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LETTER

Linking life-history theory and metabolic theory explains the offspring size-temperature relationship

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Abstract

Temperature often affects maternal investment in offspring. Across and within species, mothers in colder environments generally produce larger offspring than mothers in warmer environments, but the underlying drivers of this relationship remain unresolved. We formally evaluated the ubiquity of the temperature–offspring size relationship and found strong support for a negative relationship across a wide variety of ectotherms. We then tested an explanation for this relationship that formally links life-history and metabolic theories. We estimated the costs of development across temperatures using a series of laboratory experiments on model organisms, and a meta-analysis across 72 species of ectotherms spanning five phyla. We found that both metabolic and developmental rates increase with temperature, but developmental rate is more temperature sensitive than metabolic rate, such that the overall costs of development decrease with temperature. Hence, within a species' natural temperature range, development at relatively cooler temperatures requires mothers to produce larger, better provisioned offspring.

Keywords

Development, egg size, embryo size, incubation, larval size, maternal investment, metabolism.

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INTRODUCTION

Understanding variation in per-offspring maternal investment (offspring size) and its eco-evolutionary consequences has been a major goal of life-history theory for over 100 years (Morgulis 1909; Stearns 1992). Offspring size drives offspring performance, determines both maternal and offspring fitness, and has population- and community-level consequences (Benton *et al*. 2006; Martin & Pfennig 2010; Marshall *et al*. 2018). Theory holds that mothers balance the costs and benefits between making a few, larger and better-performing offspring, with making many smaller, poorer-performing offspring, resulting in a trade-off between size and fecundity (Smith & Fretwell 1974). A major challenge to theory is that temperature appears to alter the optimisation of this trade-off. Both among and within species, mothers in warmer conditions often (but not always) produce smaller offspring across a wide range of taxa and systems, and these effects manifest in both time (seasons) and space (latitude) (Harvey 1983; Fox & Czesak 2000; Laptikhovsky 2006; Marshall *et al*. 2012, 2018; Wootton & Smith 2014). Experimental manipulations of temperature show the same effect – cooler mothers often produce larger offspring than warmer mothers (see Atkinson *et al*. (2001) and Fig. 1 here for a formal meta-analysis). The offspring size-temperature relationship (OST) is pervasive in ectotherms, and is often associated with the more widely recognised relationship between temperature and adult body size: the temperature-size rule (TSR), where adults are often larger at cooler temperatures (Atkinson 1994). Whether the OST and TSR share the same biological drivers is unclear (Efford 1969; Yampolsky & Scheiner 1996; Hoefnagel *et al*. 2018).

Some theoretical considerations imply that the OST is a physiological by-product of the thermodynamics of development (Sinervo & Licht 1991; van der Have & de Jong 1996), but others argue that offspring size responses to the effects of temperature are maintained by selection (Sibly & Calow 1986; Yampolsky & Scheiner 1996; Partridge & Coyne 1997). For example, size-specific mortality may select for increased offspring size in colder environments (Perrin 1988). Transgenerational plasticity experiments demonstrate that changes in offspring size are adaptive responses to temperature-dependent selection (Bownds *et al*. 2010; Burgess & Marshall 2011). Similarly, experimental evolution studies have repeatedly shown evolutionary change in offspring size under different temperature regimes (Blanckenhorn 2000; Fischer *et al*. 2003). So, while the OST appears to be an adaptive response, broadly applicable explanations have not been tested comprehensively (Fox & Czesak 2000).

Here, we consider an explanation for the OST that has the potential to be widely applicable: the temperature dependence of development costs. During development, offspring are non-feeding and do not accumulate mass (i.e. there is no growth), relying entirely on endogenous reserves to meet maintenance and development requirements. Thus, the energy costs incurred during development are a product of the rate of energy expenditure (metabolic rate) and the time spent in this phase (development time Fig. 2a). The relative temperature sensitivity of these two biological rates should determine total energy costs, and hence residual energy upon completion of development. Kamler (1992) anticipated this exact hypothesis for a species of fish over 25 years ago, and similar ideas had been expressed even earlier (Efford 1969), but it has gone unexplored in other taxa since. Below, we build on these ideas to develop a simple model that formally links life-history theory with metabolic theory to explain the OST.

Following foundational theory by Vance (1973), if we assume that the primary function of maternal investment (and hence offspring size) is to provide offspring with sufficient

resources to reach a stage where they can feed for themselves (what we will call nutritional independence), then any factor that affects the costs of reaching independence should alter selection on offspring size (Pettersen *et al.* 2017; Marshall *et al.* 2018). If we assume that offspring size (OS) is shaped in part by the cost of reaching nutritional independence (C), then the minimum offspring size will scale with the cost of development,

$$OS_{\min} \propto C \quad (1)$$

and mothers must therefore produce larger offspring when C increases (Vance 1973).

From an energy perspective, C is simply a product of first, the time spent in the dependent phase, defined by total development time as a function of temperature ($D(T)$), which is inversely proportional to developmental rate ($D = 1/DR$), and second, the rate of energy expenditure during the dependent phase, metabolic rate as a function of temperature ($MR(T)$). The value of C, defined here as a function of temperature by $C(T)$, will depend on the relative temperature sensitivities of $D(T)$ and $MR(T)$,

$$C(T) = D(T) \times MR(T) \quad (2)$$

The relationship between temperature and the rate of these processes can be described by exponential functions, where a and b represent the temperature dependence of $D(T)$ and $MR(T)$, ∂ and γ are constants, α and β are the offspring mass scaling exponents for $D(T)$ and $MR(T)$ respectively, and T is temperature (°C). $C(T)$ can therefore be described by the product of development time at a given temperature, T,

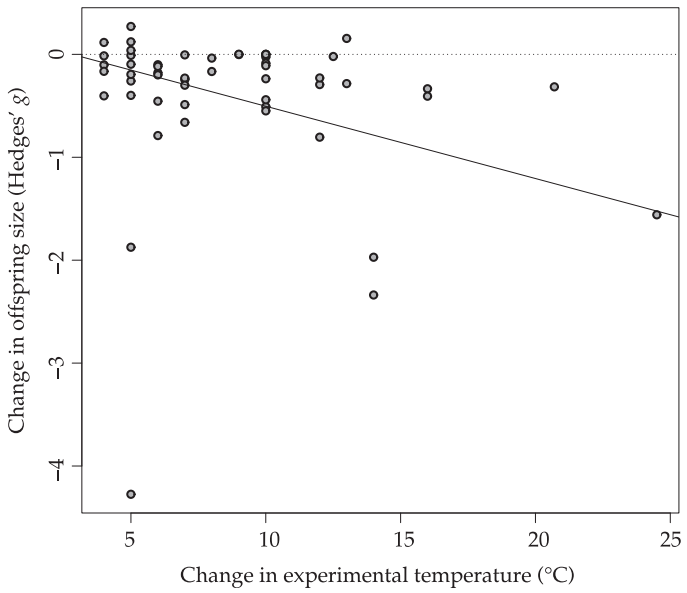

Figure 1 Relationship between Hedges' g (magnitude of change in offspring size with temperature, calculated using the mean, standard deviation and sample sizes for each temperature treatment) and change in experimental temperature (°C). Fitted line represents the final linear model for the correlation between change in experimental maternal brooding temperature and change in offspring size for 34 species (six phyla). Each dot represents a single result (12 species with more than one result was accounted for in the mixed model, see Table S1 for list of species).

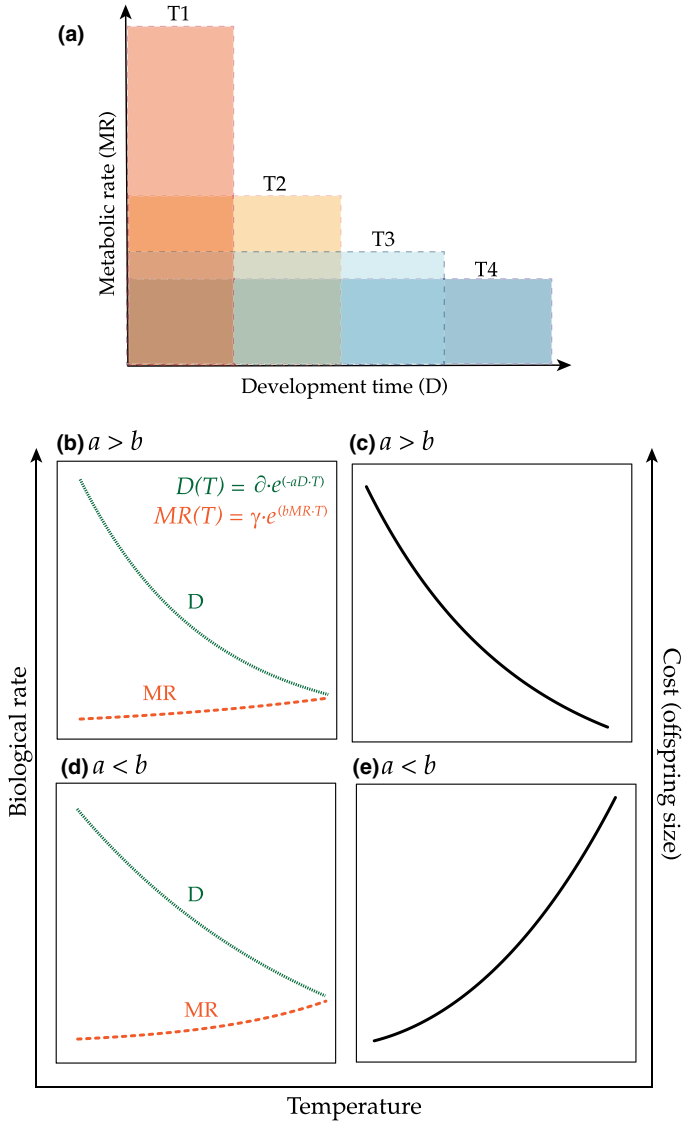

Figure 2 Schematic for the relationship between two biological rates: development time (D) and metabolic rate (MR). (a) As temperature increases from T4 to T1, development time is expected to decrease and metabolic rates will increase. Shaded areas represent the predicted costs of development (C) at each temperature where $C(T) = D(T) \times MR(T)$. In this example, C across all temperatures is equivalent. (b) Where the magnitude of the temperature sensitivity of D ($a = 0.2$) is greater than MR ($b = 0.1$), (c) total costs of development and therefore offspring size should decrease with temperature. (d) Alternatively, where the magnitude of temperature sensitivity of MR ($b = 0.2$) is greater, relative to D ($a = 0.1$), (e) total costs of development and offspring size should increase with temperature.

$$D(T) = \partial \times e^{(-aD \times T)} \times (\text{Offspring mass}^{a}) \quad (3)$$

and metabolic rate at a given temperature, T,

$$MR(T) = \gamma \times e^{(bMR \times T)} \times (\text{Offspring mass}^{\beta}) \quad (4)$$

Both development time and metabolic rate are highly temperature-dependent, and both are also affected by offspring size, albeit in complex ways (Gillooly *et al.* 2002; Clarke & Fraser

2004; Marshall & Keough 2008; Pettersen *et al.* 2015). Unless development time and metabolic rate have the same temperature dependence ($a = b$ in [3] and [4]), then the costs of development must change with temperature. If increases in temperature decrease development time more than they increase metabolic rate (i.e. $a > b$), then we would predict that the overall costs of development to independence to decrease with increasing temperature (Fig. 2b,c). Based on classic optimality theory, we would therefore expect warmer temperatures to result in decrease in offspring size because less energy is required for offspring to reach independence. Alternatively, if metabolic rate is more sensitive to temperature than development rate (i.e. $a < b$), then the reverse would be expected: increases in temperature will increase the costs of development and mothers should produce larger offspring in warmer temperatures (Fig. 2d,e).

Despite the potential for a metabolic life-history theory to provide a broad explanation for why warmer mothers produce smaller offspring, we are not aware of any systematic attempts to generate measures of the temperature dependence of metabolic rate and development rate simultaneously for a range of species. Here we took four steps: (1) We performed a phylogenetically controlled meta-analysis to determine the relationship between the temperature that mothers experience, and the size of their offspring within 34 species across six phyla. (2) We then experimentally manipulated temperature to examine the relative temperature dependencies of development time and metabolic rates during the dependent phase in two model systems, *Bugula neritina* (Linnaeus, 1758) and *Danio rerio* (Hamilton, 1822), throughout metamorphosis and embryogenesis respectively. Importantly, in both species, warmer mothers produce smaller offspring, and this relationship appears to be adaptive (Bownds *et al.* 2010; Burgess & Marshall 2011). (3) We then parameterised equations (2) through (4) for both our study species to determine how the costs of development change with temperature (4). In order to test whether our model is likely to apply more generally, we then combed the literature to compile estimates of the temperature dependence of development time and metabolic rate during development for a wide range of ectotherm species within their natural thermal range, while controlling for phylogenetic non-independence.

MATERIAL AND METHODS

Meta-analysis of temperature and offspring size

The methods used to produce a phylogenetically controlled meta-analysis were closely followed as per guidelines presented in the 'Preferred Reporting Items for Systematic Reviews and Meta-Analyses' (PRISMA) statement (Moher *et al.* 2009) – for details on methodological considerations and publication bias see Supporting information. For each study, the effect size of mean offspring/egg/larval diameter or length was calculated using Hedges' g to provide unbiased standardised mean differences in offspring size for the greatest temperature differential measured (Borenstein *et al.* 2011). To account for phylogenetic non-independence, we constructed a tree topology using the open tree of life and the 'rotl' package in R v3.3.2 (Hinchliff *et al.* 2015; Michonneau *et al.* 2016). Data were analysed using a phylogenetic mixed model implemented in 'ASReml-R' (Gilmour *et al.* 2009) and R v3.0.2, with inverse relatedness matrix calculated from the phylogenetic covariance matrix using the R package 'MCMCglmm'; Hadfield (2010). The phylogenetic mixed model approach allowed us to partition the variance between changes in offspring size with temperature (ΔT) due to the shared evolutionary history among the study species samples, relative to that independent of phylogeny.

We fit the phylogenetic mixed-effects (fixed slope, random intercepts) model including ΔT as a fixed effect and the relatedness matrix from the phylogeny as a random effect, on the effect size (Hedges' g) of temperature on offspring size. Likelihood ratio tests were then used to determine the significance of the effect of phylogeny, where phylogenetic signal was calculated as the proportion of variance – conditioned on the fixed effects – attributable to the random effect of phylogeny. This proportion of variance is equivalent to the more widely used metric of Pagel's lambda (λ) (Hadfield & Nakagawa 2010).

Empirical estimates of costs of development with temperature

Study species

In a series of experiments, offspring from two species, a marine invertebrate, *B. neritina* (Bryozoa: Cheilostomata) and a freshwater vertebrate, *D. rerio* (Chordata: Cypriniformes) were used to measure the temperature sensitivity of development time and metabolic rate (hereon referred to by genus). While offspring of *Bugula* and *Danio* exhibit very different life histories, they both possess a 'dependent phase' where early development is characterised by reliance on maternal energy investment until feeding structures are formed. Both species reproduce across a range of naturally varying temperatures, where mothers exposed to higher temperatures produce smaller offspring – and these shifts appear to be adaptive (Bownds *et al.* 2010; Burgess & Marshall 2011). Recent studies have shown the costs of development to be substantial in these species with a decline of up to 47% of initial energy in *Bugula* and 23% in *Danio* throughout the dependent phase (Pettersen *et al.* 2015, 2017). Thus, factors which exacerbate energy costs throughout the dependent phase will likely have important fitness consequences.

Bugula is an arborescent bryozoan with global distribution, colonising sheltered, subtidal structures. Reproductively mature colonies undergo internal fertilisation, brooding single larvae on individual maternal zooids. Larvae are released into the plankton, then settle onto a hard surface and undergo metamorphosis over approximately 3 days. From fertilisation until the end of metamorphosis, offspring are entirely dependent on maternally derived energy provisions. The completion of metamorphosis and the development of a feeding structure (the lophophore) thus represents the end of the 'dependent' phase where offspring commence feeding and are able to obtain external energy from the environment (Wendt 2000).

Danio is a commonly used laboratory model organism that naturally occupies slow-moving, shallow water bodies in the Indian subcontinent (Spence *et al.* 2008). *Danio* reproduces sexually by spawning gametes into the water column where fertilised eggs undergo several stages of development. Embryos rely on yolk supplies in the egg to meet energy

requirements for development until post-hatching, when feeding structures form, which occurs approximately 5 days after fertilisation under normal laboratory conditions (Bryson-Richardson *et al*. 2011; Hachicho *et al*. 2015).

Offspring sampling and size measurements

Offspring size may produce temperature-dependent or -independent effects on development and metabolic rates; therefore, the effect of offspring size was included in our estimates (Pettersen *et al*. 2015, 2017). Due to the destructive sampling of embryo mass, we used double sampling: one set of samples were used for measures of development rate or metabolic rate (outlined below) and the other to obtain estimates of offspring mass (for further detail, see Supporting information).

Development time under different temperature regimes

To determine the effect of environmental temperature on development time in *Bugula* and *Danio*, 96 larvae and 144 embryos were placed into each of four temperature treatments respectively (a total of 384 larvae and 576 embryos over six experimental runs). Treatments were representative of natural temperature ranges experienced by these species (Bownds *et al*. 2010; Scott & Johnston 2012), and parents were acclimated at temperatures within these ranges (18 ± 2 °C in *Bugula* and 28 ± 2 °C in *Danio*). Developing *Bugula* were maintained at one of the following temperature conditions: 12, 16, 20 or 24 °C; and *Danio* embryos were reared at 20, 24, 28 or 32 °C (for details, see Supporting Information).

Metabolic rate under different temperature regimes

Fluorescence-based oxygen measurements were taken throughout development of the 'dependent' phase to determine rate of oxygen consumption, or $\dot{V}O_2$ as per standard techniques (Pettersen *et al*. 2015). $\dot{V}O_2$, was measured at 24 h intervals (i.e. 'Time') from 6 h post-settlement/post-fertilisation in *Bugula* and *Danio*, respectively, throughout the dependent phase (for details, see Supporting information).

Total energy expenditure across offspring size and temperature

The $MR(T)$ estimates obtained from each nonlinear regression for each time (24 h intervals) were then multiplied by the duration spent at each time, (e.g. where D = 36 h, 24 h for Time 1, 12 h for Time 2) and where total time was calculated from the predicted $D(T)$ and combined to calculate total cost of development ($C(T)$) across the entire range of temperatures and offspring sizes measured, where $C(T) = D(T) \times MR(T)$.

Meta-analysis of temperature, development time and metabolic rate in other taxa

To determine whether the total costs of development decrease with temperature more generally, we compiled data on $D(T)$ and $MR(T)$ from studies of 72 species and analysed these data using a phylogenetically controlled meta-analysis. Due to the paucity of data on these rates under varying temperature regimes, we could not rely on search terms as per the previous meta-analysis. Rather, we combed the literature haphazardly using *ISI Web of Science* for a range of search terms and following relevant citations. We collated mean values of $MR(T)$ and $D(T)$, and natural temperature ranges ('T range') experienced by each species during the early life history when offspring are non-feeding and entirely dependent on maternally derived energy (i.e. throughout the 'dependent phase'). Where T range was not specified for the studies that measured $MR(T)$ and $D(T)$, we searched the literature for studies reporting temperature ranges for each species in similar locations. Total costs of development were then calculated by multiplying $D(T)$ and $MR(T)$ for the minimum and maximum temperature treatments used (within T range).

Most studies did not report sample size associated with measurements; for those studies that did report both sample size and estimates of error, we used generalised least squares using the 'gls' function within the 'nlme' R package (Pinheiro *et al*. 2011) to determine whether sample size was related to a higher precision of estimates. This approach has been suggested by Nakagawa & Lagisz (2016) for use in meta-analyses that measure only the absolute magnitude (i.e. mean) of the effect size on the response variable (i.e. effect of temperature on mean D and MR). We used phylogenetic generalised least squares to fit models where residuals are correlated (i.e. correlation structure taken from phylogeny) using the 'pgls' function in the R package 'caper' (Orme 2013).

The effect of temperature on the costs of development depended on the range of temperatures tested, relative to a species natural range; hence, we calculated the proportional change in the costs of development (ΔC) for a 10% increase in each species natural mean temperature (°C; ΔT). We found that the precision of the estimate (sample size) did not affect the magnitude of the relationship ($\chi^2 = 0.148$, P-value = 1); therefore, we incorporated all available data unweighted by the inverse of the precision of the estimate, and used a phylogenetically controlled approach as employed in Part 1 (Meta-analysis of temperature and offspring size), with phylogenetic signal estimated as Pagel's lambda (see detailed methods above). We again fit a mixed-effects model to test the fixed effect of ΔT and the random effect of the relatedness matrix from the phylogeny, on ΔC over a 10% increase in mean temperature.

RESULTS

Meta-analysis of temperature and offspring size

Offspring size decreased with increases in rearing temperature in 30 out of the 34 species for which we had published data (Fig. 1). The relationship between Hedges' g and ΔT for all species was significantly < 0 (Estimate ± SE: −0.06 ± 0.02, $F_{1,50} = 6.156$, $P < 0.05$). The proportion of variance attributable to phylogeny (conditioned on the fixed effects) was not significantly different from 0 (Estimate ± SE: 0.18 ± 0.22). Between and within species (between-study) variation accounted for 43 and 52% of all variance in the final model, respectively.

Table 1 Summary of scaling exponents and coefficients (± standard error; SE) for temperature (T), mass and metabolic rate (MR) of *Bugula neritina* and *Danio rerio* where $MR(T) = \gamma \times e^{(bMR \times T)} \times (\text{Offspring mass}^{\beta})$. Time 1 = 0 hps/0 hpf, Time 2 = 24 hps/24 hpf, Time 3 = 48 hps/48 hpf, Time 4 = 72 hps/72 hpf, Time 5 = 120 hps/120 hpf (where hps = hours post-settlement in *Bugula* and hpf = hours post fertilisation in *Danio*)

Time	Temperatures measured	Constant (γ)	Scaling exponent temperature (b)	Scaling exponent mass (β)
Bugula neritina				
1	24 °C, 20 °C, 16 °C, 12 °C	0.022 ± 0.002	0.065 ± 0.006	0.659 ± 0.153
2	24 °C, 20 °C, 16 °C, 12 °C	0.012 ± 0.001	0.096 ± 0.005	0.664 ± 0.114
3	16 °C, 12 °C	0.007 ± 0.001	0.196 ± 0.012	0.441 ± 0.175
4	12 °C	0.068 ± 0.015		0.609 ± 0.245
5	12 °C	0.101 ± 0.030		0.537 ± 0.270
Danio rerio				
1	32 °C, 28 °C, 24 °C, 20 °C	0.007 ± 0.001	0.085 ± 0.044	0.630 ± 0.213
2	32 °C, 28 °C, 24 °C, 20 °C	0.026 ± 0.005	0.092 ± 0.003	0.462 ± 0.160
3	28 °C, 24 °C, 20 °C	0.049 ± 0.012	0.092 ± 0.004	0.411 ± 0.180
4	24 °C, 20 °C	0.065 ± 0.022	0.094 ± 0.008	0.362 ± 0.221
5	20 °C	0.161 ± 0.109		0.629 ± 0.304

Total energy expenditure across offspring size and temperature

Development time

The temperature at which early-stage *Bugula* and *Danio* were reared significantly affected development time through the dependent phase – across the temperatures tested, development time decreased with temperature (Fig. S3). For both species, there was a main effect of Temperature (*Bugula;* $F_{1,275} = 1172.38$, $P < 0.0001$, *Danio*; $F_{1,547} = 8811.58$, $P < 0.0001$) but no effect of ln(Offspring Mass). The relationship between development time and temperature for *Bugula* was therefore best described by the exponential function,

$$\text{Development time } (\textit{Bugula}) = 6.054 \times 10^{3} \times e^{(-0.363 \times \text{Temperature})} + 3.241 \times 10^{1}$$

For *Danio*, the random effect of Experimental Run was significant ($\chi^2 = 7.11$, $P < 0.05$); however, its interactions with Temperature and ln(Offspring Mass) were not (i.e. slopes among runs were homogenous), so Experimental Run could be excluded from the final model. The temperature dependence of development time for *Danio* was described by,

$$\text{Development time } (\textit{Danio}) = 1.234 \times 10^{4} \times e^{(-0.224 \times \text{Temperature})} + 3.527 \times 10^{1}$$

Metabolic rate

We found a significant, positive relationship between Temperature and ln(MR) throughout the dependent phase across all time stages for both species (Fig. S4). The random effect of Run had a significant effect on ln(MR) for both species across almost all times measured (Supporting information, Table S4). Although there was considerable variation in the relationship between ln(Offspring mass) and ln(MR) among runs for each temperature, we found no support for fitting a random-slopes model overall. For each time, a single model was fit for the relationship between metabolic rate, mass and temperature (Table 1).

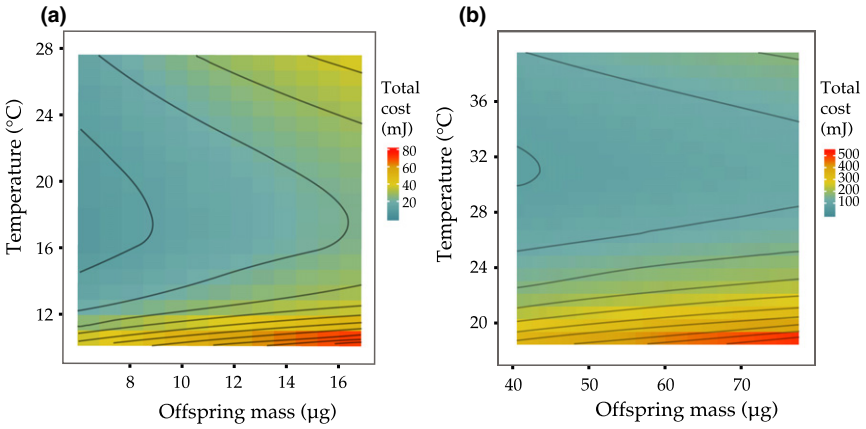

Figure 3 Predicted total costs of development (total mJ used) throughout the dependent phase in (a) *Bugula neritina* from larval settlement through to emergence of the lophophore over 10–30 °C and in (b) *Danio rerio* from fertilisation through to hatching as a larva over 18–40 °C. Warmer colours represent higher costs of development, where costs initially decrease with temperature, then increase at the upper limit of each species natural temperature range (>24 °C and >36 °C in *Bugula* and *Danio* respectively).

Total energy consumption

We found that total energy expenditure as a product of development time and metabolic rate was negatively related to temperature for both *Bugula* and *Danio* offspring – individuals developing at higher temperatures expended less energy overall than individuals at lower temperatures (Fig. 3, Table S5). We found higher energy costs associated with extending the dependent phase at lower temperatures, relative to increased metabolic rate at higher temperatures. However, the relationship between temperature and costs of development were not monotonic. At extreme temperatures (i.e. at the highest temperature treatment for *Bugula*; > 24 °C and those outside the natural temperature range of *Danio*; > 36 °C), our model predicted that the costs of development would begin to increase with temperature (Fig. 3).

Meta-analysis of temperature, development time and metabolic rate in other taxa

In line with our empirical estimates for the temperature-dependent costs of development in *Bugula* and *Danio*, we found similar patterns for the majority of the 72 species investigated. A 10% increase in natural mean developmental temperature was associated with a decrease in the costs of development (Fig. 4). Phylogeny explained less than 1% of the variance between costs of development and temperature ($\lambda \pm$ SE: 0.09 ± 0.14; $\chi^2 = 1.37$, $P = 1$); therefore, the final analysis was run as a linear model. The intercept for the relationship between a 10% increase in mean natural temperature (ΔT) and proportional change in the costs of development (ΔC) was significantly < 1 (Estimate ± SE: 0.79 ± 0.04; $P < 0.0001$) such that development costs decreased significantly when temperatures increased.

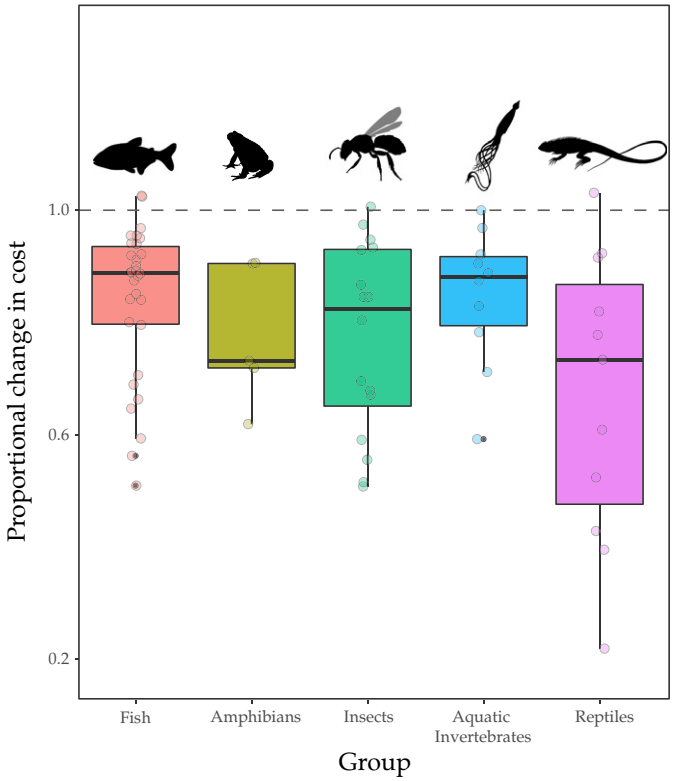

Figure 4 Proportional change in the costs of development with a 10% increase in temperature (relative to natural temperature range for each species), for 72 species (red = fish, yellow = amphibians, green = insects, blue = aquatic invertebrates, purple = reptiles). Each data point represents an individual species for which the costs of development were calculated (as per eqn 2; Table S6). A less than proportional change in the costs of development (values < 1) signifies a decrease in the costs of development with a 10% increase in natural mean temperature.

DISCUSSION

Costs of development as an explanation for the offspring size–temperature relationship

Through the use of metabolic life-history theory, we first show that OSTs are taxonomically widespread, and second, provide a potentially broad explanation for these patterns (Thorson 1936; Atkinson *et al.* 2001; Marshall *et al.* 2012). Building on proximal physiological mechanisms suggested by Kamler (1992), we propose an ultimate cause for the OST – the temperature-dependent costs incurred during development. Colder temperatures can elicit an adaptive response via offspring size, whereby mothers offset the increased costs associated with developing under colder environments by making larger offspring that possess greater amounts of energy. Repeatedly over the last 30 years, authors have speculated that the costs of development might decrease with temperature in a disparate range of species (Efford 1969; Gutzke *et al.* 1987; Booth & Thompson 1991; Angilletta *et al.* 2000; Irlich *et al.* 2009; DuRant *et al.* 2011) but none has provided an explicit and unifying mechanism until now. We show empirically that for two (very different) species, *B. neritina* and *D. rerio*, development time is more temperature sensitive than metabolic rate ($a > b$), such that the overall costs of development decrease with temperature. We also find that this pattern applies more broadly – for 72 species across five phyla, the costs of development are higher at cooler temperatures. In *Oncorhynchus mykiss*, for example, a 5 °C decline in incubation temperature incurred a 40% increase in the costs of development – this cost reflects an equivalent decrease in energy content of newly hatched larvae (Kamler 1992; Table 4.6). Our model also quantitatively predicts offspring size (and associated energy provisioning) changes in response to acute temperature change. We predict that a decrease from 25 °C to 19 °C during development increases the cost of development in *Bugula* by 5% and according to Burgess & Marshall (2011), this is exactly the increase in offspring size that is observed when mothers are reared under such conditions. While these values are remarkably congruent, there is no reason to expect that offspring size increases will perfectly match the increased costs of development for all species (Sniegula *et al.* 2016). Nevertheless, if minimum offspring size (OS_{min}) must at least provide for the costs of completing development, then our results could serve as a general explanation for why colder mothers produce larger offspring (Vance 1973).

Mechanisms driving the temperature dependence of the costs of development

While the effect of temperature on the costs of development may serve to explain the OST, the underlying biophysical mechanisms driving this relationship are less clear. Our data support suggestions by Zuo *et al*. (2012), that differences in the activation energies (i.e. temperature dependencies) of development and metabolism serve as potential drivers of change in developmental costs, but do not explain why the temperature dependencies of developmental processes differ. An explanation for why development is more temperature sensitive than metabolism may be physical. Development and metamorphosis require the division and differentiation of cells – there is some evidence that cell cleavage is extremely temperature-dependent because cell protoplasm viscosity mediates cell cleavage speeds (Marsland 1950; McLaren 1965). In a study on sea urchin eggs, Costello (1934) found an exponential decrease in cell viscosity with temperature, where the temperature sensitivity of protoplasm viscosity was greater than the temperature sensitivity of oxygen consumption, and viscosity decreased (and therefore development rate increased) more rapidly than the rate of oxygen consumption (metabolic rate) (Loeb & Wasteneys 1911; Loeb & Chamberlain 1915).

The costs of development increase at highest temperatures

Our model predicts that at temperatures beyond moderate temperature increases, the costs incurred during development increase. This prediction is supported for organisms from a wide range of phyla (Gophen 1976; Booth 1987; DuRant *et al*. 2011; Mueller *et al*. 2015; Akbar *et al*. 2016; Caamal-Monsreal *et al*. 2016). In *Pseudophryne bibronii*, costs of development decrease steadily with temperatures between 7 and 17 °C then increase at 22 °C (Seymour *et al*. 1991). We find the same pattern – beyond a particular threshold (24 °C in *Bugula* and 36 °C in *Danio*), the temperature sensitivity of metabolic rate becomes higher than the temperature sensitivity of development time ($b > a$) such that the costs of development increase with temperature. We predict that within the temperature range offspring usually experience, increasing temperatures will initially increase the energy efficiency (energy lost during development relative to initial investment) of offspring. Mothers, released from high per-offspring investment demands at warmer temperatures could therefore respond by increasing their fecundity. But, beyond certain temperatures, our model predicts that developmental costs should increase with further temperature increases, and mothers should increase offspring size in order to allow offspring to survive more costly development. These predictions are supported in *Danio* where mothers make smaller offspring when temperature is increased slightly but much larger offspring when temperature is increased substantially (Bownds *et al*. 2010). Similarly, the energy efficiency of development initially increases, then decreases with temperature in fish larvae (reviewed by Blaxter 1969a), and this relationship reflects natural variation in egg yolk size across seasons (Blaxter 1969b). Thus, our results have implications for global changes in temperature– under more extreme temperature increases, we expect developmental costs to increase, requiring mothers to make fewer, larger offspring that then waste more energy in order to complete development. These effects will be particularly strong for species living under cold temperature regimes. For example, in Antarctic krill *Euphausia superba*, our model predicts that an increase of 2 °C above its natural temperature range will increase the costs of development by 37% (Ross *et al*. 1988). Furthermore, future increases in temperature may result in fecundity decreases, but with no concomitant increase in offspring performance as development becomes more costly. Such effects would reduce the productivity of populations of ectotherms across a wide variety of taxa. Our model only applies for acute responses within natural temperature limits – above these ranges, the temperature dependence of development time and metabolic rate may reverse [see Forster *et al*. (2011)]. Measuring thermal performance across extreme temperature ranges, to gain full reaction norms of development time and metabolic rate is an important next step.

Alternative explanations for the relationship between offspring size and temperature

Our explanation of why warmer mothers reduce offspring size does not preclude other adaptive explanations [e.g. Perrin (1988); Yampolsky & Scheiner (1996); Atkinson *et al*. (2001)]. We recognise that the costs of development do not represent the sole source of selection on both offspring size and size at the completion of development (independence). Oxygen diffusion during incubation can pose physical constraints on offspring size (Fleming & Gross 1990; Seymour & Bradford 1995; Lee & Strathmann 1998). However, studies of the size-dependent fitness consequences of oxygen limitation are ambivalent (Woods 1999; Einum *et al*. 2002). While we did not detect any temperature-dependent mortality during development, oxygen limitation could be driving these effects for temperatures outside those of a species natural range that is if size-dependent oxygen limitation is exacerbated at higher temperatures such that larger eggs are more sensitive to increases in developmental temperature. Alternatively, because offspring size can be constrained by maternal body size, the OST may be merely a consequence of the TSR, enabling mothers to increase the size of their offspring in response to selection in colder environments (Congdon & Gibbons 1987). While this is a plausible explanation for field-based studies, laboratory manipulations of maternal rearing temperature can control for maternal size, and is therefore unlikely to serve as a general explanation for the OST. It is feasible that the proximal constraints discussed here may not be mutually exclusive explanations, but work complementarily with the temperature-dependent costs of development to drive the OST.

CONCLUSIONS

Through a combination of experimental manipulations and meta-analyses, we show that the energy costs incurred during development change with temperature. Over natural temperature ranges, development in cooler environments is more energetically expensive than development in warmer temperatures, and mothers must provision their offspring accordingly. We

also predict that beyond natural temperature ranges experienced by a species, the costs of development should increase. These findings have worrying implications for the effects of global warming on ectotherm life histories – initially costs will decrease with temperature, yet beyond this point higher temperatures will force mothers to increase their per offspring investment to offset more costly development, at the expense of fecundity. How the costs of development change with temperature can extend beyond individual-level fitness consequences, to inform life-history theory and our understanding of population- and community-level dynamics. By formally linking two largely disparate disciplines, metabolic life-history theory can serve as a framework for understanding and predicting other key patterns in life histories under environmental change.

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AUTHORSHIP

DJM and AKP conceived of the study; all authors developed the study design. AKP and DJM collected the data. DJM and CRW developed the analyses; CRW developed phylogenetic analyses; AKP analysed the data and wrote the first draft of the manuscript; and all authors contributed substantially to revisions.

DATA ACCESSIBILITY STAEMENT

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.bh14n51

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.
[Correction added on 28 February 2020, after first online publication: Table S6 has been amended]

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