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Developmental cost theory predicts thermal environment and vulnerability to global warming

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Supplementary Information

1. Functions characterising the relationship between temperature and metabolic rate, and temperature and development

In a previously published study ¹, we characterised the relationship between temperature and our traits of interest (Supplementary Table 1) using simple exponential functions. We used these functions for mathematical simplicity, and because they are the formal notation for longstanding ‘ Q_{10} ’ measures of temperature dependence in classic physiology studies (e.g.²).

In the present study however, we were particularly interested in understanding how developmental costs change across a broader thermal range. Furthermore, we repeatedly observed that simple exponential equations linking development to temperature tended to systematically underestimate development times at relatively higher temperatures.

Consequently, we modified the simple exponential equation for development to include a constant. An exponential equation with a constant also has a long history in studies of developmental physiology ³ and so is equally in keeping with physiological tradition. The biological interpretation of an exponential with a constant is that while development time may be highly temperature dependent, above a certain temperature, development time can never equal 0 (where $c > 1$). In other words, an exponential with a constant has the intuitive appeal in that, at very high temperatures, development is not instantaneous.

Perhaps more importantly, including a constant is supported by the data. **Supplementary Figure 1** shows the fit of a simple exponential versus one including a constant – the function lacking the constant consistently underestimated development times at the highest temperatures. Formal statistical analyses for species for which we had high levels of replication confirmed this difference in fit (Supplementary Table 2). In hindsight we should

have fit this more complex function in our earlier study, but when we re-analysed the results presented there with our more complex function - our results were qualitatively unchanged.

We considered fitting a more complex function for metabolic rate as well (i.e. including a constant), but we found no evidence for better fits with a more complex function across the temperature ranges for which metabolism was explored (Supplementary Table 2). As such, we retained a simple exponential function for this parameter, which carries the reasonable assumption that metabolic rate will fall to essentially zero at sufficiently cold temperatures, outside of the range of temperatures considered here.

Our goal here was not to explore the mechanistic drivers of why development and temperature covary with temperature the way they do, instead we were interested in the consequences of their covariance for shaping the costs of development and the thermal niche. However, we should note that our functions bear very close resemblance to more mechanistic descriptions of the temperature-dependence of metabolic rate and development⁴⁻⁶. An interesting next step would be to integrate the mechanistic drivers of these temperature dependencies into Developmental Cost Theory but this is beyond the scope of our endeavour here.

2. The relationship between temperature, metabolism and development beyond the usual temperature range.

Throughout our analyses, we use exponential functions to describe the relationship between temperature and metabolism, and temperature and development. In reality however, the relationship between temperature and our traits of interest are more complex. At extreme temperatures (for a particular organism), metabolic processes will fail and development will slow. Thus across a large temperature range, metabolism and development almost certainly

show more complex relationships with temperature and probably resemble classic Thermal Performance Curves (TPCs; ⁷). We used exponential functions instead of more complex polynomials that resemble TPCs for several reasons.

Despite our expectation that metabolism and development show a TPC-like form, there are only a few data to support that expectation (see **Supplementary Figures 2 & 3**). Instead, for the most part, it seems that physiologists tend to measure traits like metabolism and development within temperature ranges that do not suppress metabolism and cause mortality. Thus, while we might suspect more complex relationships between temperature and our traits of interest across all possible temperatures, the available data across all of the taxa here only support the exponential functions used here. In other words, more complex functions cannot be parameterised based on the available data for most species. The lack of data on metabolism and development outside of unstressful temperature ranges may explain why other frameworks that focus on the temperature-dependence of traits use similar functions to ours (e.g. ⁴⁻⁶).

Importantly, while we must therefore restrict our inferences about developmental costs and their minimisation to a temperature range that excludes more stressful temperatures, the exclusion of these temperatures does not influence our conclusions. To explain, our theory finds that a single (usually intermediate) temperature minimises the costs of development. Within that temperature range we also find that mortality is extremely low and weakly affected by temperature (see Results). Consequently, any consideration of temperatures beyond that range would cause additional mortality and reduce fitness even further. Thus, restricting our theory to within the natural or nonstressful temperature range captures the space that both minimises mortality and energy costs, so T_{opt} is likely to be a good predictor of the temperature that maximises fitness.

3. Description of environmental temperature

For those species that overlapped with ¹, we used the estimates of environmental temperature compiled there. As reported in ¹, we collated mean values of 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 (see ¹ for details). The level of detail, and the resolution of data regarding temperature ranges provided by different studies varied enormously. In some instances, daily temperature estimates were provided throughout the relevant developmental period while other studies reported only maximum and minimum temperatures for the area in which the species live.

Importantly however, there are likely to be systematic differences between the temperatures experienced by terrestrial species and aquatic species. Relative to aquatic environments, terrestrial habitats are far more thermally heterogeneous, with ubiquitous microhabitat variation in the temperatures that developing organisms experience. For example, shaded and unshaded microhabitats can differ by 11°C within the same m² ⁸ and clearly some species select oviposition sites based on local thermal conditions. Perfectly characterising the thermal environment of species that select specific thermal microhabitats is unfeasible for a meta-analysis such as this ⁹ but we took several steps in order to assess the reliability of our analyses.

First, we compared regressions of T_{opt} with T_{min} and T_{max} in addition to T_{mid} . We found the same qualitative patterns regardless of the temperature descriptor we used but T_{opt} was a

better fit in terms of R^2 (Supplementary Table 3). Thus, there is a relationship between T_{opt} and environmental temperature, regardless of how environmental temperature is characterised.

Second, because creating a nest for developing eggs can alter the thermal environment of the developing embryos profoundly, we compared terrestrial species that did or did not nest. We defined nesting as any non-egg material or structure that parents create or shape to house developing offspring. We found that metabolism and development have evolved to minimise development costs in temperatures in both groups but that in nesting species, T_{opt} is systematically warmer than T_{mid} . These results suggest that terrestrial nesting species have the capacity to significantly alter the thermal environment that their offspring experience. Nevertheless, across both nesting and non-nesting species, there was a strong positive relationship between T_{opt} and T_{mid} .

Supplementary Table 1. Studies included in meta-analysis for the temperature sensitivity of development time (D), metabolic rate (MR), Survival in different temperatures (S), and Temperature range (TR) for 71 species. Where only one study was used for all available parameters, no specific parameter is specified.

Taxon	Temperature range (°C)	Reference
<i>Chordata</i>		
Actinopterygii (class):		
<i>Chanos chanos</i>	23-33	1 (D,MR,TR)
<i>Chondrostoma nasus</i>	10-19	2

<i>Clarias gariepinus</i>	20-30	3 (D, MR), 4 (TR)
<i>Clupea harengus</i>	8-12	5(D), 6 (MR,TR)7(S)
<i>Coregonus clupeaformis</i>	0.5-8	8(D,MR,TR) 9 (S)
<i>Danio rerio</i>	20-32	10
<i>Dicentrarchus labrax</i>	10-20	11 (D,TR), 12 (MR) 13(S)
<i>Gadus morhua</i>	4-10	14(D,S), 15 (MR), 16 (TR)
<i>Hypomesus pretiosus</i>	10-16	17 (D,MR,TR) 18 (S)
<i>Leuciscus cephalus</i>	12-28	19 (D,TR), 20 (MR)
<i>Leuresthes tenuis</i>	12-25	21 (D, S), 22 (MR,TR)
<i>Melanogrammus</i>		
<i>aeglefinus</i>	4-10	23 (D), 15 (MR), 16 (TR, S)
<i>Merluccius productus</i>	11-14	24 (D,MR,TR)
<i>Mugil cephalus</i>	20-27	25 (D,S,TR), 26 (MR)
<i>Oncorhynchus mykiss</i>		27 (D S,MR), 28 (TR) 29 (S)
<i>(Salmo gairdneri)</i>	6-13	
<i>Oncorhynchus</i>		30 (D, MR), 31(TR) 32 (S)
<i>tshawytscha</i>	3-16	
<i>Oryzias latipes</i>	20-29	33

<i>Pseudopleuronectes americanus</i>	2-8	34 (D,MR,TR)
<i>Pleuronectes platessa</i>	3-10	35 (D, S), 6 (MR), 36 (TR)
<i>Rutilus rutilus</i>	8-24	37 (D,TR), 20 (MR)
<i>Salmo salar</i>	0-16	38 (D,S), 39 (MR), 40 (TR)
<i>Salmo trutta fario</i>	3-11	41,42 (D,MR), 43 (TR)
<i>Salvelinus alpinus</i>	4-8	44
<i>Salvelinus fontinalis</i>	5-9	45 (D,S), 46 (MR,TR)
<i>Scardinius erythrophthalmus</i>	10-22	47 (D), 20 (MR), 48 (TR)
<i>Scomber japonicus</i>	11-23	49 (D, MR, TR)
<i>Scomber scombrus</i>	8-18	50 (D,TR, S), 51 (MR)
<i>Tautoga onitis</i>	16-22	52 (D,MR,TR) 53 (S)
<i>Xyrauchen texaus</i>	10-22	54
Amphibia (class):		
<i>Bufo terrestris</i>	13-40	55 (DT), 56 (MR,TR)
<i>Crinia nimbus</i>	0-15	57 (D, MR, TR)

<i>Neoceratodus forsteri</i>	15-25	58 (D, MR, TR)
<i>Pseudophryne bibronii</i>	7-22	59 (D, MR), 60 (TR)
<i>Rana pipiens</i>	6-28	61 (D), 56 (MR,TR) 62 (S)
Chondrichthyes (class):		
<i>Heterodontus</i>	15-22	63 (D), 64 (MR,TR, S)
<i>portusjacksoni</i>		
Reptilia (class):		
<i>Apalone spinifera</i>	18-29	65 (D,MR,TR) 66 (S)
<i>Bassiana duperreyi</i>	17-24	67 (D,MR),68 (TR) 69 (S)
<i>Caretta caretta</i>	24-31	70 (D,MR), 71 (TR,S)
<i>Chelonia mydas</i>	22-29	72 (D,MR),73 (TR)70(S)
<i>Crocodylus johnsoni</i>	28-34	74 (D,MR,TR)
<i>Lampropholis guichenoti</i>	24-28	67 (D,MR, S), 75 (TR)
<i>Macrochelys temminckii</i>	18-29	65 (D,MR,TR) 76 (S)
<i>Sphenodon punctatus</i>	15-25	77 (DR,MR), 78 (S, TR)
<i>Trachemys scripta</i>	18-29	65 (D,MR,TR) 79 (S)

<i>Trionyx triunguis</i>	24-33	80
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Arthropoda		
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Insecta (class):		
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<i>Brevicoryne brassicae</i>	10-30	81 (D,MR,TR)
<i>Chironomus sp.</i>	13-33	82 (D,TR), 83 (TR) 84 (S)
<i>Culex pipiens</i>	15-33	85 (D,MR), 86 (TR)
<i>Drosophila melanogaster</i>	16-29	87 (D), 88 (MR), 89 (S,TR)
<i>Erynnis propertius</i>	-12-26	90 (MR, TR), 91 (D)
<i>Gynaephora</i>	0-32	92 (MR, T) 93 (D)
<i>groenlandica</i>		
<i>Hippodamia convergens</i>	10-35	94 (D), 95 (MR, TR)
<i>Melanoplus differentialis</i>	16-32	85 (D,MR), 96 (TR)
<i>Melanoplus sanguinipes</i>	14-39	97 (D,TR), 98 (MR) 99 (S)
<i>Oncopeltus fasciatus</i>	13-35	100 (D,MR), 101(TR)
<i>Ostrinia nubialis</i>	15-30	85 (D,MR), 102 (TR)
<i>Polypedilum sp.</i>	5-15	103(D), 83 (MR,TR)
<i>Solenopsis invicta</i>	17-24	104 (D,TR), 105 (MR)

<i>Tribolium confusum</i>	18-38	106 (D,S,TR), 85 (MR)
<i>Neohelice granulata</i> (<i>Chasmagnathus granulata</i>)	15-24	107
<i>Euphausia superba</i>	-1-2	108 (D,TR), 109 (MR) 110 (S)
<i>Hyas araneus</i>	3-15	111 (D,S,TR), 112 (MR)

Bryozoa

<i>Bugula neritina</i>	12-24	10
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Echinodermata

<i>Dendraster excentricus</i>	8-16	113 (D,MR), 114 (TR, S))
<i>Strongylocentrotus purpuratus</i>	4-20	115 (D), 116 (MR), 117 (TR, S)
<i>Odontaster validus</i>	-0.5-0	118

Mollusca

<i>Chorus giganteus</i>	10-16	119
<i>Loligo opalescens</i>	7-14	120 (D), 121 (MR), 122 (TR)
<i>Loligo reynaudii</i>	12-17	123 (D,TR, S), 124 (MR)
<i>Mytilus edulis</i>	6-18	125 (D,TR), 126 (MR)
<i>Octopus maya</i>	15-27	127 (D,MR,TR)

Stramonita

128

canaliculata (*Thais*

22-28

haemastoma

canaliculata)

110

111 Supplementary Table 2. Comparison of fits for exponential functions with and without a

112 constant included for those species for which there was sufficient data.

Species	Trait	Model	Akaike's Information Criterion
<i>Bugula neritina</i>	Metabolism	$MR(T) = \delta e^{a.T}$	191
		$MR(T) = \delta e^{a.T} + g$	193
	Development	$D(T) = de^{-bT}$	2052
		$D(T) = de^{-bT} + c$	1563
<i>Danio rerio</i>	Metabolism	$MR(T) = \delta e^{a.T}$	586
		$MR(T) = \delta e^{a.T} + g$	588
	Development	$D(T) = de^{-bT}$	4001
		$D(T) = de^{-bT} + c$	3536

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Supplementary Table 3. Comparison of regressions between T_{mid} , T_{min} or T_{max} and T_{opt} , their fit and whether the slope and intercept significantly differ from 1 and 0 respectively. Note that these are simple (nonphylogenetic) regressions.

Temperature parameter	Regression equation	Slope different to 1?	Intercept different to 0?	R^2
T_{opt}	$T_{\text{opt}} = 1.05 \times T_{\text{opt}} + 0.39$	No	No	0.84
T_{min}	$T_{\text{opt}} = 0.99 \times T_{\text{min}} + 7.07$	No	Yes	0.75
T_{max}	$T_{\text{opt}} = 0.789 \times T_{\text{max}} - 0.27$	Yes	No	0.66

118 Supplementary Table 4. Summary table of T_{mid} , T_{opt} , Predicted percentage increase in
 119 developmental costs at 20% above T_{opt} and equivalent decrease in survival for same
 120 temperature change.

Species	T_{mid}	T_{opt}	Costs @ $T_{opt}+20\%$	Survival @ $T_{opt}+20\%$
<i>Apalone spinifera</i>	23.5	29.3	7.2	0
<i>Bassiana duperreyi</i>	20.9	27.1	6.7	0
<i>Brevicoryne brassicae</i>	18	16.7	3	
<i>Bryobatrachus nimbus</i>	10	13	1	
<i>Bufo terrestris</i>	26.5	25.2	3.2	
<i>Bugula</i>	18	18.3	3.1	
<i>Caretta caretta</i>	27.3	30.6	6.9	0
<i>Chanos chanos</i>	28	32	2.5	2.3
<i>Chasmagnathus granulata</i>	19.5	20.7	1.7	0
<i>Chelonia mydas</i>	25.5	28.9	16.1	0
<i>Chironomus sp</i>	23.8	21.6	3.4	0
<i>Chondrostoma nasus</i>	14.5	15.5	10.5	12
<i>Chorus giganteus</i>	13	14.4	3	8.2
<i>Clarias gariepinus</i>	25	30.3	21.6	
<i>Clupea harengus</i>	10	11.3	4.4	0
<i>Coregonus clupeaformis</i>	4.3	5.6	1.3	0
<i>Coregonus lavaretus</i>	6	8.7	3.3	
<i>Crinia nimbus</i>	7.5	13.9	4.5	

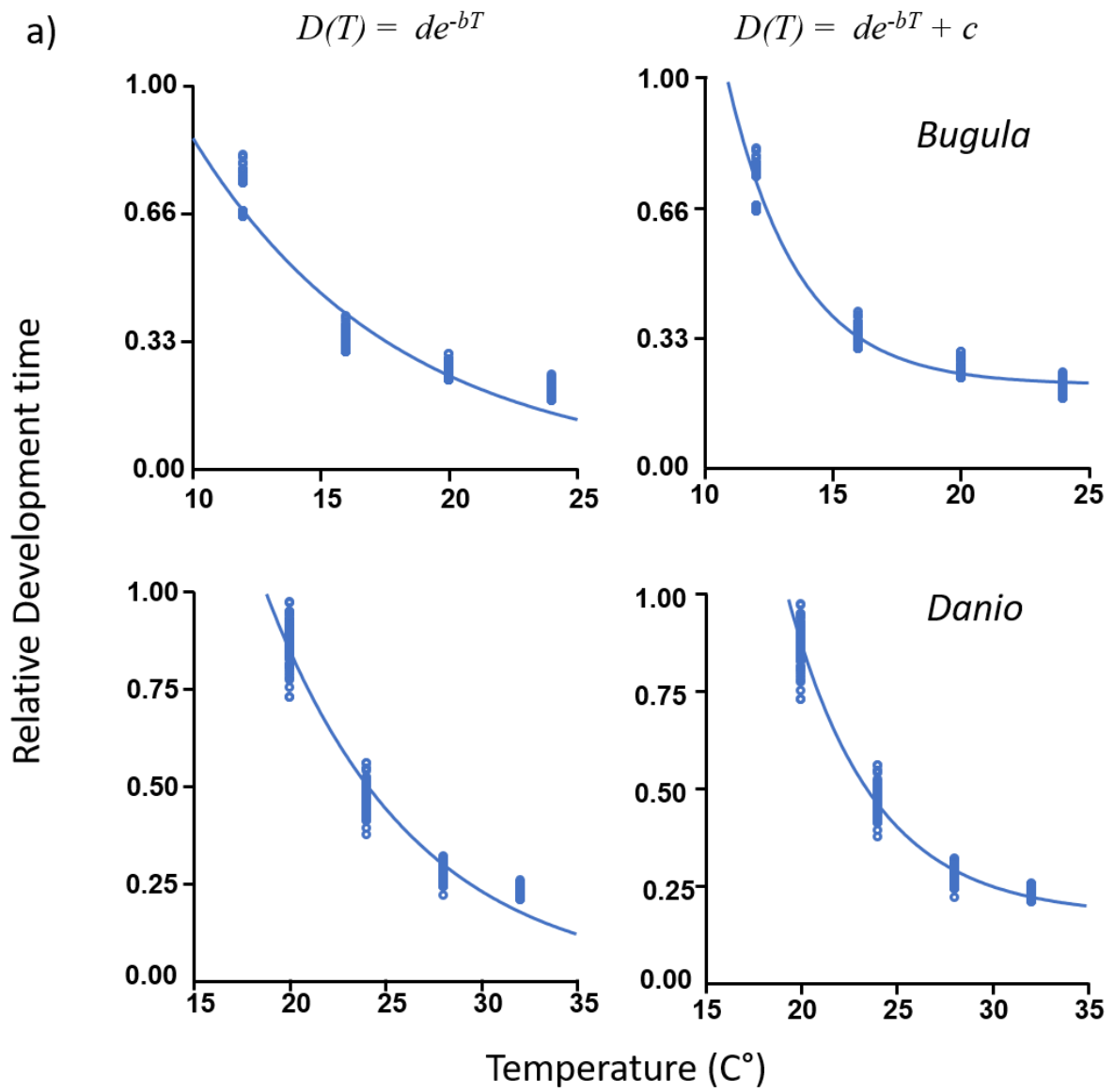
<i>Crocodylus johnstoni</i>	31	42.2	15.2	
<i>Culex pipiens</i>	24	21.2	16.2	
<i>Danio</i>	26	28.7	17.5	
<i>Dendraster excentricus</i>	12	20.4	5.6	0
<i>Dicentrarchus labrax</i>	15	21.3	4.9	0.6
<i>Drosophila melanogaster</i>	22.5	25	10.5	6.4
<i>Erynnis propertius</i>	7	4.6	1.3	
<i>Euphuasia superba</i>	0.5	-0.8	4.5	0
<i>Gadus morhua</i>	7	10.2	4.6	0
<i>Gynaephora groenlandica</i>	16	13.7	1.2	
<i>Heterodontus portusjacksoni</i>	18.5	19.6	11.6	0
<i>Hyas araneus</i>	8.8	12.8	4.4	0
<i>Hypomesus pretiosus</i> <i>pretiosus</i>	13	6.7	3.2	0
<i>Lampropholis guichenoti</i>	26	26.5	45.4	14.3
<i>Leuciscus cephalus</i>	19.9	16.3	12.6	
<i>Leuresthes tenuis</i>	18.5	22.2	7.0	0
<i>Loligo opalescens</i>	10.8	6.7	0.2	
<i>Loligo reynaudii</i>	14.5	11.9	7.7	0
<i>Macrochelys temminckii</i>	23.5	31.8	2	
<i>Melanogrammus aeglefinus</i>	7	8.5	0.8	3
<i>Melanoplus differentialis</i>	23.9	23.3	21	

<i>Melanoplus sanguinipes</i>	26.5	23.3	4.1	0
<i>Merluccius productus</i>	12.5	11.4	0.6	
<i>Mugil cephalus</i>	23.5	21	6.4	0
<i>Mytilus edulis</i>	12	14.9	6.2	
<i>Neoceratodus forsteri</i>	20	24.4	11.4	
<i>Octopus maya</i>	21	17.4	1.4	
<i>Odontaster validus</i>	-0.3	-0.8	0.7	0
<i>Oncopeltus fasciatus</i>	24	21	21.7	
<i>Oncorhynchus mykiss</i>	9.5	10.5	1.5	0.3
<i>Oncorhynchus tshawytscha</i>	9.5	9.4	3.3	0
<i>Oryzias latipes</i>	24.5	22.2	6.5	0
<i>Ostrinia nubilalis</i>	22.5	24.6	10.6	
<i>Pleuronectes platessa</i>	6.5	7.9	6.4	2
<i>Polypedium sp</i>	10	5.5	0.3	
<i>Pseudophryne bibronii</i>	14.5	16.7	9	
<i>Rana pipiens</i>	17	22.6	14.3	8
<i>Rutilus rutilus</i>	15.8	17.9	8.6	
<i>Salmo salar</i>	8	11.9	10.6	8
<i>Salmo trutta fario</i>	7	9	3.4	0
<i>Salvelinus alpinus</i>	6	6.2	1.6	0
<i>Salvelinus fontinalis</i>	6	9.1	2.3	0
<i>Scardinius erythrophthalmus</i>	16	11	1.1	
<i>Scomber japonicus</i>	17	17	6.7	0
<i>Scomber scombrus</i>	13	13.9	7.5	3.5

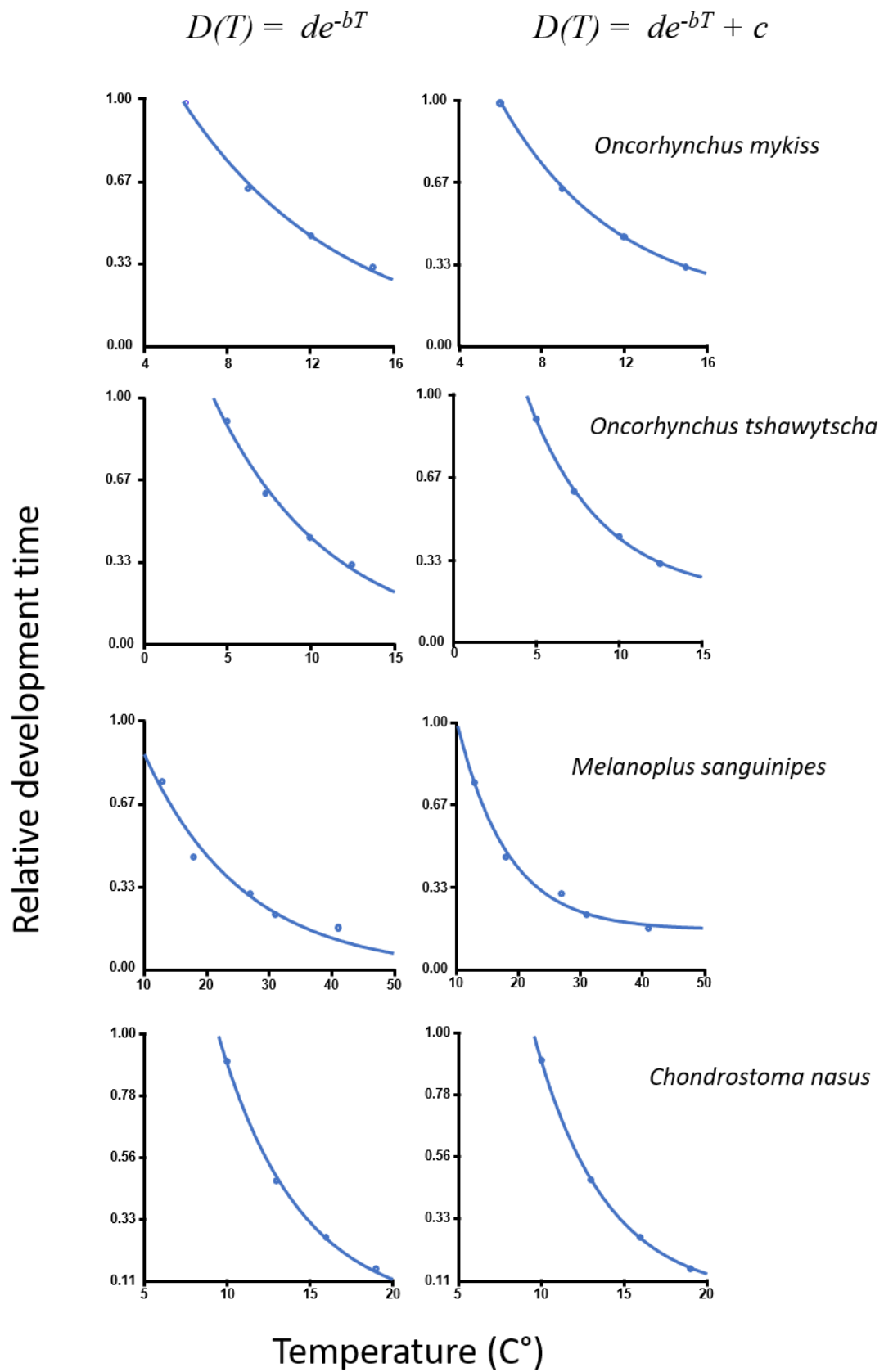
<i>Sphenodon punctatus</i>	20	22.2	12	0
<i>Strongylocentrotus purpuratus</i>	12	11.9	2.4	0
<i>Tautoga onitis</i>	19	17.8	14.8	8
<i>Thais canaliculata</i>	25	25.3	10.1	0
<i>Trachemys scripta</i>	23.5	29.9	17.1	
<i>Tribolium confusum</i>	27.5	27.1	20.6	5
<i>Trionyx triunguis</i>	28.5	33.8	10.8	35
<i>Xyrauchen texanus</i>	16	17.3	2.4	0

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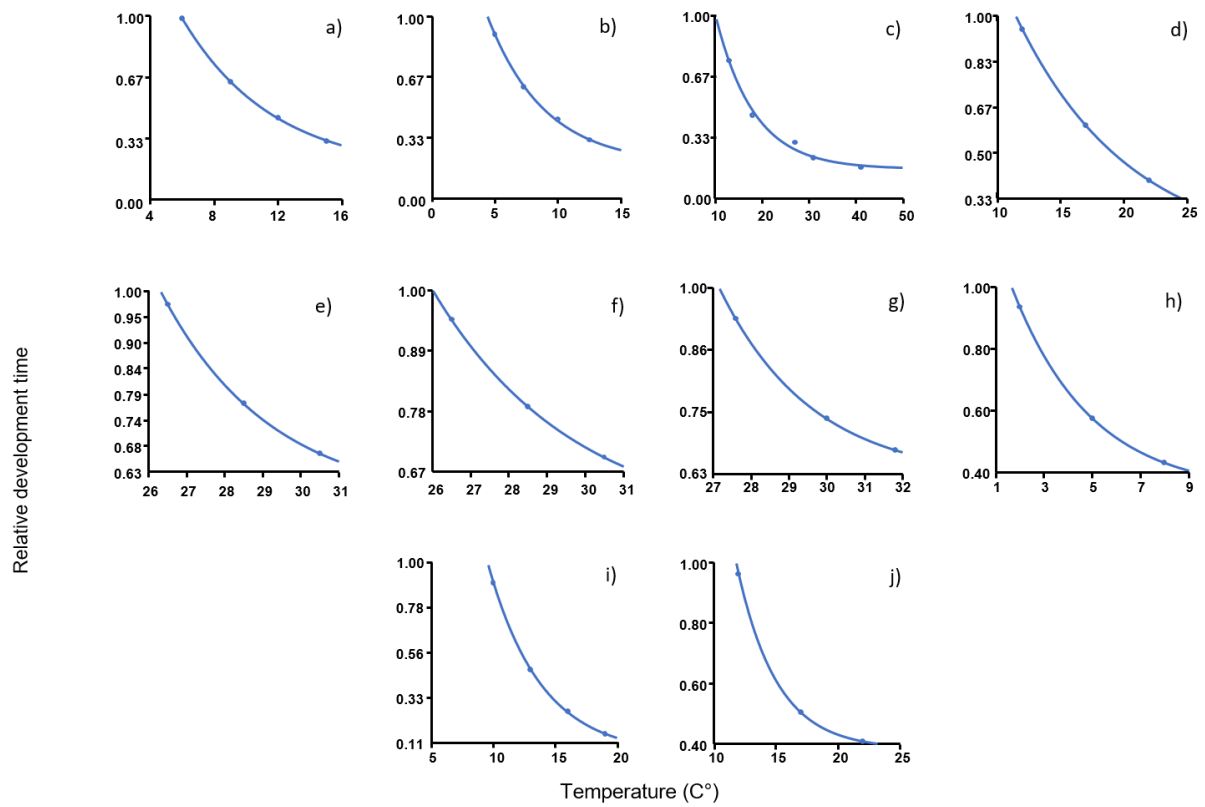
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b)



125 Supplementary Figure 1 a) & b) Examples of comparison of models describing the
126 temperature dependence of development time with and without a constant for those
127 species for which we have data obtained at four or more temperatures. For most species,
128 dots represent means for those temperatures; lines are the predicted lines of best fit given
129 the model. For *Danio rerio* and *Bugula neritina*, because we had access to the raw data,
130 we included all of the replicates rather than just the means.



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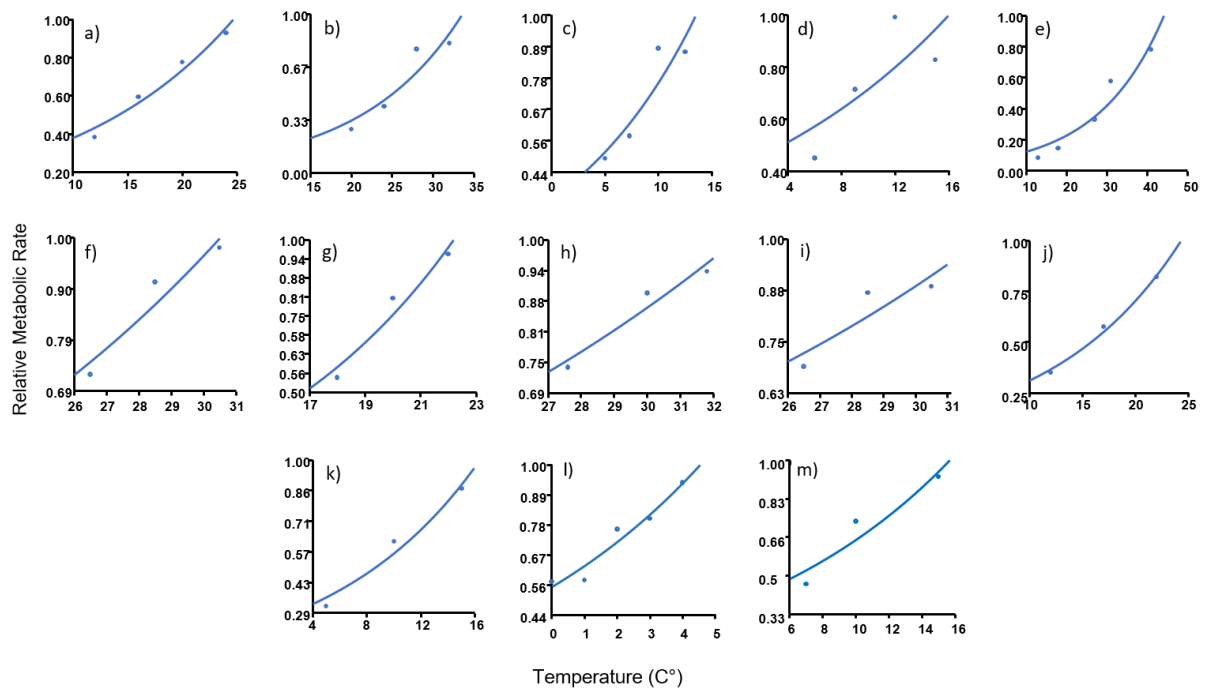
132 Supplementary Figure 2. Examples of relationships between temperature and (relative)

133 development time. Species shown are a) *Oncorhynchus mykiss*; b) *Oncorhynchus*

134 *tshawytscha*; c) *Melanoplus sanguinipes*; d) *Dendraster excentricus*; e) *Apalone spinifera*;

135 f) *Trachemys scripta*; g) *Caretta caretta*; h) *Coregonus clupeaformis*; i) *Chondrostoma*

136 *nasus*; j) *Pseudophryne bibronii*.



137

138 Supplementary Figure 3. Examples of relationships between temperature and (relative)
 139 metabolic rate. Species shown are a) *Bugula sp.*; b) *Danio sp.*; c) *Oncorhynchus*
 140 *tshawytscha*; d) *Oncorhynchus mykiss*; e) *Melanoplus sanguinipes*; f) *Apalone spinifera*; g)
 141 *Sphenodon punctatus*; h) *Caretta caretta*; i) *Trachemys scripta*; j) *Pseudophryne bibronii*;
 142 k) *Bryobatrachus nimbus*; l) *Euphausia superba*; m) *Clupea harengus*.

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