PHILOSOPHICAL TRANSACTIONS B

royalsocietypublishing.org/journal/rstb

Opinion piece

Cite this article: Naug D. 2024 Metabolic scaling as an emergent outcome of variation in metabolic rate. *Phil. Trans. R. Soc. B* **379**: 20220495.
https://doi.org/10.1098/rstb.2022.0495

Received: 22 May 2023
Accepted: 6 November 2023

One contribution of 13 to a theme issue 'The evolutionary significance of variation in metabolic rates'.

Subject Areas:
behaviour, theoretical biology

Keywords:
metabolic rate, scaling, interindividual variation, heterogeneity, social insects, honeybees

Author for correspondence:
Dhruba Naug
e-mail: dhruba@colostate.edu

Metabolic scaling as an emergent outcome of variation in metabolic rate

Dhruba Naug

Department of Biology, Colorado State University, 1878 Campus Delivery, Fort Collins, CO 80523, USA

DN, 0000-0001-9252-8037

The allometric scaling of metabolic rate and what drives it are major questions in biology with a long history. Since the metabolic rate at any level of biological organization is an emergent property of its lower-level constituents, it is an outcome of the intrinsic heterogeneity among these units and the interactions among them. However, the influence of lower-level heterogeneity on system-level metabolic rate is difficult to investigate, given the tightly integrated body plan of unitary organisms. In this context, social insects such as honeybees can serve as important model systems because unlike unitary organisms, these superorganisms can be taken apart and reassembled in different configurations to study metabolic rate and its various drivers at different levels of organization. This commentary discusses the background of such an approach and how combining it with artificial selection to generate heterogeneity in metabolic rate with an analytical framework to parse out the different mechanisms that contribute to the effects of heterogeneity can contribute to the various models of metabolic scaling. Finally, the absence of the typical allometric scaling relationship among different species of honeybees is discussed as an important prospect for deciphering the role of top-down ecological factors on metabolic scaling.

This article is part of the theme issue 'The evolutionary significance of variation in metabolic rates'.

1. Introduction

The allometric scaling of metabolic rate is one of those fundamental questions in biology that has been extensively debated for a century [1–7]. It refers to the widespread observation that metabolic rate scales hypometrically with body size, which means that the mathematical relationship between the two can be defined by a power function with an exponent less than one. More popularly, this scaling phenomenon is often illustrated with the example of a mouse having a higher mass-specific metabolic rate than an elephant. Although there is considerable variation in the exact value of the observed scaling exponent, which might suggest a diversity of mechanisms at work (see [8–11] and [12] this issue), the search for a possible singular mechanism that underlies this biological rule has been a major pursuit in theoretical biology [13,14]. The question has increasingly attracted attention from a wider range of biologists with the advent of broad concepts such as the metabolic theory of ecology [15] and the pace-of-life hypothesis [16], ideas that place metabolic rate at the centre of all biological processes.

A mechanistic understanding of the scaling relationship is challenging, given the large number of correlated factors that might simultaneously contribute to it and the largely correlative support for the different competing hypotheses [17,18]. Any analysis of scaling based on measuring metabolic rate in whole organisms is problematic because such measurements are confounded by the several other variables that co-vary with body size [19]. This problem could be overcome to some extent if one were able to 'build' animals of different sizes using a set of parts with known metabolic rates and then predict the metabolic rate of the whole animal based on the metabolic rates of its parts [20], a possibility that is offered by colonial or modular animals [21–24]. The to-be-assembled parts

THE ROYAL SOCIETY PUBLISHING

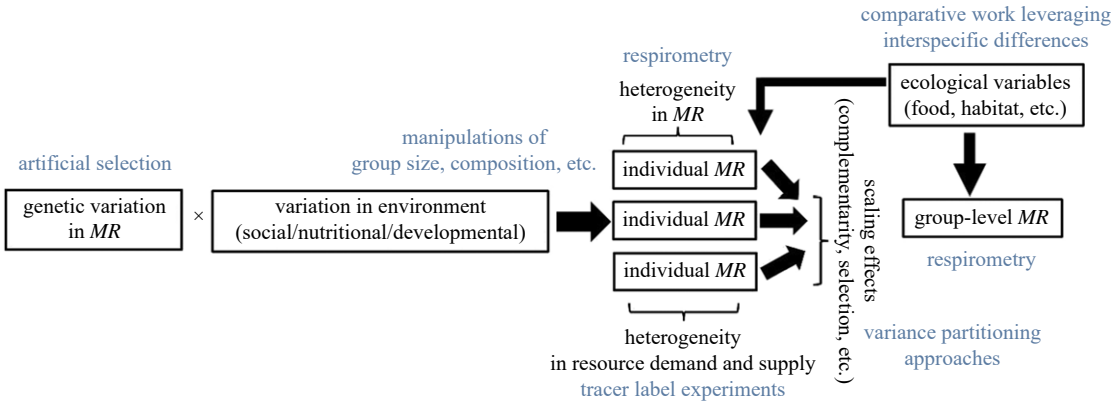

Figure 1. Schematic representation of the conceptual outline consisting of experimental and analytical frameworks that can potentially be used to pursue questions about metabolic scaling using honeybees (and other social insects) as a model system. Text in black represents the parameters of interest and text in blue represents the approaches to control and measure these parameters. MR, metabolic rate.

could either be homogeneous for simplicity or be sourced from a heterogeneous assortment that better reflects biological reality, in which case the exact composition of the admixture becomes an important variable. Such a bottom-up approach can in principle be extended across different levels of biological organization, spanning organs, tissues, cells, mitochondria, or even the enzymatic complex of respiration, to decipher how processes operating at these different levels contribute to the scaling process [25–29]. The goal of this paper is to discuss how such a bottom-up approach can be pursued at the organismal level using social insects as a model. A case is made specifically for honeybees, based on their amenability to a wide range of experimental techniques including artificial breeding that can generate individuals and therefore groups (colonies) with different metabolic rates, the suitability of such experimental data to some novel analytical approaches and the differences in metabolic rate among their different species that do not fit the usual size scaling relationship (figure 1).

2. Social insects as a model for metabolic scaling

The conceptual outline in which the property of a biological entity is the emergent outcome of its lower-level units is perfectly mirrored in a social insect colony. Often referred to as superorganisms, each of these colonies is defined by the sum of the attributes of all its members and their interactions. This means that the phenotypic expression at the higher level is an outcome of the phenotypic diversity at the lower level, comprised of a dynamic set of entities, which is also subject to the top-down modulatory influence of the social environment that they define [30]. In such cases, selection will act simultaneously on both the individual phenotypes and the group-level phenotype, defined by the group composition in terms of both the average and the variance, thereby generating phenotypic covariance among the interacting units [31,–33]. In the context of scaling, this means that the group-level metabolic rate depends on the group composition due not only to the intrinsic heterogeneity in metabolic rates among group members but also due to the social processes that can influence their metabolic rates. This suggests that the process by which a system-level metabolic rate emerges from the metabolic rate of its constituent parts is complex, being subject to both direct and indirect genetic effects on metabolic rate.

The major advantage social insects provide for understanding system-level properties such as metabolic scaling is that unlike most other biological organizations, a colony can both be easily separated into its constituent units as well as be reassembled in different configurations. This allows one to measure a given biological property at both the individual and the system level with relative ease, an approach that has been extensively leveraged to understand how the colony phenotype emerges from the processes operating at these two levels [34]. The large background in terms of such an approach in social insects provides a sophisticated framework, both in terms of theory and experiments, that can be applied to pursue questions regarding metabolic scaling. Using this approach to assemble groups of various sizes and/or phenotypic compositions that vary in their individual metabolic rates, one can test the relative influence of the various factors that have been proposed to explain metabolic scaling. Despite a substantial amount of research on metabolic rate in social insects, the potential of this framework has not been sufficiently leveraged—except for manipulations of group size to some extent—to address questions regarding metabolic scaling, with some notable exceptions that are discussed below.

(a) Size

Early studies with ants and honeybees demonstrated that metabolic rate indeed scales with increasing group size, but with substantial variation in the value of the scaling exponent across species and contexts [35–37]. More recently, a detailed test of metabolic scaling using interspecific comparisons showed that larger colonies use relatively less energy, which translates into lower rates of growth and reproduction but longer lifespan at the colony level, thereby demonstrating a possible functional connection between energetics and sociality [38]. Based on the general congruence of this scaling pattern in social insect colonies with what is seen in unitary organisms, it is parsimonious to assume that the organizational principles that dictate scaling are likely universal [39], and that social insects could be valid model systems for deciphering these mechanisms. However, the observed variation in scaling across taxa and contexts can also be interpreted as the reflection of a diversity in the mechanisms underlying scaling. It has therefore been pointed out that one should be cautious in generalizing the results of scaling

in social insects because, being mostly laboratory studies thus far, their lack of an ecological context might not have allowed the expression of the whole range of variables that are involved in driving the scaling process [7].

The importance of the ecological context is clear from the results of a series of experimental studies in scaling with seed-harvester ants (*Pogonomyrmex californicus*), which showed that isolated groups of workers display isometric scaling of metabolic rate, strongly suggesting that the social environment plays a critical role in driving the hypometric scaling relationship [40,41]. These studies, by controlling for possible constraints such as food supply, identified a higher disparity in activity rates among members in larger colonies to be the likely basis for the observed scaling. The social environment, however, may not be a simple function of colony size, as a different study found that a higher density or crowding, independent of colony size, can lead to an increase in colony-level metabolic rate [42]. Such studies point to the importance of understanding the various mechanisms that shape the interactions among lower-level units because there are numerous attributes of colony social organization such as phenotypic diversity, demography and structural organization, each of which contributes to heterogeneity in terms of the various parameters that are parts of the various models of metabolic scaling.

(b) Heterogeneity

Increase in body size in unitary organisms or colony size in colonial organisms is accompanied by increasing levels of morphological and behavioural complexity or heterogeneity among the constituent units [40,43–45]. This has led to the hypothesis that the observed variation in metabolic rate among animals and the scaling process are outcomes of the difference in the relative sizes of metabolically active organs or tissues [29]. It has been shown that organs with high metabolic activity are relatively smaller in larger animals, which can explain the observed hypometric scaling [25,46–48]. Similarly, it has also been argued that the relationship between metabolic rate and body size is primarily driven by the correlated change in cellular diversity [49,50]. However, until more recently, these so-called system composition models of metabolic scaling have been less appreciated [5] and this suggests that disentangling the correlation between size and heterogeneity can provide important insights for our understanding of metabolic scaling.

In social insects, heterogeneity is an integral part of social organization and the basis for division of labour in the colony [51,52]. Heterogeneity in worker size, or morphological caste differentiation, can result in not only an assortment of production and maintenance costs [39,53,54] but also of what these different caste members add to the colony in terms of energy provisioning. In ants, larger workers were shown to have lower mass-specific metabolic rates, which suggests that metabolic scaling in social insect colonies could result from a higher proportion of such large workers in larger colonies [55,56]. This suggests that colony composition, and thus heterogeneity, is the critical variable that drives the value of the scaling exponent. Manipulating morphological caste ratios independently of colony size can therefore test for this hypothesis, although it has limitations because individual body size can still confound the influence of other biological variables that co-vary with body size.

In this context, genetic lines with different metabolic rates, produced through artificial selection while controlling for other variables such as body size, offer opportunities for more direct experimental tests of metabolic scaling [25,57,58]. In social insects, such an approach is currently possible only with the honeybee, *Apis mellifera*, in which artificial crosses can be made using instrumental insemination. In *A. mellifera*, there is significant interindividual variation in metabolic rate associated with allelic variation in the malate dehydrogenase (MDH-1) locus [59–61]. Using MDH-1 as a convenient marker, bees with low and high metabolic rates can therefore be bred by making suitable crosses. While such bees with different metabolic rates have been bred and used for asking questions about the influence of metabolic rate on behaviour [62,63], they have not been used yet for testing ideas about metabolic scaling.

These low and high metabolic rate phenotypes, by allowing us to create colony admixtures with different proportions of these bees, can provide a rigorous experimental test of the influence of heterogeneity on metabolic scaling. The experimental methodology can be combined with an equally powerful analytical approach, based on the additive partitioning method of the Price equation, which can quantify the effect of heterogeneity as a diversity effect, defined as the deviation in a trait value of a polymorphic group from the null additive expectation set for the value by the same morphs in monomorphic groups [64,65]. This diversity effect can be further separated into two components, which itemize the two different processes through which diversity, positively or negatively, shapes a trait value. One of these is the selection effect, the disproportionate effect of any one morph on the trait, and the other is the complementarity effect, the degree to which interactions between the different morphs influence the trait. Diversity effects are frequency dependent processes in which the frequency of a phenotype has either a positive or a negative influence on the outcome of its expression, measured as differences in performance as a function of frequency [66].

A recent study with honeybees used the above approach to show that heterogeneity in metabolic rate at the individual level had a significant and complex influence on group-level metabolic rate, an effect that also varied depending upon the richness of the resource environment [63]. The metabolic rate of polymorphic groups was higher than expected in a low resource environment and lower than expected in a high resource environment. This resulted from significant diversity effects, which comprised nonsignificant selection effects but significant positive and negative complementarity effects, respectively. It is also worth noting that diversity effects are thought to be mediated by mechanisms related to resource competition [67] since all models of metabolic scaling are directly or indirectly tied to resource dynamics. Although the specific goals of this study were different, it nonetheless shows the promise of such an approach toward addressing questions about metabolic scaling.

(c) Resource demand and supply

It is interesting that the observed effects of heterogeneity on metabolic rate in honeybees depended on the resource environment. The lower than expected metabolic rate and consumption rate observed for heterogeneous groups in

the high resource environment [63] should translate to a hypometric scaling in terms of both of these parameters, arising from a negative effect of diversity. On the other hand, in a low resource environment, metabolic rate (but not consumption rate) was higher than expected in heterogeneous groups, which should lead to hypermetric scaling being an outcome of a positive diversity effect. These results suggest that there is an interactive effect between heterogeneity and the resource environment that influences metabolic rate at a higher level of organization.

The resource-based models of metabolic scaling explain it as either an outcome of constraints in resource supply [13,28], or a reduction in energetic (and therefore resource) demand [48,68] with increasing body size. However, the generally tight coupling between these two parameters at the level of the whole animal in unitary organisms [69] makes it difficult to test these alternative hypotheses. But in superorganisms such as honeybees, these two parameters are decoupled to some extent because the foraging rates of individual workers comprising the supply chain are dictated not so much by their own metabolic demands but rather more by the collective demand at the colony level. This allows opportunities to manipulate the two parameters partially independently of each other to create different supply demand ratios at the colony level. Colony demand can be manipulated by changing the amount of brood and/or food storage space, while the supply chain can be manipulated by taking advantage of the behavioural heterogeneity among workers in terms of their levels of foraging activity.

While activity level is an important part of ideas about metabolic scaling, based on its strong influence on the value of the scaling exponent [70,71], it is almost always based on how activity influences energy demand. In social insects, the primary idea in this context is that activity levels are expected to be lower in larger colonies and lead to energy savings [40,55,72]. This is due to the scaling effects seen in terms how work is organized in the colony [73]: larger colonies have more specialist workers, which allows more parallel processing of tasks, leading to increased work efficiency [74,75] and a higher proportion of inactive workers at any time [76]. However, it is important to recognize that rates of certain activities such as foraging, which are tied to individual metabolic rates [77,78], can also influence the scaling process by impacting the supply of energy and it is therefore important to distinguish between the two different outcomes of activity.

How activity levels are tied to differences in metabolic rate and energy dynamics is not simple. It depends on the proportion of the metabolic output that is allocated to fueling behavioural activities such as foraging, which supply energy into the system, versus what is allocated to other activities that consume energy [79]. There can be potentially opposite relationships between activity and (resting) metabolic rate as proposed by the performance and the allocation models, depending respectively on whether the measured metabolic rate represents the energy available for activity or the energy left over after provisioning for activity [80]. If hypometric scaling is explained by lower activity rates in larger groups, the associated energy savings come from an implicit assumption of a positive relationship between activity and metabolic rate (the performance model). However, an opposite relationship between activity and metabolic rate, as predicted by the allocation model, would imply that a lower activity level translates into a higher metabolic rate, which would lead to an observed hypermetric scaling in larger groups. It is therefore critically important to be careful and contextual about how metabolic rate is measured for a more fine-grained view regarding how activity can be expected to influence metabolic scaling.

Integrating behaviour can provide such contextually important information to some of these resource- and activity-based models of metabolic scaling. For example, size can have very different implications for unitary animals where it usually refers to body size, compared to group-living animals where it refers to group size. Just as in unitary organisms, constraints in supply can apply in larger colonies due to bottlenecks in the food distribution chain as the interaction network becomes increasingly non-random, with increase in colony size and higher spatial heterogeneity in the nest [81–84]. A constraint can also act at the level of resource collection as resource depletion can reduce foraging success in both the short term [85,86] and the long term [45,87]. Energy-poor environments are known to have a significant negative impact on metabolic rate [88,89], which in turn can lead to a lower value of the scaling exponent [90]. However, it is important to note that a larger colony, due to its better information-gathering abilities as a distributed network, can also expand the size of its foraging supply chain [76,91–94]. Therefore, while increasing size is generally proposed to pose limits to resource supply and distribution in the context of unitary organisms, larger groups can in fact be better at harvesting resources from the environment.

Models of metabolic scaling that are based on limitations in resource supply due to delivery constraints in the resource transport networks [28,95] require the measurement of supply demand levels at different levels of biological organization, which is a challenging task in unitary animals. By contrast, measuring these parameters in both isolated individuals and in experimental groups of different sizes or phenotypic compositions, is relatively simpler in social insects. Specifically, adult honeybees, which almost exclusively depend on ingested carbohydrates to fuel their metabolic activity and store little of the ingested amount [96,97] are ideal for testing the link between supply and demand at the individual level. For colony-level measurements of resource flow, various tracer-based techniques have been successfully used to measure the spatial and temporal dynamics of the supply chain network [98–100]. Such experiments can provide information regarding the nature of supply limitations at a group level and test the key idea of whether metabolic rates of lower-level units are mass-independent *in vitro* but not *in vivo*, where the rate would correspond to the scaling of the supply network. Since there is substantial heterogeneity in supply demand ratios across individual honeybees that is correlated to their metabolic rates [101], it also suggests that resource flow within the colony, and thereby any supply limitations, can be influenced by the phenotypic composition of the group.

(d) Interspecific comparisons

The theory of metabolic scaling is most conspicuously illustrated by interspecific comparisons (such as mouse versus elephant), largely because such data allow for the large range in body mass that is required to robustly demonstrate this principle. However, such comparisons have the potential to be confounded by the large ecological and evolutionary

differences among species [102–104]. A few such comparisons in social insects, while being consistent with the general allometric principle, show a wide range in terms of the exact value of the scaling exponent [38]. A key finding from such studies is that species with low activity rates or 'tempo' tend to show a lower metabolic rate than those with high tempo [56,73], which might suggest that the fundamental mechanisms that contribute to metabolic scaling are universal and apply at both intra- and interspecific levels, largely overshadowing any ecological and evolutionary differences among them.

Honeybees, being a monophyletic group, present the opportunity to study the evolutionary modification of a common phylogenetic plan that has been subject to different ecological pressures [105]. In honeybees, interspecific differences in metabolic rate are strongly associated with differences in nesting habit and correlated differences in worker tempo. The workers of the two cavity-nesting, high tempo species *Apis mellifera* and *Apis cerana* have significantly higher metabolic rates than workers of the two open-nesting, low tempo species, *Apis florea* and *Apis dorsata*, a pattern that also extends to the colony level [105] and lines up with several behavioural and life-history differences, but not with body size, along expected lines [106]. This independence of interspecific differences in metabolic rate from differences in body size, which is a departure from the allometric principle of metabolic scaling, strongly points to the important role of ecology (nesting habit in this case) and other top-down factors acting at a higher level of organization (the colony in this case) in shaping the metabolic rate of lower-level units. The two species with low metabolic rate span the two ends of the body size range in honeybees, with the largest species, *A. dorsata*, being about five times as large as the smallest species, *A. florea*, while the two species with high metabolic rate are intermediate in body size. Given this independence of metabolic rate from body size, determining the scaling relationships in the four different species, combined with other behavioural and life-history measures, can provide a more comprehensive analysis of how top-down and bottom-up forces interact to drive metabolic scaling, an opportunity that has surprisingly attracted relatively little interest so far. The importance of understanding the influence of such myriad life history and ecological differences on scaling is also highlighted by a finding that the scaling of metabolic rate changes from a hypermetric to a hypometric relationship at a certain body size in flying insects, possibly due to an advantage of lower flight costs in smaller species [107].

3. Conclusion

The metabolic theory of ecology suggests that the functional properties at any level of biological organization, from cells to societies and ecosystems, are a composite function of the metabolic rate of its constituent parts [15]. Since heterogeneity is an intrinsic component at each of these levels, having the experimental ability to disintegrate the system into its component parts and to understand the interactions among them allows tests of the various hypotheses of metabolic scaling at different levels. The effects of heterogeneity go beyond the obvious that different constituent units of the whole system have their own unique energy dynamics. The critical role of heterogeneity is embedded in the interactions among the different parts and how that in turn defines their expression, leading to a seemingly infinite feedback loop. Several authors have advocated for more multidimensional and integrative models of metabolic scaling [3,9,108–110], and while such models may better reflect the biological reality, they are probably not as appealing as a more general and grand unified theory from a more reductionist perspective [13]. Despite such different opinions, what is indisputable is that metabolic scaling is clearly an emergent outcome of the complex set of interactions among heterogeneous units that define a biological system, and social insects such as honeybees offer a convenient model to explore the various bottom-up and top-down processes operating across its different levels of organization.

Data accessibility. This article has no additional data.

Authors' contributions. D.N.: conceptualization, funding acquisition, writing—original draft, writing—review and editing.

Conflict of interest declaration. I declare I have no competing interests.

Funding. National Science Foundation USA, Foundation for Food and Agricultural Research, and the Fulbright Program.

Acknowledgements. I would like to thank Amanda Pettersen and Neil Metcalfe for inviting me to be a part of the symposium and this special section on the evolutionary significance of variation in metabolic rate. Two referees who read an earlier version of the manuscript made several suggestions that clarified, improved and tightened-up the perspective presented here. Thanks are also due to the National Science Foundation USA, the Fulbright Program and the Foundation for Food and Agricultural Research, the funding from which have allowed my explorations in metabolic rate.

References

1. Kleiber M. 1932 Body size and metabolism. *Hilgardia* **6**, 315–353. (doi:10.3733/hilg.v06n11p315)
2. Savage VM, Gillooly JF, Woodruff WH, West GB, Allen AP, Enquist BJ, Brown JH. 2004 The predominance of quarter-power scaling in biology. *Funct. Ecol.* **18**, 257–282. (doi:10.1111/j.0269-8463.2004.00856.x)
3. O'Connor MP, Kemp SJ, Agosta SJ, Hansen F, Sieg AE, Wallace BP, McNair JN, Dunham AE. 2007 Reconsidering the mechanistic basis of the metabolic theory of ecology. *Oikos* **116**, 1058–1072. (doi:10.1111/j.0030-1299.2007.15534.x)
4. Isaac NJB, Carbone C. 2010 Why are metabolic scaling exponents so controversial? Quantifying variance and testing hypotheses. *Ecol. Lett.* **13**, 728–735. (doi:10.1111/j.1461-0248.2010.01461.x)
5. Glazier D. 2014 Metabolic scaling in complex living systems. *Systems* **2**, 451. (doi:10.3390/systems2040451)
6. Maino JL, Kearney MR, Nisbet RM, Kooijman SALM. 2014 Reconciling theories for metabolic scaling. *J. Anim. Ecol.* **83**, 20–29. (doi:10.1111/1365-2656.12085)
7. Harrison JF *et al.* 2022 An integrated perspective on the causes of hypometric metabolic scaling in animals. *Integr. Comp. Biol.* **62**, 1395–1418. (doi:10.1093/icb/icac136)
8. White CR, Cassey P, Blackburn TM. 2007 Allometric exponents do not support a universal metabolic allometry. *Ecology* **88**, 315–323. (doi:10.1890/05-1883)
9. Glazier DS. 2010 A unifying explanation for diverse metabolic scaling in animals and plants. *Biol. Rev.* **85**, 111–138. (doi:10.1111/j.1469-185X.2009.00095.x)
10. Glazier DS. 2022 Variable metabolic scaling breaks the law: from 'Newtonian' to 'Darwinian' approaches. *Proc. R. Soc. B* **289**, 20221605. (doi:10.1098/rspb.2022.1605)
11. Pettersen AK, Marshall DJ, White CR. 2018 Understanding variation in metabolic rate. *J. Exp. Biol.* **221**, jeb166876. (doi:10.1242/jeb.166876)
12. Pettersen A, Metcalfe N. 2023 Consequences of the cost of living: is variation in metabolic rate

evolutionary significant? *Phil. Trans. R. Soc. B* **378**, 20220498. (doi:10.1098/rstb.2022.0498)

13. West GB, Brown JH, Enquist BJ. 1997 A general model for the origin of allometric scaling laws in biology. *Science* **276**, 122–126. (doi:10.1126/science.276.5309.122)
14. West GB, Brown JH, Enquist BJ. 1999 The fourth dimension of life: fractal geometry and allometric scaling of organisms. *Science* **284**, 1677–1679. (doi:10.1126/science.284.5420.1677)
15. Brown JH, Gillooly JF, Allen AP, Savage VM, West GB. 2004 Toward a metabolic theory of ecology. *Ecology* **85**, 1771–1789. (doi:10.1890/03-9000)
16. Réale D, Garant D, Humphries MM, Bergeron P, Careau V, Montiglio P-O. 2010 Personality and the emergence of the pace-of-life syndrome concept at the population level. *Phil. Trans. R. Soc. B* **365**, 4051–4063. (doi:10.1098/rstb.2010.0208)
17. Kearney MR, White CR. 2012 Testing metabolic theories. *Am. Nat.* **180**, 546–565. (doi:10.1086/667860)
18. Harrison JF. 2018 Approaches for testing hypotheses for the hypometric scaling of aerobic metabolic rate in animals. *Am. J. Physiol.-Regul. Integr. Comp. Physiol* . **315**, R879–R894. (doi:10.1152/ajpregu.00165.2018)
19. McNab BK. 1988 Complications inherent in scaling the basal rate of metabolism in mammals. *Q. Rev. Biol.* **63**, 25–54. (doi:10.1086/415715)
20. Krebs HA. 1950 Body size and tissue respiration. *Biochim. Biophys. Acta* **4**, 249–269. (doi:10.1016/0006-3002(50)90032-1)
21. Nakaya F, Saito Y, Motokawa T. 2005 Experimental allometry: effect of size manipulation on metabolic rate of colonial ascidians. *Proc. R. Soc. B* **272**, 1963–1969. (doi:10.1098/rspb.2005.3143)
22. White CR, Kearney MR, Matthews PGD, Kooijman SALM, Marshall DJ. 2011 A manipulative test of competing theories for metabolic scaling. *Am. Nat.* **178**, 746–754. (doi:10.1086/662666)
23. Barneche DR, White CR, Marshall DJ. 2017 Temperature effects on mass-scaling exponents in colonial animals: a manipulative test. *Ecology* **98**, 103–111. (doi:10.1002/ecy.1624)
24. Burgess SC, Ryan WH, Blackstone NW, Edmunds PJ, Hoogenboom MO, Levitan DR, Wulff JL. 2017 Metabolic scaling in modular animals. *Invertebr. Biol.* **136**, 456–472. (doi:10.1111/ivb.12199)
25. Konarzewski M, Diamond J. 1995 Evolution of basal metabolic rate and organ masses in laboratory mice. *Evolution* **49**, 1239–1248. (doi:10.2307/2410448)
26. Hulbert AJ, Else PL. 2000 Mechanisms underlying the cost of living in animals. *Annu. Rev. Physiol.* **62**, 207–235. (doi:10.1146/annurev.physiol.62.1.207)
27. Kozłowski J, Konarzewski M, Gawelczyk AT. 2003 Cell size as a link between noncoding DNA and metabolic rate scaling. *Proc. Natl Acad. Sci. USA* **100**, 14 080–14 085. (doi:10.1073/pnas.2334605100)
28. West GB, Woodruff WH, Brown JH. 2002 Allometric scaling of metabolic rate from molecules and mitochondria to cells and mammals. *Proc. Natl Acad. Sci. USA* **99**, 2473–2478. (doi:10.1073/pnas.012579799)
29. Konarzewski M, Książek A. 2013 Determinants of intra-specific variation in basal metabolic rate. *J. Compar. Physiol. B* **183**, 27–41. (doi:10.1007/s00360-012-0698-z)
30. Farine DR, Montiglio P-O, Spiegel O. 2015 From individuals to groups and back: The evolutionary implications of group phenotypic composition. *Trends Ecol. Evol.* **30**, 609–621. (doi:10.1016/j.tree.2015.07.005)
31. Moore AJ, Brodie III ED, Wolf JB. 1997 Interacting phenotypes and the evolutionary process: I. Direct and indirect genetic effects of social interactions. *Evolution* **51**, 1352–1362. (doi:10.2307/2411187)
32. Wolf JB, Brodie ED, Cheverud JM, Moore AJ, Wade MJ. 1998 Evolutionary consequences of indirect genetic effects. *Trends Ecol. Evol.* **13**, 64–69. (doi:10.1016/S0169-5347(97)01233-0)
33. Wolf JB, Brodie ED, Moore AJ. 1999 Interacting phenotypes and the evolutionary process. II. Selection resulting from social interactions. *Am. Nat.* **153**, 254–266. (doi:10.1086/303168)
34. Wilson EO. 1985 The sociogenesis of insect colonies. *Science* **228**, 1489–1495. (doi:10.1126/science.228.4707.1489)
35. Galle L. 1978 Respiration as one of the manifestations of the group effect in ants. *Acta Biologica Szeged* **24**, 111–114.
36. Southwick EE. 1985 Allometric relations, metabolism and heart conductance in clusters of honey bees at cool temperatures. *J. Comp. Physiol. B* **156**, 143–149. (doi:10.1007/BF00692937)
37. Fonck C, Jaffé K. 1996 On the energetic cost of sociality. *Physiol. Behav.* **59**, 713–719. (doi:10.1016/0031-9384(95)02028-4)
38. Hou C, Kaspari M, Vander Zanden HB, Gillooly JF. 2010 Energetic basis of colonial living in social insects. *Proc. Natl Acad. Sci. USA* **107**, 3634–3638. (doi:10.1073/pnas.0908071107)
39. Gillooly JF, Hou C, Kaspari M. 2010 Eusocial insects as superorganisms. *Commun. Integr. Biol.* **3**, 360–362. (doi:10.4161/cib.3.4.11887)
40. Waters JS, Holbrook CT, Fewell JH, Harrison JF. 2010 Allometric scaling of metabolism, growth, and activity in whole colonies of the seed-harvester ant *Pogonomyrmex californicus*. *Am. Nat.* **176**, 501–510. (doi:10.1086/656266)
41. Waters JS, Ochs A, Fewell JH, Harrison JF. 2017 Differentiating causality and correlation in allometric scaling: ant colony size drives metabolic hypometry. *Proc. R. Soc. B* **284**, 20162582. (doi:10.1098/rspb.2016.2582)
42. Cao TT, Dornhaus A. 2008 Ants under crowded conditions consume more energy. *Biol. Lett.* **4**, 613–615. (doi:10.1098/rsbl.2008.0381)
43. Bell G, Mooers AO. 1997 Size and complexity among multicellular organisms. *Biol. J. Linnean Soc.* **60**, 345–363. (doi:10.1111/j.1095-8312.1997.tb01500.x)
44. Bonner JT. 2004 The size–complexity rule. *Evolution* **58**, 1883–1890. (doi:10.1111/j.0014-3820.2004.tb00476.x)
45. Naug D. 2009 Structure and resilience of the social network in an insect colony as a function of colony size. *Behav. Ecol. Sociobiol.* **63**, 1023–1028. (doi:10.1007/s00265-009-0721-x)
46. Itazawa Y, Oikawa S. 1986 A quantitative interpretation of the metabolism-size relationship in animals. *Experientia* **42**, 152–153. (doi:10.1007/BF01952441)
47. Daan S, Masman D, Groenewold A. 1990 Avian basal metabolic rates: their association with body composition and energy expenditure in nature. *Am. J. Physiol.-Regul. Integr. Compar. Physiol.* **259**, R333–R340. (doi:10.1152/ajpregu.1990.259.2.R333)
48. Wang Z, O'Connor TP, Heshka S, Heymsfield SB. 2001 The reconstruction of Kleiber's law at the organ-tissue level. *J. Nutr.* **131**, 2967–2970. (doi:10.1093/jn/131.11.2967)
49. McCarthy MC, Enquist BJ. 2005 Organismal size, metabolism and the evolution of complexity in metazoans. *Evol. Ecol. Res.* **7**, 681–696.
50. Takemoto K. 2015 Heterogeneity of cells may explain allometric scaling of metabolic rate. *Biosystems* **130**, 11–16. (doi:10.1016/j.biosystems.2015.02.003)
51. Oster GF, Wilson EO. 1978 *Caste and ecology in the social insects*. Princeton, NJ: Princeton University Press.
52. Oldroyd BP, Fewell JH. 2007 Genetic diversity promotes homeostasis in insect colonies. *Trends Ecol. Evol.* **22**, 408–413. (doi:10.1016/j.tree.2007.06.001)
53. Wilson EO. 1968 The ergonomics of caste in the social insects. *Am. Nat.* **102**, 41–66. (doi:10.1086/282522)
54. Lighton JRB, Bartholomew GA, Feener DH. 1987 Energetics of locomotion and load carriage and a model of the energy cost of foraging in the leaf-cutting ant *Atta colombica* Guer. *Physiol. Zool.* **60**, 524–537. (doi:10.1086/physzool.60.5.30156127)
55. Shik J. 2010 The metabolic costs of building ant colonies from variably sized subunits. *Behav. Ecol. Sociobiol.* **64**, 1981–1990. (doi:10.1007/s00265-010-1009-x)
56. Mason KS, Kwapich CL, Tschinkel WR. 2015 Respiration, worker body size, tempo and activity in whole colonies of ants. *Physiol. Entomol.* **40**, 149–165. (doi:10.1111/phen.12099)
57. Konarzewski M, Książek A, Łapo IB. 2005 Artificial selection on metabolic rates and related traits in rodents. *Integr. Comp. Biol.* **45**, 416–425. (doi:10.1093/icb/45.3.416)
58. Videlier M, Careau V, Wilson AJ, Rundle HD. 2021 Quantifying selection on standard metabolic rate and body mass in *Drosophila melanogaster*. *Evolution* **75**, 130–140. (doi:10.1111/evo.14126)
59. Coelho JR, Mitton JB. 1988 Oxygen consumption during hovering is associated with genetic variation of enzymes in honey-bees. *Funct. Ecol.* **2**, 141–146. (doi:10.2307/2389688)
60. Harrison JF, Fewell JH. 2002 Environmental and genetic influences on flight metabolic rate in the honey bee, *Apis mellifera*. *Compar. Biochem. Physiol.*

A **133**, 323–333. (doi:10.1016/S1095-6433(02)00163-0)

61. Cassano J, Naug D. 2022 Metabolic rate shapes differences in foraging efficiency among honeybee foragers. *Behav. Ecol.* **33**, 1188–1195. (doi:10.1093/beheco/arac090)
62. Harrison JF, Nielsen DI, Page Jr RE. 1996 Malate dehydrogenase phenotype, temperature and colony effects on flight metabolic rate in the honey-bee, *Apis mellifera*. *Funct. Ecol.* **10**, 81–88. (doi:10.2307/2390265)
63. Mugel SG, Naug D. 2022 Metabolic rate diversity shapes group performance in honeybees. *Am. Nat.* **199**, E156–E169. (doi:10.1086/719013)
64. Loreau M, Hector A. 2001 Partitioning selection and complementarity in biodiversity experiments. *Nature* **412**, 72–76. (doi:10.1038/35083573)
65. Takahashi Y, Tanaka R, Yamamoto D, Noriyuki S, Kawata M. 2018 Balanced genetic diversity improves population fitness. *Proc. R. Soc. B* **285**, 20172045. (doi:10.1098/rspb.2017.2045)
66. Arathi HS, Spivak M. 2001 Influence of colony genotypic composition on the performance of hygienic behaviour in the honeybee, *Apis mellifera* L. *Anim. Behav.* **62**, 57–66. (doi:10.1006/anbe.2000.1731)
67. Wennersten L, Forsman A. 2012 Population-level consequences of polymorphism, plasticity and randomized phenotype switching: a review of predictions. *Biol. Rev.* **87**, 756–767. (doi:10.1111/j.1469-185X.2012.00231.x)
68. Harrison JF. 2017 Do performance–safety tradeoffs cause hypometric metabolic scaling in animals? *Trends Ecol. Evol.* **32**, 653–664. (doi:10.1016/j.tree.2017.05.008)
69. Weibel ER, Hoppeler H. 2005 Exercise-induced maximal metabolic rate scales with muscle aerobic capacity. *J. Exp. Biol.* **208**, 1635–1644. (doi:10.1242/jeb.01548)
70. Niven JE, Scharlemann JPW. 2005 Do insect metabolic rates at rest and during flight scale with body mass? *Biol. Lett.* **1**, 346–349. (doi:10.1098/rsbl.2005.0311)
71. Glazier DS. 2009 Activity affects intraspecific body-size scaling of metabolic rate in ectothermic animals. *J. Comp. Physiol. B* **179**, 821–828. (doi:10.1007/s00360-009-0363-3)
72. Cao TT, Dornhaus A. 2013 Larger laboratory colonies consume proportionally less energy and have lower per capita brood production in *Temnothorax* ants. *Insectes Soc.* **60**, 1–5. (doi:10.1007/s00040-012-0256-4)
73. Fewell JH, Harrison JF. 2016 Scaling of work and energy use in social insect colonies. *Behav. Ecol. Sociobiol.* **70**, 1047–1061. (doi:10.1007/s00265-016-2097-z)
74. Jeanne RL. 1986 The organization of work in *Polybia occidentalis*: costs and benefits of specialization in a social wasp. *Behav. Ecol. Sociobiol.* **19**, 333–341. (doi:10.1007/BF00295706)
75. Karsai I, Wenzel JW. 1998 Productivity, individual-level and colony-level flexibility, and organization of work as consequence of colony size. *Proc. Natl Acad. Sci. USA* **95**, 8665–8669. (doi:10.1073/pnas.95.15.8665)
76. Dornhaus A, Powell S, Bengston S. 2012 Group size and its effects on collective organization. *Annu. Rev. Entomol.* **57**, 123–141. (doi:10.1146/annurev-ento-120710-100604)
77. Feuerbacher E, Fewell JH, Roberts SP, Smith EF, Harrison JF. 2003 Effects of load type (pollen or nectar) and load mass on hovering metabolic rate and mechanical power output in the honey bee *Apis mellifera*. *J. Exp. Biol.* **206**, 1855–1865. (doi:10.1242/jeb.00347)
78. Mugel SG, Naug D. 2020 Metabolic rate shapes phenotypic covariance among physiological, behavioral, and life-history traits in honeybees. *Behav. Ecol. Sociobiol.* **74**, 129. (doi:10.1007/s00265-020-02901-5)
79. Biro PA, Stamps JA. 2010 Do consistent individual differences in metabolic rate promote consistent individual differences in behavior? *Trends Ecol. Evol.* **25**, 653–659. (doi:10.1016/j.tree.2010.08.003)
80. Careau V, Thomas D, Humphries MM, Réale D. 2008 Energy metabolism and animal personality. *Oikos* **117**, 641–653. (doi:10.1111/j.0030-1299.2008.16513.x)
81. Crailsheim K. 1998 Trophallactic interactions in the adult honeybee (*Apis mellifera* L.). *Apidologie* **29**, 97–112. (doi:10.1051/apido:19980106)
82. Naug D. 2008 Structure of the social network and its influence on transmission dynamics in a honeybee colony. *Behav. Ecol. Sociobiol.* **62**, 1719–1725. (doi:10.1007/s00265-008-0600-x)
83. Naug D. 2009 Nutritional stress due to habitat loss may explain recent honeybee colony collapses. *Biological Conservation* **142**, 2369–2372. (doi:10.1016/j.biocon.2009.04.007)
84. Pinter-Wollman N, Wollman R, Guetz A, Holmes S, Gordon DM. 2011 The effect of individual variation on the structure and function of interaction networks in harvester ants. *J. R. Soc. Interface* **8**, 1562–1573. (doi:10.1098/rsif.2011.0059)
85. Jun J, Pepper JW, Savage VM, Gillooly JF, Brown JH. 2003 Allometric scaling of ant foraging trail networks. *Evol. Ecol. Res.* **5**, 297–303.
86. Naug D, Wenzel JW. 2006 Constraints on foraging success due to resource ecology limit colony productivity in social insects. *Behav. Ecol. Sociobiol.* **60**, 62–68. (doi:10.1007/s00265-005-0141-5)
87. Roulston TAH, Goodell K. 2011 The role of resources and risks in regulating wild bee populations. *Annu. Rev. Entomol.* **56**, 293–312. (doi:10.1146/annurev-ento-120709-144802)
88. Lebeau J, Wesselingh RA, Van Dyck H. 2016 Nectar resource limitation affects butterfly flight performance and metabolism differently in intensive and extensive agricultural landscapes. *Proc. R. Soc. B* **283**, 20160455. (doi:10.1098/rspb.2016.0455)
89. Tomlinson S, Dixon KW, Didham RK, Bradshaw SD. 2017 Landscape context alters cost of living in honeybee metabolism and feeding. *Proc. R. Soc. B* **284**, 20162676. (doi:10.1098/rspb.2016.2676)
90. Finkel ZV, Irwin AJ, Schofield O. 2004 Resource limitation alters the 3/4 size scaling of metabolic rates in phytoplankton. *Mar. Ecol. Progr. Ser.* **273**, 269–279. (doi:10.3354/meps273269)
91. Fewell JH, Ydenberg RC, Winston ML. 1991 Individual foraging effort as a function of colony population in the honey bee, *Apis mellifera* L. *Anim. Behav.* **42**, 153–155. (doi:10.1016/S0003-3472(05)80618-9)
92. Pacala S, Gordon DM, Godfray HCJ. 1996 Effects of social group size on information transfer and task allocation. *Evol. Ecol.* **10**, 127–165. (doi:10.1007/BF01241782)
93. Mailleux A-C, Deneubourg JL, Detrain C. 2003 How does colony growth influence communication in ants? *Insectes Soc.* **50**, 24–31. (doi:10.1007/s000400300004)
94. Donaldson-Matasci MC, DeGrandi-Hoffman G, Dornhaus A. 2013 Bigger is better: honeybee colonies as distributed information-gathering systems. *Anim. Behav.* **85**, 585–592. (doi:10.1016/j.anbehav.2012.12.020)
95. Banavar JR, Damuth J, Maritan A, Rinaldo A. 2002 Supply–demand balance and metabolic scaling. *Proc. Natl Acad. Sci. USA* **99**, 10 506–10 509. (doi:10.1073/pnas.162216899)
96. Panzenböck U, Crailsheim K. 1997 Glycogen in honeybee queens, workers and drones (*Apis mellifera carnica* Pollm.). *J. Insect. Physiol.* **43**, 155–165. (doi:10.1016/S0022-1910(96)00079-0)
97. Hrassnigg N, Crailsheim K. 1999 Metabolic rates and metabolic power of honeybees in tethered flight related to temperature and drag (Hymenoptera: Apidae). *Entomologia Generalis* **24**, 23–30. (doi:10.1127/entom.gen/24/1999/23)
98. Naug D, Smith B. 2007 Experimentally induced change in infectious period affects transmission dynamics in a social group. *Proc. R. Soc. B* **274**, 61–65. (doi:10.1098/rspb.2006.3695)
99. Feigenbaum C, Naug D. 2010 The influence of social hunger on food distribution and its implications for disease transmission in a honeybee colony. *Insectes Soc.* **57**, 217–222. (doi:10.1007/s00040-010-0073-6)
100. Brodschneider R, Libor A, Kupelwieser V, Crailsheim K. 2017 Food consumption and food exchange of caged honey bees using a radioactive labelled sugar solution. *Plos One* **12**, e0174684. (doi:10.1371/journal.pone.0174684)
101. Reade AJ, Dillon M, Naug D. 2019 Spare to share? How does interindividual variation in metabolic rate influence food sharing in the honeybee? *J. Insect. Physiol.* **112**, 35–38. (doi:10.1016/j.jinsphys.2018.11.006)
102. Glazier DS. 2005 Beyond the '3/4-power law': variation in the intra-and interspecific scaling of metabolic rate in animals. *Biol. Rev.* **80**, 611–662. (doi:10.1017/S1464793105006834)
103. McNab BK. 2008 An analysis of the factors that influence the level and scaling of mammalian BMR. *Comp. Biochem. Physiol. A: Mol. Integr. Physiol.* **151**, 5–28. (doi:10.1016/j.cbpa.2008.05.008)

104. McNab BK. 2009 Ecological factors affect the level and scaling of avian BMR. *Comp. Biochem. Physiol. A: Mol. Integr. Physiol.* **152**, 22–45. (doi:10.1016/j.cbpa.2008.08.021)
105. Dyer FC, Seeley TD. 1991 Nesting behavior and the evolution of worker tempo in four honey bee species. *Ecology* **72**, 156–170. (doi:10.2307/1938911)
106. Bhagavan H, Brockmann A. 2019 *Apis florea* workers show a prolonged period of nursing behavior. *Apidologie* **50**, 63–70. (doi:10.1007/s13592-018-0618-7)
107. Duell ME, Klok CJ, Roubik DW, Harrison JF. 2022 Size-dependent scaling of stingless bee flight metabolism reveals an energetic benefit to small body size. *Integr. Comp. Biol.* **62**, 1429–1438. (doi:10.1093/icb/icac131)
108. Darveau C-A, Suarez RK, Andrews RD, Hochachka PW. 2002 Allometric cascade as a unifying principle of body mass effects on metabolism. *Nature* **417**, 166–170. (doi:10.1038/417166a)
109. Suarez RK, Darveau C-A, Childress JJ. 2004 Metabolic scaling: a many-splendoured thing. *Comp. Biochem. Physiol. B: Biochem. Mol. Biol.* **139**, 531–541. (doi:10.1016/j.cbpc.2004.05.001)
110. Suarez RK, Darveau CA. 2005 Multi-level regulation and metabolic scaling. *J. Exp. Biol.* **208**, 1627–1634. (doi:10.1242/jeb.01503)