

REPRODUCTIVE COST

Metabolic loads and the costs of metazoan reproduction

Samuel C. Ginther^{1*}, Hayley Cameron^{1,2}, Craig R. White¹, Dustin J. Marshall¹

Reproduction includes two energy investments—the energy in the offspring and the energy expended to make them. The former is well understood, whereas the latter is unquantified but often assumed to be small. Without understanding both investments, the true energy costs of reproduction are unknown. We present a framework for estimating the total energy costs of reproduction by combining data on the energy content of offspring (direct costs) and the metabolic load of bearing them (indirect costs). We find that direct costs typically represent the smaller fraction of the energy expended on reproduction. Mammals pay the highest reproductive costs (excluding lactation), ~90% of which are indirect. Ectotherms expend less on reproduction overall, and live-bearing ectotherms pay higher indirect costs compared with egg-layers. We show that the energy demands of reproduction exceed standard assumptions.

Reproduction is energetically costly, but these costs have been poorly quantified. The energy invested by parents includes a direct cost, which is the energy content within the offspring themselves, and an indirect cost, which is the energy expended to synthesize and carry offspring before their release—the metabolic load of reproduction (Fig. 1A). The direct costs of reproduction are well understood, but the indirect costs remain

unknown. Without a complete accounting of the total energy costs of reproduction, it is impossible to reconstruct how metazoans allocate energy to growth and reproduction across their ontogeny. Despite our incomplete understanding, fundamental biological theory makes strong assumptions about these energy flows (1–3).

Different theories make conflicting assumptions about the metabolic load of reproduction. Most assume that it is relatively small, whereas others do not distinguish between metabolic loads and total reproductive energy investment (table S1 and Fig. 1B). Life history models tend to assume that the energy contained in offspring represents most of the

energy devoted to reproduction, whereas the indirect costs of synthesizing, packaging, and carrying offspring are either unspecified or assumed to be zero. Mechanistic theories, on the other hand, include explicit estimates of indirect costs but assume that they are trivial, ranging from 5 to 25% of the total energy spent on reproduction. Unsurprisingly, these different assumptions yield very different conclusions about the fundamental drivers of metazoan life histories.

Because growth and reproduction are intimately linked by energy, fierce debates about the evolution of life histories, metabolic scaling, and the drivers of body size hinge on how much energy mothers invest into reproduction (4–7). For example, some theories posit that the redirection of energy from growth to reproduction eventually decelerates growth after maturation (3), whereas others maintain that the energy devoted to reproduction is minor and irrelevant to the slowing of growth later in life (table S1). These debates are insoluble as long as the costs of reproduction remain ambiguous, which hampers our ability to predict how organisms will grow and reproduce now and in the future (8).

The total costs of reproduction

In this work, we develop a quantitative framework for estimating the total energy costs of reproduction (Fig. 1) (9). Our approach borrows from classic physiological methods for estimating the costs of growth and the so-called heat of gestation in mammals (10, 11). Note that our use of the word cost here refers

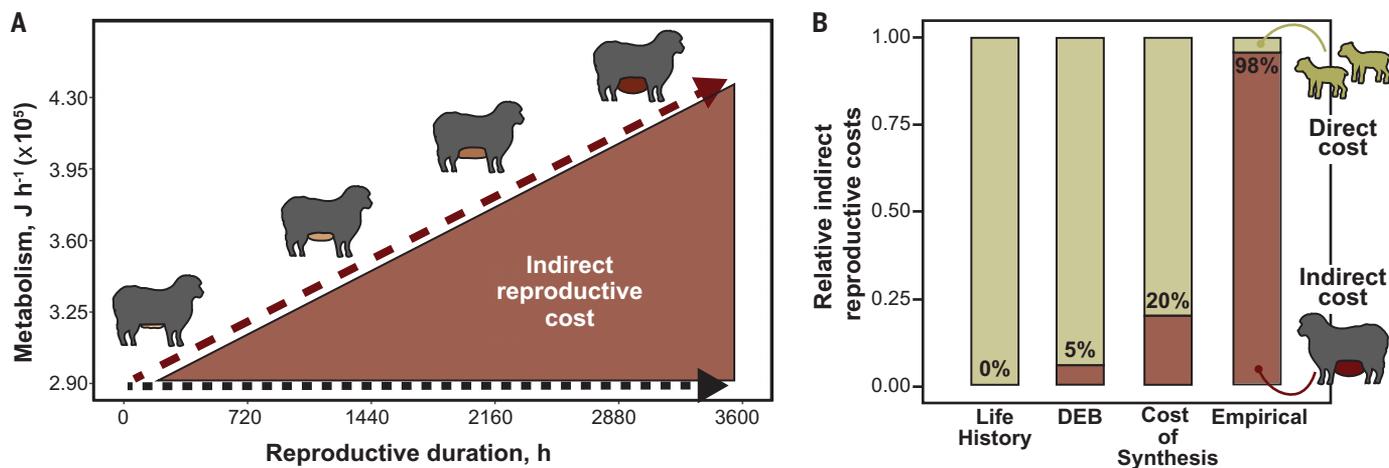


Fig. 1. The calculus of indirect costs of reproduction and contemporary theoretical assumptions. (A) Illustration of our framework for calculating indirect reproductive costs using empirical data from the sheep, *Ovis aries*, as an example. The key equation is $I = (L \times T)/2$ (Eq. 3), where I is indirect cost (in joules), L is the component of metabolic rate that is attributable to reproduction [i.e., the difference between nongravid (black line) and gravid metabolism (red line); joules per hour], and T is reproductive duration (hours). We assume that reproductive metabolism increases as a linear function of reproductive duration

(so the product of L and T is halved); this assumption was well supported by our data and was conservative (table S3) (9). (B) Relative indirect costs (R_i ; shown in red) are calculated as a proportion of total reproductive costs (indirect + direct costs). Relative direct costs (R_D) are also shown in yellow. Schematic shows assumed values of R_i for several prominent theory bases and the empirical value for the sheep example. DEB, dynamic energy budget theory. See table S1 for a summary of theoretical assumptions regarding the indirect costs of reproduction.

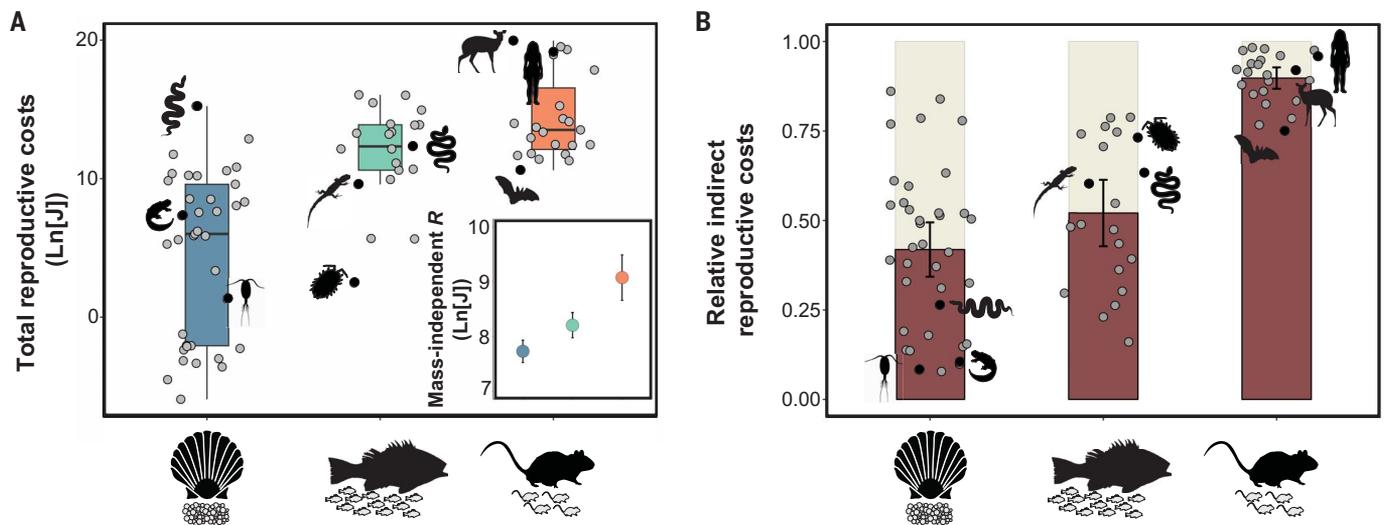


Fig. 2. Total reproductive costs and relative indirect costs are greatest in mammals. (A) Distribution of total reproductive costs (R ; joules) for oviparous ectotherms (spp. = 37; shown in blue), viviparous ectotherms (spp. = 21; green), and mammals (spp. = 23; orange). Shaded boxes and whiskers represent interquartile ranges, and horizontal lines show median values. Points represent individual species, and silhouettes of representative taxa correspond to the nearest black point. Inset shows mean estimate (\pm SE) of mass-independent reproductive costs (joules) (9). (B) Indirect reproductive costs relative to R (means \pm 95% confidence intervals; shown in red) for oviparous ectotherms, viviparous ectotherms, and mammals; mean direct costs relative to R are shown in pale yellow.

to energy costs in a physiological sense and differs from classic life history considerations that usually refer to reproductive costs as fitness trade-offs [in the sense of Stearns (12)]. We consider the energy content of the offspring (i.e., direct costs) and the metabolic load of reproduction (i.e., indirect costs) as

$$R = D + I \quad (1)$$

where R is the total energy expended on reproduction (reproductive costs; measured in joules). D (direct costs) is the total energy content of offspring (joules), estimated as the product of the mass of offspring from a single reproductive bout (M ; grams) and the average energy density of offspring tissue (E ; joules per gram), or

$$D = M \times E \quad (2)$$

I (indirect costs) is the metabolic load of reproduction (joules), which is estimated as the product of the increase in maternal metabolic rate attributable to reproduction (L ; joules per hour) and reproductive duration (T ; hours), or

$$I = \frac{L \times T}{2} \quad (3)$$

where the product of L and T is halved based on the assumption that reproductive metabolic rate increases linearly with reproductive duration (Fig. 1A) (9). Our definition of reproductive metabolic loads and durations only consider the phase of reproduction before offspring release and excludes postnatal care (e.g., lactation in mammals). Using this framework, we estimated the total costs of reproduc-

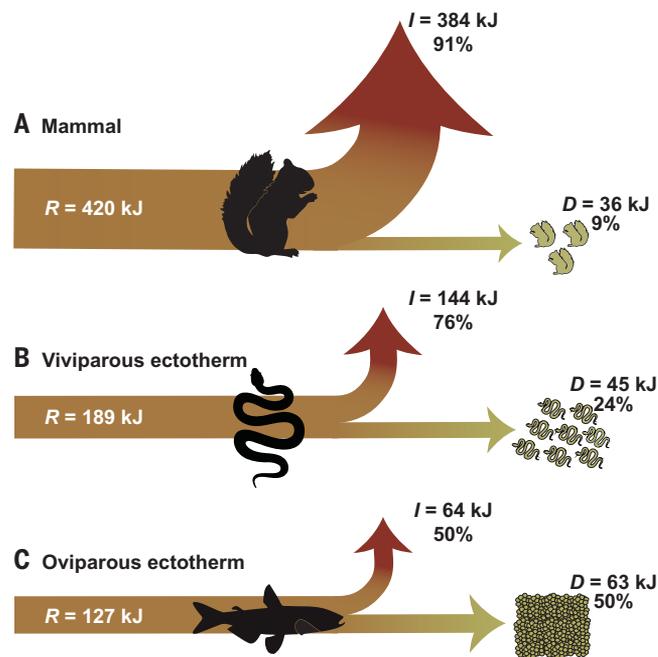


Fig. 3. Schematic showing the allocation of total reproductive energy to indirect and direct reproductive costs. Reproductive energy (R) is shown in orange, indirect reproductive costs (I) are indicated by red arrows, and direct reproductive costs (D) are indicated by yellow arrows. (A to C) Empirical estimates are provided for three species of comparable size: the mammal, *Glaucomys volans* (squirrel) (A); the viviparous ectotherm, *Tomodon dorsatus* (snake) (B); and the oviparous ectotherm, *Mallotus villosus* (fish) (C). Percentages describe the proportion of each component of reproductive costs (direct and indirect) relative to R for each species.

tion (R) and its constituents (D and I) with data for L , T , M , and E collated for 81 metazoans—from rotifers to humans. Our analyses did not include birds because we could only find data for two species (but see supplementary text 6).

Indirect costs of reproduction exceed direct costs in most animals

Across the animal kingdom, the total energy invested in reproduction spanned ~11 orders of magnitude, from 0.000003 kJ in a rotifer (*Brachionus plicatilis*) to 470,037 kJ in the

white-tailed deer (*Odocoileus virginianus*). Mammals expend more energy on reproduction compared with ectotherms (i.e., amphibians, arthropods, fish, marine invertebrates, and reptiles) overall—the energy invested in reproduction in the period up to the release of offspring is, on average, three times greater in mammals than ectotherms, after accounting for body size (Fig. 2A). In most species (48 of 81), indirect costs represented more than half of the total energy invested into reproduction, and in the most extreme case, indirect costs represented ~98% of the total reproductive energy (Fig. 2B).

Downloaded from https://www.science.org at Deakin University on March 17, 2026

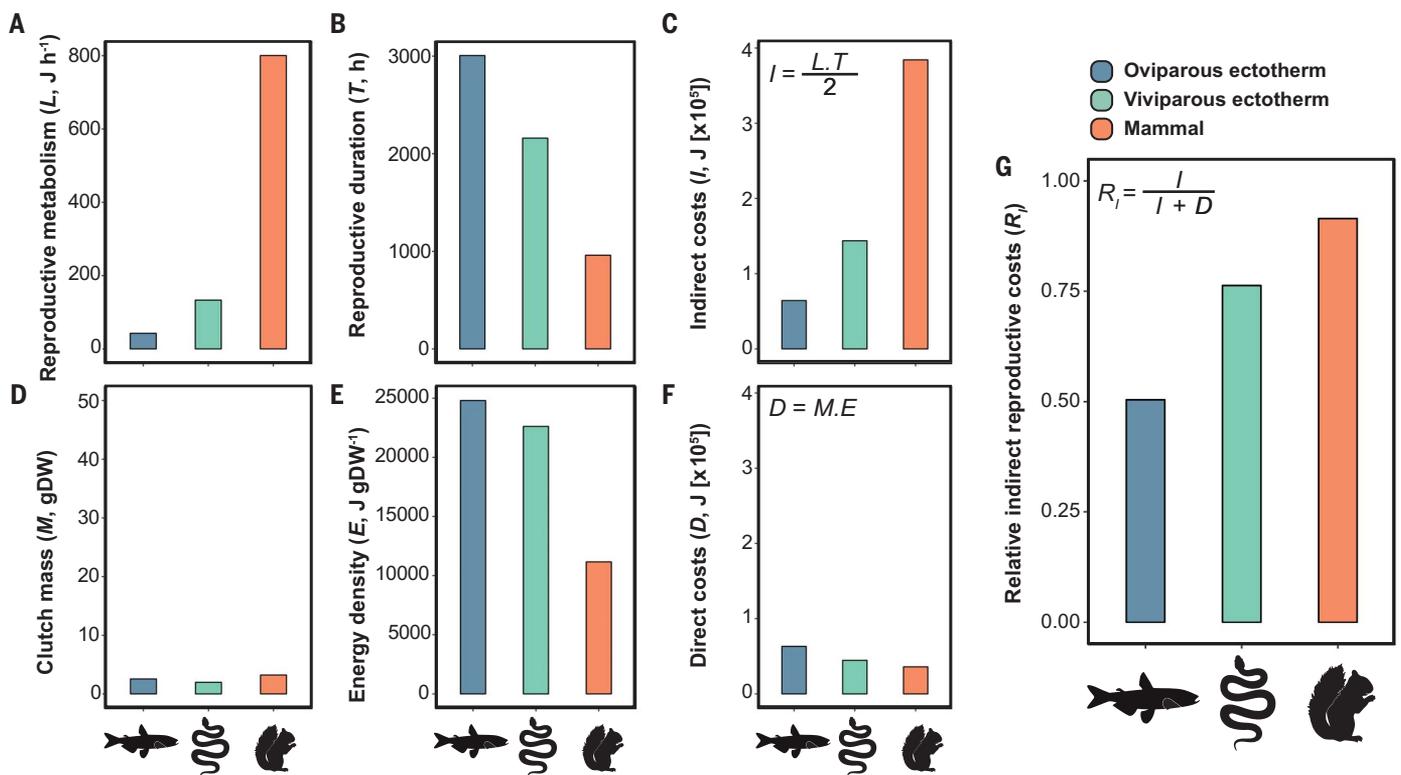


Fig. 4. The energy dynamics of reproduction differ across metazoans.

Empirical estimates for each component of reproductive costs are illustrated for species of similar size from each group—the oviparous ectotherm [*M. villosus* (fish); blue], the viviparous ectotherm [*T. dorsatus* (snake); green], and the mammal [*G. volans* (squirrel); orange]. (A to C) The product of reproductive metabolism (L ; joules per hour) (A) and reproductive duration

(T ; hours) (B) is used to calculate the indirect reproductive cost (I ; joules) (C). (D to F) The product of the mass of a single reproductive bout [M ; grams dry weight (gDW)] (D) and the energy density (E ; joules per gDW) (E) is used to calculate the direct reproductive cost (D ; joules) (F). (G) Relative indirect reproductive cost (R_i) is calculated as a proportion of total reproductive cost ($I + D$).

Ectotherms pay lower indirect costs compared with mammals (table S2, Fig. 2B, and fig. S1). In live-bearing ectotherms, indirect costs of reproduction were slightly higher than direct costs [average ratio of indirect to direct costs: $1.21:1 \pm 0.12$ standard error (SE)], but in egg-laying species, indirect costs were relatively lower ($0.44:1 \pm 0.20$ SE). In other words, viviparous species spend most (55%) of their reproductive energy on indirect costs, whereas oviparous species spend only 31% (Fig. 2B and fig. S1).

In mammals, indirect costs are approximately nine times greater than direct costs; offspring energy contents account for only 10% of the total energy spent on reproduction (average ratio: $8.62:1 \pm 0.97$ SE; table S2, Fig. 2B, and fig. S1). Humans have some of the highest metabolic loads of reproduction (96% of total costs), whereas the brown bat, *Myotis lucifugus*, has the lowest—yet, 75% of its reproductive energy is still spent on indirect costs (Fig. 2B and fig. S1).

Our findings about the indirect costs of gestation in mammals mirror those of the indirect costs of lactation: The energy expended by mothers to produce milk can exceed the

energy contained in the milk itself (13–15). Combining both pre- and postpartum investments, we find that the energy content of weaned offspring represents only one-twentieth of the total energy that is actually invested on average by mammalian mothers (supplementary text 1). In other words, 95% of the energy that mammalian mothers devote to reproduction is lost to metabolism.

Our framework shows that reproductive energy flows differ between mammals and ectotherms. To illustrate, we compare three representative species of similar size from these groups (Fig. 3). Based on classic measures of direct reproductive costs, oviparous ectotherms appear to invest the most in reproduction. But, by including indirect costs, we reveal that mammals expend more than triple the total reproductive energy of oviparous ectotherms and more than double that of viviparous ectotherms. Failing to account for indirect costs of reproduction therefore always underestimates the total energy expended on reproduction, particularly in mammals.

Mammals pay higher (prepartum) indirect costs than ectotherms, but within each of these

groups, reproductive metabolic loads (indirect costs) increase proportionally with the energy content of offspring [direct costs: ectotherms, scaling exponent (b) = 1.00 ± 0.03 SE; mammals, $b = 1.08 \pm 0.08$ SE] (table S2 and fig. S1). In other words, within each of our broad taxonomic groups, the ratio of indirect and direct costs remains the same, regardless of total reproductive investment.

The energy dynamics of reproduction and the costs of viviparity

Although indirect costs are consistently proportional to offspring energy content within animal groups, the energy dynamics of reproduction fundamentally differ between mammals and ectotherms (Fig. 4). Ectotherms and mammals produce similar cumulative masses of offspring per reproductive bout (Fig. 4D and supplementary text 2), but mammalian litters have lower energy densities (Fig. 4E and supplementary text 3) such that total direct costs are slightly lower for mammals on average (Fig. 4F). Nevertheless, these groups show stark differences in indirect reproductive costs: Although the time taken to produce and bear offspring

is less for mammals than that for ectotherms (Fig. 4B and supplementary text 4), mammals have an approximately sixfold higher increase in metabolism attributable to reproduction (Fig. 4A and supplementary text 5). When the duration of gestation and reproductive metabolism are combined, mammalian mothers experience much higher reproductive metabolic loads (indirect costs) compared with their ectothermic counterparts (Fig. 4C). On the other hand, endotherms are generally more active and have higher foraging and energy intake rates than ectotherms; consequently, viviparous ectotherms may commit the highest proportion of their available energy budget to reproduction overall (16, 17).

We suspect that high indirect costs of reproduction in mammals emerge from the synergistic effects of endothermy and viviparity. Endothermy increases energy expenditure per unit time (3); Mammalian mothers have higher absolute metabolic rates, as do their developing embryos. Viviparity exacerbates reproductive metabolic loads more generally: Indirect costs were higher in viviparous relative to oviparous ectotherms (table S2 and Fig. 4C). The increased metabolic load of viviparity could be due to offspring metabolism or metabolically expensive matrotrophic structures, such as placentas (18, 19). For the few birds for which we could find data, indirect costs of reproduction were comparable to those of live-bearing ectotherms (supplementary text 6), which implies that endothermy or viviparity alone do not incur the high costs of having both (as in mammals). More estimates of indirect reproductive costs in birds and monotremes should further resolve this issue. Either way, viviparity incurs higher indirect costs relative to oviparity within both thermoregulatory modes, and theory on the evolution of viviparity should be revised to reflect this. Theorized benefits of viviparity (e.g., higher rates of fertilization and reduced vulnerability of offspring during development) may be higher than has been appreciated to offset the higher energy costs of viviparous reproduction (20). Viviparous species have long been recognized to have lower fecundity relative to oviparous sister taxa (21, 22)—the increased metabolic load due to viviparity may contribute to this difference (23).

That mammals expend so much energy on reproduction before the birth of their offspring (relative to other clades) may shape their life history. Because mammalian mothers expend much more energy gestating their offspring, selection for ensuring the survival of these offspring should be stronger and may partially explain the increased intensity of postpartum care in mammals relative to other groups. Consequently, life history strategies common in other clades, such as brood reduction and bet-hedging, may be less beneficial in mammals (24, 25).

Reproductive costs are sensitive to global warming

Our study identifies a pathway by which temperature may affect the energy dynamics of ectothermic reproduction. Warmer temperatures decrease reproductive duration (reducing costs) but increase metabolic rates (raising costs) (26); their net effect depends on the relative temperature dependencies of both processes (27). Reproductive energy expenditure will increase with warmer temperatures whenever metabolic rate depends on temperature more strongly than does reproductive duration (27). For example, in the skink *Chalcides ocellatus*, a 3°C increase in temperature raises indirect costs by 20% (supplementary text 7). Temperature-mediated indirect costs may explain why mothers produce smaller offspring at warmer temperatures—higher reproductive metabolic loads reduce the energy that mothers can directly invest into their offspring unless resource acquisition also increases with temperature. Smaller offspring are often lower quality (28), such that changes in reproductive energy flows have worrying implications for population replenishment under global warming.

Reproductive costs shape life histories

Given that the energetic costs of reproduction for females have been underestimated, sometimes by an order of magnitude, the same may be true for males. A fundamental tenet of sexual selection theory is that both sexes expend equivalent energy on reproduction, albeit in different ways. Females spend energy on bearing and nourishing offspring, whereas males expend theirs on competition and attracting mates (29–31). Assuming that the tenet of equal energy expenditure between sexes remains true, our results imply that we have been underestimating the costs of producing ejaculates, the costs of securing mates, or both (32, 33). Estimating the metabolic load of sperm production seems like an important next step.

Indirect costs of reproduction have long gone unquantified and have traditionally been assumed to represent a minor fraction of the energy devoted to reproduction (table S1). We show that for most species, the opposite is true: Indirect costs account for more than half of reproductive energy expenditure. In other words, the total costs of reproduction have been systematically underestimated until now. That reproduction is more costly than was previously thought fundamentally challenges the calculus of biological models of metazoan growth and life histories (1, 3, 5–8, 34–36). For example, some models of growth assume that the fraction of total energy devoted to reproduction remains constant through time (1)—however, we show that it increases markedly during any one reproductive bout (9).

Other theories assume that the indirect costs of reproduction (or even the total costs of reproduction) represent a minor fraction of an organism's energy budget (5, 6). Instead, we show that the energy invested in reproduction can be an order of magnitude higher than is typically assumed. Our results imply that reproduction presents a massive energy demand, and the initiation of reproduction alters the energy flows within organisms profoundly. We suspect that metazoan ontogenies have evolved to anticipate and accommodate the substantial energy demands of reproduction (37).

REFERENCES AND NOTES

1. S. A. L. M. Kooijman, *Dynamic Energy Budget Theory for Metabolic Organisation* (Cambridge Univ. Press, 2010).
2. J. H. Brown, C. A. S. Hall, R. M. Sibly, *Nat. Ecol. Evol.* **2**, 262–268 (2018).
3. C. R. White, L. A. Alton, C. L. Bywater, E. J. Lombardi, D. J. Marshall, *Science* **377**, 834–839 (2022).
4. J. Kozłowski, J. Weiner, *Am. Nat.* **149**, 352–380 (1997).
5. D. Pauly, *Sci. Adv.* **7**, eabc6050 (2021).
6. M. R. Kearney, M. Jusup, *Science* **380**, eade9521 (2023).
7. C. R. White, D. J. Marshall, *J. Exp. Biol.* **226**, jeb245426 (2023).
8. M. Álvarez-Noriega, C. R. White, J. Kozłowski, T. Day, D. J. Marshall, *PLoS Biol.* **21**, e3002114 (2023).
9. Materials and methods are available as supplementary materials.
10. S. Brody, "Growth and development with special reference to domestic animals: XLVI. Relation between heat increment of gestation and birth weight." Research Bulletin 283 for Missouri Agricultural Experiment Station (University of Missouri, 1938).
11. W. Wieser, *Biol. Rev.* **69**, 1–33 (1994).
12. S. Stearns, *The Evolution of Life Histories* (Oxford Univ. Press, 1992).
13. O. T. Oftedal, in *Bioenergetics of Wild Herbivores*, R. J. Hudson, R. G. White, Eds. (CRC Press, 1985), pp. 215–238.
14. A. M. Prentice, A. Prentice, *Annu. Rev. Nutr.* **8**, 63–79 (1988).
15. T. H. Clutton-Brock, *The Evolution of Parental Care* (Princeton Univ. Press, 1991).
16. J. M. McNamara, A. I. Houston, *Evol. Ecol.* **6**, 170–185 (1992).
17. K. A. Nagy, *J. Exp. Biol.* **208**, 1621–1625 (2005).
18. I. Filin, *J. Theor. Biol.* **364**, 168–178 (2015).
19. K. R. Morrison, V. Ngo, R. A. Cardullo, D. N. Reznick, *Proc. R. Soc. B* **284**, 20171342 (2017).
20. R. Shine, *J. Theor. Biol.* **75**, 417–424 (1978).
21. S. Meiri, J. H. Brown, R. M. Sibly, *Glob. Ecol. Biogeogr.* **21**, 592–602 (2012).
22. D. Pincheira-Donoso et al., *Glob. Ecol. Biogeogr.* **30**, 1299–1310 (2021).
23. T. Foucart, O. Lourdaux, D. F. DeNardo, B. Heulin, *J. Exp. Biol.* **217**, 4049–4056 (2014).
24. D. Haig, *Am. Nat.* **136**, 550–556 (1990).
25. H. Olofsson, J. Ripa, N. Jonzén, *Proc. R. Soc. B* **276**, 2963–2969 (2009).
26. J. F. Gillooly, J. H. Brown, G. B. West, V. M. Savage, E. L. Charnov, *Science* **293**, 2248–2251 (2001).
27. D. J. Marshall, A. K. Pettersen, M. Bode, C. R. White, *Nat. Ecol. Evol.* **4**, 406–411 (2020).
28. D. J. Marshall, A. K. Pettersen, H. Cameron, *Funct. Ecol.* **32**, 1436–1446 (2018).
29. A. J. Bateman, *Heredity* **2**, 349–368 (1948).
30. G. C. Williams, *Adaptation and Natural Selection: A Critique of Some Current Evolutionary Thought* (Princeton Univ. Press, 1966).
31. R. I. Trivers, in *Sexual Selection and the Descent of Man*, B. Campbell, Ed. (Aldine, 1972), pp. 136–179.
32. G. A. Parker, M. E. Begon, *Proc. R. Soc. Lond. B* **253**, 255–262 (1993).
33. G. A. Parker, T. Pizzari, *Biol. Rev.* **85**, 897–934 (2010).
34. J. R. Burger, C. Hou, C. A. S. Hall, J. H. Brown, *Ecol. Lett.* **24**, 1262–1281 (2021).
35. M. R. Kearney, *Biol. Rev.* **96**, 557–575 (2021).

36. C. R. White, L. A. Alton, C. L. Bywater, E. J. Lombardi, D. J. Marshall, *Science* **380**, eadf5188 (2023).
37. J. R. Speakman, *Phil. Trans. R. Soc. B* **363**, 375–398 (2008).
38. S. C. Ginther, H. Cameron, C. R. White, D. J. Marshall, Data in support of “Metabolic loads and the costs of metazoan reproduction,” dataset, Zenodo (2024); <https://doi.org/10.5281/ZENODO.10460483>.

ACKNOWLEDGMENTS

We thank J. Van Dyke and M. Finkler for kindly supplying raw data, G. Jarvis for thoughtful discussions and technical advice with phylogenetic analyses, and the MEEG laboratory for their support. We are also grateful to N. Phillips, J. Shima, and the Wellington University Coastal Ecology Laboratory for providing S.C.G. with

office space. **Funding:** This study received funding from the Centre for Geometric Biology, Monash University (S.C.G., H.C., C.R.W., and D.J.M.). **Author contributions:** Conceptualization: S.C.G., H.C., C.R.W., and D.J.M. Data curation: S.C.G. Formal analysis: S.C.G., H.C., C.R.W., and D.J.M. Investigation: S.C.G. Methodology: S.C.G., H.C., C.R.W., and D.J.M. Project administration: S.C.G. and D.J.M. Visualization: S.C.G., H.C., C.R.W., and D.J.M. Writing – original draft: S.C.G., H.C., C.R.W., and D.J.M. Writing – review & editing: S.C.G., H.C., C.R.W., and D.J.M. **Competing interests:** The authors declare that they have no competing interests. **Data and materials availability:** The data needed to reproduce our results are hosted at Zenodo (38). **License information:** Copyright © 2024 the authors, some rights reserved; exclusive licensee American Association for the Advancement of Science. No claim to

original US government works. <https://www.science.org/about/science-licenses-journal-article-reuse>

SUPPLEMENTARY MATERIALS

[science.org/doi/10.1126/science.adk6772](https://doi.org/10.1126/science.adk6772)

Materials and Methods

Supplementary Text

Figs. S1 and S2

Tables S1 to S16

References (39–117)

MDAR Reproducibility Checklist

Submitted 7 September 2023; accepted 9 April 2024

[10.1126/science.adk6772](https://doi.org/10.1126/science.adk6772)



Metabolic loads and the costs of metazoan reproduction

Samuel C. Ginther, Hayley Cameron, Craig R. White, and Dustin J. Marshall

Science **384** (6697), . DOI: 10.1126/science.adk6772

Editor's summary

Reproduction is one of the biggest energy investments that an animal will make. It has also been well studied over many years, leading to much knowledge about how much energy is directly invested in the production of offspring. However, the other half of this investment, the cost of caring for offspring, was not clear. Ginther *et al.* developed a framework for estimating the overall costs of reproduction across taxa and teased apart the factors that contribute to the total. They found that caring for offspring is as much as 10 times more energy expensive than producing them, and this higher expense is the case not just in mammals (in which costs are the highest), but in other taxa as well. —Sacha Vignieri

View the article online

<https://www.science.org/doi/10.1126/science.adk6772>

Permissions

<https://www.science.org/help/reprints-and-permissions>

Use of this article is subject to the [Terms of service](#)

Science (ISSN 1095-9203) is published by the American Association for the Advancement of Science. 1200 New York Avenue NW, Washington, DC 20005. The title *Science* is a registered trademark of AAAS.

Copyright © 2024 The Authors, some rights reserved; exclusive licensee American Association for the Advancement of Science. No claim to original U.S. Government Works