it recognizes both contingent effects and physical constraints. Other prominent theoretical models based strictly on internal physical constraints cannot explain these patterns (see Section 3.1). The MLBH is part of a more general theory, the contextual multimodal theory, which includes multiple mechanisms that act in contingent ways ([10]; also see Section 5).

3.2.2. Suggestions for Future Research

I recommend future research that attempts to explain the diversity of metabolic scaling and its sensitivity to a variety of intrinsic and extrinsic factors, rather than a non-existent universal metabolic scaling law (e.g., 3/4-power law) (see [10,16,23,32,105]). Potentially productive approaches include comparative and experimental studies exploring how various intrinsic and extrinsic factors interact to produce a variety of metabolic scaling relationships, and how biological regulation mediates these interactions.

Further studies of how T_a affects metabolic scaling are required for comparisons both within and among species. As predicted by the MLBH (as amended in Section 3.1), in the laboratory mouse (*Mus musculus domesticus*), metabolic level is higher at 21 versus 29 °C, but the metabolic scaling slope is lower [106]. Varied patterns occur for other rodents, but these analyses suffer from very small body-mass ranges [107]. In addition, as predicted by the MLBH, the metabolic rate of marine zooplankton (including diverse taxa) increases in the order of boreal, temperate and tropical species, whereas the interspecific scaling exponent (based on dry masses) decreases (0.830, 0.691, and 0.538, respectively) [108], though this may not be true for planktonic crustaceans [109]. Although inverse relationships between T_a and the exponent (slope) for ontogenetic metabolic scaling are common in ectotherms, other patterns are also possible, including non-significant, positive and nonlinear relationships (reviewed in [16,26]). In this study, I suggest that thermoregulatory lifestyle (ectothermy versus endothermy) can affect the temperature-sensitivity of interspecific metabolic scaling. Other

differences in lifestyle may also help explain the varied responses of intraspecific metabolic scaling to T_a observed in ectotherms. One key lifestyle feature may be activity level. According to the MLBH, for resting (inactive) metabolism, increasing metabolic level should be associated with decreasing scaling exponents, whereas for active metabolism, increasing metabolic level should be associated with increasing scaling exponents (because of an increase in the relative influence of volume-related locomotor power production) ([16,23,26]; cf. [92]). Therefore, in sedentary (immobile) organisms, a thermally increased metabolic level should result in a lowered metabolic scaling exponent, whereas, in actively mobile animals, a thermally increased metabolic level may result in a variety of effects on the metabolic scaling exponent, depending on the relative size-specific effects of T_a on activity level (also see [26]). Consistent with this hypothesis, sedentary or mostly stationary organisms (including plants, oysters, mussels, chitons, and ascidians) usually show strong negative associations between T_a and the resting metabolic scaling exponent (e.g., [110–114]), whereas actively mobile animals show a variety of responses (as reviewed in [16,26]; and as shown in an unpublished data set). As further evidence, when the effects of activity are removed in an actively mobile species, such as the fish *Coregonus albula*, T_a and the resting metabolic scaling exponent are strongly negatively correlated [115], as predicted by the MLBH [16,26]. Further studies of the effects of various abiotic and biotic ecological factors on metabolic scaling would also be worthwhile (see also [10,16,22,26,32,41,44–46,48]).

My study suggests that not only T_a , but also the mode of regulation of T_b , affect metabolic scaling. My interpretation of these contingent thermal effects contributes to a growing revival of the old, controversial view that thermoregulation is importantly involved in the metabolic scaling of endotherms ([10–12,16,23–28,32,56,58,87,89,93], but see [9,21,22,33,92,116,117]). This thermoregulatory view is testable. For example, since thermal insulation scales allometrically (slope ~ 0.17) in mammals with a body mass < 10 kg, but remains constant in larger mammals [6], the thermoregulatory view predicts that at low T_a below the thermoneutral zone, the scaling exponent for metabolic rate should approach 0.50 in small mammals, but be near 0.67 in large mammals (cf. Section 3.1). The data provided in Figure 4 are only for mammals ≤ 14 kg, which show metabolic scaling exponents of 0.39–0.56 at T_a below the thermoneutral zone, which encompass the predicted slope of 0.50. As a further test, we now need data for larger mammals exposed to the cold. A thermoregulatory view may also help explain the curvilinearity of the scaling of mammalian basal metabolic rate in the thermoneutral zone, showing a slope near $2/3$ in small mammals, and a higher slope ($\geq 3/4$) in larger mammals (e.g., [93,118,119]). Is it a coincidence that the breakpoint in the scaling of mammalian basal metabolic rate occurs near a body mass of 10 kg (4.25 or 20 kg, according to the two-segmented linear models of Kozłowski and Konarzewski [120] and Makarieva and colleagues [121], respectively)?

Furthermore, I suggest that contingent effects on metabolic scaling are often mediated by various biological regulatory systems. Although the importance of regulation in metabolic scaling was discussed over 50 years ago (e.g., [20,106,122]), it has been a neglected focus of research in recent years (but see [10,27,96,123,124]). The effects of regulation can be dramatic, as seen when mammals engage in regulated depression of their T_b and metabolic rate during torpor and hibernation [125]: as a result, their metabolic scaling slope shifts markedly from ~ 0.67 – 0.75 to ~ 1 , as predicted by the MLBH [10,23,26,93]. This observation also reinforces the view that thermoregulation plays a major role in the metabolic scaling of endotherms. Therefore, I recommend that increased attention should be given to how various regulatory systems at various levels of biological organization (from biochemical signaling pathways to neuroendocrine systems) affect metabolic scaling. Metabolic scaling is not merely the result of physical constraints, but is also mediated by various regulated processes involving resource supply and demand, metabolic waste removal, and heat dissipation [10,27,96].

I also encourage investigators to employ well-controlled experiments and incisive comparative analyses to test further the relative merits of multiple theoretical models. All too often investigators have tested single models without considering the relative merits of alternative models. Testing “multiple working hypotheses” [126] simultaneously in a variety of taxa under diverse physiological and ecological conditions is a promising approach for resolving heated debates about the relative

importance and range of applicability of various proposed mechanisms determining metabolic scaling (see e.g., [10,39,40,44,94,95,127,128]). In addition, attempts should be made to synthesize multiple models and mechanisms [10,32]. For example, synthesizing the MLBH with cell-size theory may expand the predictive power of both [26,129]. Although cell-size theory by itself cannot explain effects of T_a on the metabolic scaling exponent (see Section 3.1), it can, if combined with the MLBH. Thermally increased metabolic level may cause decreases in the scaling exponent for resting metabolic rate, not only because of the increased influence of surface-area related metabolic processes at the whole body level, but also at the cellular level, a hypothesis requiring testing [10,26,129]. Other examples of multi-mechanistic models of metabolic scaling are reviewed in [10,32].

4. Materials and Methods

The data sets used in this study were the best that I could find that showed the effects of ambient temperature on the scaling of metabolic rate, based on large samples of species with broad body-mass ranges. The ectotherm data sets [48,53] were the only ones available that used typical, native habitat temperatures (thus minimizing acute thermal stress responses). The endotherm data sets [56,58] were the only ones available that examined effects of ambient temperature on interspecific metabolic scaling in birds and mammals under normal atmospheric conditions. Resting/routine metabolic rate was estimated as the rate of oxygen consumption during fasting for crustaceans [53] fish [48] and mammals [58], and as rate of metabolized food energy (ingested–excreted energy) over several days for caged birds with stable body masses and essentially no extra energy demand beyond mere existence, i.e., “existence metabolism” [56]. Existence metabolism included energy used for maintenance, temperature regulation, food-processing and minimal locomotor activity, but excluded energy required for growth, reproduction, molting, migratory activity and fat deposition. Estimates of metabolized energy intake required determining the caloric content of ingested food and excreta. This method is comparable to that based on oxygen consumption during fasting because T_a affects the scaling slopes of existence metabolism and oxygen consumption rates in similar ways. As shown for existence metabolism (Figure 3), the interspecific scaling slope for oxygen consumption rate of birds decreases at lower T_a (30 °C: summer and winter scaling slopes = 0.658, 0.688 for passerines, and 0.701, 0.728 for non-passerines; 0 °C: summer and winter scaling slopes = 0.528, 0.531 for passerines, and 0.571, 0.594 for non-passerines [56]). Figure 3 depicts scaling relationships for existence metabolism, because they had larger sample sizes (and thus were more reliable) than those for oxygen consumption.

5. Conclusions

In my opinion, it is no longer a question of whether contingency or constraints affect metabolic scaling, but what are the relative roles of each. Continuing efforts to develop metabolic scaling theory based only on a single, universally applicable, physical mechanism are misguided. A comprehensive theory of metabolic scaling should be “meta-mechanistic”, i.e., it should recognize multiple, interactive mechanisms whose relative effects depend on various contingent intrinsic (biological) and extrinsic (ecological) conditions, within specified constraints [10]. The recently proposed contextual multimodal theory [10] offers one possible conceptual framework requiring further development and testing [32]. The challenge is to explain the actually observed diversity of metabolic scaling, not an idealized, non-existent 3/4-power law.

Acknowledgments: I thank the anonymous reviewers for their useful comments.

Conflicts of Interest: The author declares no conflict of interest.

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