

1 **Body size shifts influence effects of increasing temperatures on ectotherm metabolism**

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37 Key words: Metabolic rate, ectotherms, warming temperatures, indirect effects, body size,
38 metabolic theory of ecology, physiology

39

40 Running title: Indirect effect of temperature on ectotherm metabolism

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42 Number of words (abstract): 299

43 Number of words (main body): 4,195

44 Number of references: 55

45

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47 INTRODUCTION

48

49 Environmental temperature influences organisms in many ways; temperature increases or
50 decreases rates of physiological processes (Brown et al., 2012), determines timing of
51 reproduction (Olive, 1995), and even directly affects mortality (Pauly, 1980). Because of the far-
52 reaching influence of temperature, projected increases in global temperatures due to climate
53 change are expected to substantially alter diverse species characteristics. Increased temperatures
54 have already been implicated in shifts in species geographic distributions (e.g., Buckley et al.,
55 2010), and in the phenology of species' life history and development (e.g., Wolkovich et al.,
56 2012).

57 It is predicted that global warming will also increase metabolic rates of ectotherms
58 (Seebacher et al., 2015; Dillon et al., 2010). Metabolic rate is a key physiological process that
59 represents the rate of energy required for the maintenance, growth, and reproduction of
60 organisms. Temperature influences metabolic rates in ectotherms through its influence on the
61 kinetic energy available for chemical reaction. Because the relationship between temperature and
62 metabolic rate is positive and exponential until an upper temperature threshold, small changes in
63 temperature can have substantial impacts on metabolic rate (Gillooly et al., 2001). By directly
64 increasing ectotherm metabolic rates, warmer temperatures would have considerable impacts on
65 the ecology of communities and ecosystems (Anderson-Teixeira et al., 2012; Lemoine &
66 Burkepile, 2012; O'Connor et al., 2011; Rall et al., 2010). Changes in metabolic rate affect many
67 aspects of organismal biology and ecology, including individual fitness (Burton et al., 2011),
68 population dynamics (Buckley et al., 2014), community composition (Marquet et al., 2004), and
69 even ecosystem processes such as ecosystem respiration and nutrient cycling (Gilbert et al.,

70 2014; McIntyre et al., 2008). Therefore, understanding the impact of temperature increases on
71 metabolic rates is critical to determining how ectotherm organisms, and the ecological
72 communities in which they perform key roles, will response to climate change.

73 While the direct effect of temperature on ectotherm metabolic rates is well-known,
74 temperature also affects other aspects of organismal biology which in turn influence metabolic
75 rate. One such organismal characteristic that influences metabolic rate and is influenced by
76 temperature is body size. Temperature affects body size, a phenomenon often referred to as the
77 size-temperature rule in which ectothermic individuals commonly develop to a smaller adult size
78 when raised at higher temperatures (Forster et al., 2011a; Angilletta, 2004; Atkinson, 1994). This
79 shift in adult size occurs quickly, with individual body size often responding to temperature
80 change after a single generation (e.g., fruit flies in Partridge et al., 1994). Smaller ectotherms
81 then have decreased metabolic rate due to the positive allometric relationship between body size
82 and metabolic rate (Kleiber, 1932; West et al., 1997; Brown et al., 2004). Thus, in addition to its
83 direct effect on metabolic rate, temperature influences metabolic rate indirectly via body size
84 shifts.

85 Predictions of ectothermic metabolic response to warming temperatures have focused on
86 the direct effect of temperature on metabolic rate while neglecting the indirect effects from size
87 shifts (Dillon et al., 2010). This occurs even though the relationships between temperature and
88 metabolic rate, size and metabolic rate (Gillooly et al., 2001; Brown et al., 2004), and
89 temperature and size (Walters & Hassall, 2006) are well documented. Indirect effects often
90 emerge in ecology because ecological systems are complex systems composed of multiple, and
91 sometimes antagonistic, interactions. These indirect effects can be strong enough to modify
92 outcomes, rendering predictions that only consider direct interactions incorrect (e.g., apparent

93 competition in Holt, 1977). While warmer temperatures from climate change will directly result
94 in increased metabolic rates, this increase could be offset by a decrease in metabolic rates due to
95 the concurrent indirect effect of smaller body size.

96 Here we examine how predictions of ectotherm metabolic rates differ when the indirect
97 effect of increased global temperatures on size is included in addition to the direct effect. While
98 higher temperatures cause metabolic rates to increase when size is constant (i.e., direct effect),
99 this increase could be dampened when size is allowed to vary (i.e., indirect effect) consistent
100 with empirical data, if not result in an overall decreased metabolic rate. To estimate how much
101 size changes in response to temperature, we collect experimental data on observed ectothermic
102 size shifts in response to temperature changes. We then use a previously established model that
103 integrates size and temperature effects on metabolic rate to estimate metabolic rates when size is
104 constant and when size varies. We compare these metabolic rates to determine how this
105 established indirect effect of increased temperature alters the magnitude and direction of existing
106 predictions that use only the direct effect.

107

108 **METHODS**

109

110 **Data**

111 We used data from published experimental studies that raised individuals of ectotherm
112 species at constant temperatures. From these studies, we obtained average adult size of all
113 individuals grown at each temperature treatment. Criteria for inclusion were that (1) in each
114 study individuals were raised at a minimum of two experimental temperatures, (2) individuals
115 were either lab-bred or collected at an early life stage, and (3) sufficient food was provided so

116 that resource limitation did not influence ontogenetic growth. These criteria were laid out by
117 Forster et al. (2011a), which was also the source of most of our data, and we collected some
118 additional data from the literature that also conformed to these criteria (Coker, 1993; Berven,
119 1982; Stacey & Fellowes, 2002; Marti & Carpenter, 2008; Oetken et al., 2009). Some studies had
120 multiple trials to compare responses of individuals from different latitudes or elevations; we
121 retained data for all trials and they were kept separate for the analysis. If length was the only size
122 metric provided, we converted it to mass using allometric relationships (Appendix S1 in
123 Supporting Information).

124 Studies examined body size response to temperature across a range of temperatures (2°C
125 $- 36^{\circ}\text{C}$) that differed from each other by various temperature increments ($1^{\circ}\text{C} - 29^{\circ}\text{C}$ difference
126 in temperature between experiments within studies). To simplify this analysis and focus on our
127 core question of whether the indirect temperature effect on body size could, on average, offset or
128 substantively ameliorate the direct effect of temperature on metabolic rate, we further filtered
129 this data by only considering pairs of experiments within a study that differed by 3°C in
130 experimental temperature. We chose 3°C as our temperature difference because it is within the
131 bounds of predicted future temperature change from climate models, though particular species
132 may or may not experience this specific temperature increase in their native ranges. From each
133 3°C experimental pair, we considered the mass value associated with the lower temperature to
134 represent that species' mass before temperature increase while mass value reported for the higher
135 temperature represented size response to a 3°C increase in temperature. Some studies had
136 multiple experimental pairs whose experimental temperatures differed by 3°C (i.e., one pair of
137 15°C and 18°C , and a second pair of 18°C and 21°C); in these cases we kept all 3°C pairs. This
138 filtered subset of the data had temperature ranges of 3°C to 30°C for the lower temperature and

139 6°C to 33°C for the higher temperature.

140 The final dataset contained 191 pairs of average adult masses for 45 species across 40
141 studies. This dataset includes species from seven taxonomic classes, ranging from Insecta to
142 Amphibia, and terrestrial species from every continent except Antarctica and aquatic species
143 from every ocean and many large bodies of water. Most species are very small (<100 mg)
144 invertebrates because available data for larger ectotherms was limited. Mass values span five
145 orders of magnitude, from 2 µg to 100 mg. Data and code have been deposited in the online
146 Dryad Data Repository (<http://datadryad.org>).

147

148 **Metabolic rates**

149 Size-temperature studies do not typically measure metabolic rate. Therefore, we used a
150 model to calculate species' metabolic rates from the experimental temperature-mass dataset. This
151 model is central to the metabolic theory of ecology (MTE) (Brown et al., 2004) and combines
152 both mass and temperature effects on metabolic rates:

153

$$154 R = r_0 M^b e^{-E/kT}$$

155

156 where R = metabolic rate, r_0 = scaling constant, M = mass (g), b = unitless scaling exponent, E =
157 activation energy of respiration (eV), k = Boltzmann's constant (8.617×10^{-5} eV/K), and T =
158 temperature (K). Though the mechanism underlying the MTE equation has been questioned
159 (O'Connor et al., 2007), it provides a reasonable empirical approximation across a wide range of
160 taxa (Gillooly et al., 2001) and has been used previously to estimate metabolic rates response to
161 temperature change (e.g., Dillon et al., 2010). An advantage of this equation for our study is that

162 it allows us to incorporate both the direct effect of temperature on metabolic rate ($e^{-E/kT}$) and the
163 indirect effect through organismal size (M^b).

164 We used values of b and E specific to each taxonomic class to allow for taxon-specific
165 responses of metabolism to temperature. Because availability of class-specific b and E values
166 varied widely among the classes, we used different approaches for determining these values.
167 When data on organismal metabolic rate available for a class also contained size and temperature
168 information (Branchiopoda, Amphibia, Malacostraca, Maxillopoda; Makarieva et al., 2008;
169 White et al., 2012), we used a multiple regression method (White et al., 2012) to calculate b and
170 E . Values for Actinopterygii were estimated using fish species from several classes (Gillooly et
171 al., 2001) and values for Insecta were acquired from literature sources (Chown et al., 2007; Irlich
172 et al., 2009), while the average values of $b = 0.75$ and $E = 0.63$ eV (Brown et al., 2004) were
173 used for Entognatha, the most data-limited class. Data used to calculate b and E were non-
174 overlapping with our experimental temperature-mass dataset.

175 For each species, we used the MTE equation to calculate how much metabolic rate
176 changed due to only the direct effect of temperature increase, and from both the direct effect of
177 temperature and indirect effect of the empirical body size response to temperature. To do so, we
178 calculated three metabolic rates for each 3°C experimental pair in the temperature-size dataset
179 (Fig. 1A):

- 180 i. “Starting metabolic rate” represents the metabolic rate prior to temperature increase, and
181 was calculated using size and temperature data from the lower temperature experiment of
182 each pair.
- 183 ii. “Constant size metabolic rate” is the hypothetical metabolic rate including only the direct
184 effect of temperature increase. It was calculated with the size from the lower temperature

185 of each experimental pair, and temperature from the higher temperature of each pair (i.e.,
186 the assumption that size at the lower temperature does not change as temperature
187 increases).

188 iii. “Varying size metabolic rate” represents the empirical metabolic rate that includes both
189 the direct and indirect effects of temperature increase. It was calculated using both size
190 and temperature data from the higher temperature of each pair.

191

192 *Comparison*

193 To visualize the difference between the metabolic predictions including only the direct
194 effect of temperature versus including both the direct and indirect effects of temperature, we
195 examined how much varying size metabolic rate increased from initial compared to constant size
196 metabolic rate. Because some species had data from multiple 3°C experimental pairs, we
197 condensed the data by calculating species averages for starting metabolic rate, constant
198 metabolic rate, and varying size metabolic rate (Fig. 1A). We used these average values to
199 calculate i) “constant size metabolic rate change”: the percent change from starting metabolic
200 rate to constant size metabolic rate and ii) “varying size metabolic rate change”: the percent
201 change from starting metabolic rate to varying size metabolic rate. These two change metrics
202 represent how much metabolic rate changes due to only the direct effect of temperature increase
203 (i.e., constant size metabolic rate change), and when the indirect effect of temperature, in
204 addition to the direct effect, is included (i.e., varying size metabolic rate change). Positive
205 percent change showed an increase in metabolic rate from starting metabolic rate for each
206 species. To assess the difference between metabolic rates with and without the indirect effect,
207 each species' constant size and varying size metabolic rates were log-transformed and compared

208 across species with a paired t-test.

209

210 *Linear mixed model*

211 We used a mixed model to determine if other factors, besides the body size response,
212 impacted the difference between constant size and varying size metabolic rates. The response
213 variable for the model was the log of the ratio between each pair's constant size and varying size
214 metabolic rates, where a positive log-ratio indicated that the pair's varying size metabolic rate
215 was smaller than its constant size metabolic rate. In addition to the model results, likelihood ratio
216 tests were used to determine each effect's significance. We included absolute temperature, as
217 represented by the lower temperature for each pair, as a fixed effect because higher starting
218 temperatures are expected to have a disproportionate effect on metabolic rates due to their
219 exponential relationship. The random effects in the model were the taxonomic classifications of
220 species and class, as metabolic rate varies amongst these groupings due to biology and ecology.
221 We initially included study and trial as random effects, to take into account differences in
222 experimental setups, but these were not included in the final model because their maximum
223 likelihood estimates for variance were near zero and they therefore had no impact on the final
224 model. Similarly, because metabolic rate depends on the relative size of organisms, we included
225 mass from the lower temperature of each pair as a fixed effect but it was removed because it did
226 not have a substantial effect on the metabolic rate log-ratio ($\chi^2 = 0.7015$; $df = 1$; $p = 0.4$). We ran
227 the linear mixed model using the R package lme4 version 1.1.9 (Bates et al., 2015; Winter,
228 2013).

229

230 **Compensation mass**

231 We assessed the magnitude of size response to temperature needed to offset the direct
232 effect of temperature on metabolic rate, and how close each species' observed size response to
233 temperature came to reaching this predicted value (Fig. 1B). To calculate the predicted size
234 necessary to offset the 3°C increase in temperature for an experimental pair (M_N), we rearranged
235 the MTE equation to solve for size:

236

$$237 \quad M_N = (R / e^{-E/kT})^{1/b}$$

238

239 where R is the starting metabolic rate and T is the observed temperature from the higher
240 temperature experiment for each pair. Thus, needed mass (M_N) is the mass a species would have
241 to be under higher temperature conditions in order for metabolic rate to not change.

242 We calculated how much each species' size actually changed with increased temperature,
243 (“observed mass change” = percent change from initial mass to actual mass), and how much size
244 theoretically needed to change to maintain metabolic rate with increased temperature
245 (“compensation mass change” = percent change from initial mass to needed mass) (Fig. 1B).
246 Observed mass changes or compensation mass changes of less than 100% indicated that the mass
247 of a species either did or needed to decrease, respectively. A paired t-test was used to compare
248 log-normalized actual and needed mass values. All analyses were completed using R version
249 3.3.1 (R Core Team, 2016).

250

251 **RESULTS**

252

253 **Metabolic rates comparison**

254 Metabolic rates differed when the indirect effect of temperature increase was included
255 with the direct effect. All varying size metabolic rate changes, which included the indirect effect
256 of temperature on size, were positive (average percent change = 23%; Fig. 2), indicating that
257 ectotherm metabolic rate will still increase with temperature despite decreases in body size.
258 However, most species' metabolic rates did not increase as much when the indirect effect was
259 included, as shown by smaller varying size metabolic rate changes than constant size metabolic
260 rate changes (Fig. 2). There was also a statistically significant difference between these
261 metabolic rate changes, with varying size metabolic rate being consistently smaller than constant
262 size ($t_{44} = 3.34$; $p = 0.002$; 95% CI = 0.017 – 0.070). While the majority of species had a smaller
263 increase in metabolic rate with the body size response included, for 9 of the 45 species
264 incorporating size shifts actually caused metabolic rate to increase even more than expected from
265 just the direct effect of temperature.

266

267 **Linear mixed model**

268 Similarly, most pairs had smaller varying size metabolic rates than constant size
269 metabolic rates. Of 191 pairs, 82% had positive log-ratios, which represent the difference
270 between constant size and varying size metabolic rates. These log-ratios were not explained by
271 the three factors of interest we included in the model. While absolute temperature ($\chi^2 = 9.27$; $df =$
272 1 ; $p = 0.002$), taxonomic class ($\chi^2 = 3.90$; $df = 1$; $p = 0.048$), and taxonomic species ($\chi^2 = 5.48$; df
273 $= 1$; $p = 0.019$) did influence the differences between metabolic rates, they were not sufficiently
274 biologically significant. With increasing absolute temperature, varying size metabolic rate tended
275 to get increasingly smaller than constant size metabolic rate, as shown by a slightly positive
276 slope in the relationship between absolute temperature and log-ratio (slope = 0.004 ± 0.001).

277 However, this increasing difference had minimal biological relevance because it was between
278 one and two orders of magnitude smaller than the actual difference between metabolic rates.
279 Similarly, species classification explained only 17% of the variability in random effects, while
280 class explained a more substantial 43% of random effects variability (Fig. 2).

281

282 **Compensation mass**

283 No species' mass decreased enough for their metabolic rate to remain constant regardless
284 of temperature increase. To retain constant metabolic rates, all species would need to get smaller
285 (Fig. 3). Actual mass (i.e., empirical mass in response to temperature increase) and needed mass
286 (i.e., theoretical mass required in order for metabolic rate to not change due to temperature
287 increase) were statistically significantly different, with needed masses smaller than actual masses
288 ($t_{44} = 17.707$; $p < 2.2 \times 10^{-16}$; $CI = 0.25 - 0.32$). While most species empirically decreased in size,
289 20% of species actually increased in size in response to temperature increase (observed mass
290 change mean \pm standard deviation: $-4\% \pm 11\%$). These were the same species that had a greater
291 increase in metabolic rate when the body size response was included (Fig. 2).

292

293 **DISCUSSION**

294

295 Consistent with expectations, predictions of most species' metabolic rates were smaller
296 when the indirect effect of temperature was included with the direct effect. While all metabolic
297 rates increased with increased temperatures whether or not the indirect effect was included,
298 incorporating the body size response to temperature significantly dampened the increase in
299 metabolic rate for most species (Fig. 2). Species decreased in size by up to 20% (Fig. 3). Though

300 there is no accepted quantitative description of the relationship between temperature and size for
301 ectotherms (Forster et al., 2011b), the magnitude of size decrease by these species was similar to
302 results from previous studies. For example, worm species *Caenorhabditis elegans* was 6%
303 smaller when raised at a temperature increase of 5°C (Voorhies, 1996) and two mayfly species
304 *Ameletus ludens* and *Ephemerella subvaria* were 6% and 26% smaller, respectively, at a 3.1°C
305 warmer temperature (Sweeney & Vannote, 1978). None of the species in this study decreased
306 sufficiently in size for the indirect effect of temperature to offset the direct effect. All species
307 would have needed to decrease between 15% and 35% in size for their metabolic rates to remain
308 constant with temperature increase (Fig. 3).

309 A small proportion of species increased in size, instead of decreasing as expected, in
310 response to increased temperature. Of 36 species, 9 species increased in size (Fig. 3) and
311 therefore had a greater increase in metabolic rate when the indirect effect of temperature was
312 included (Fig. 2). These included four crustacean species from two classes (*Artemia salina*,
313 *Farfantepenaeus californiensis*, *Hyas coarctus*, *Pandalus borealis*) and insect species including
314 two butterfly species (*Aglais urticae*, *Polygonia c-album*), two out of 11 fruit fly species
315 (*Drosophila equinoxialis*, *Drosophila subobscura*), and one crop pest (*Ptero alternus*). This
316 opposing size response is consistent with previous research as, for example, 12% of the studies
317 in the meta-analysis by Atkinson (1994) showed a positive relationship between temperature and
318 size. While it is unknown why some species exhibit this opposing response, many explanations
319 have been proposed based on growth rates (Angilletta & Dunham, 2003; Walters & Hassall,
320 2006), abiotic conditions (Atkinson, 1994), extreme temperatures (Kingsolver & Huey, 2008),
321 and life history characteristics (Walters & Hassall, 2006; Forster et al., 2012). Regardless of the
322 mechanism, these anomalous species will have relatively greater metabolic rates and body sizes

323 from increased temperatures, with the accompanying higher energy requirements. Their greater
324 use of space, food, and other resources could result in disproportionately greater ecological
325 impacts and ecological mismatches, such as substantial changes in prey abundances due to
326 increased consumption by predators (Rall et al., 2010).

327 Though there was a significant difference in species metabolic rates when the indirect
328 effect of temperature was included, the biological relevance of this difference is unknown.
329 Including the indirect effect of temperature on size generally resulted in small changes in the
330 predicted metabolic rate. Species that declined in size with increasing temperature experienced,
331 on average, a 9% reduction in the predicted metabolic rate increase, while those that increased in
332 size saw an average 11% increase in metabolic rate from that expected due to the direct effect of
333 temperature alone. This magnitude of difference in metabolic rate seems relatively small, but its
334 ecological relevance could depend on context. For example, Gilbert et al. (2014) showed that
335 small changes in biomass potential resulted in large and unpredictable fluctuations in food web
336 stability but only when biomass potential was low. Thus, whether or not these small changes in
337 expected metabolic rates due to the size response to increasing temperature will have cascading
338 effects on the ecology of those species or the communities they inhabit may depend on the
339 productivity of the system and their trophic interactions. Further work would be needed to
340 determine if there is an ecological impact due to the difference in metabolic rate caused by the
341 body size response.

342 Because none of the species in this study decreased enough in size to offset the expected
343 direct effect of temperature on metabolic rate, increasing metabolic rates is still likely to be a
344 widespread response of ectotherms to warming. The overall increase in ectotherm metabolic
345 rates will have substantial consequences for every aspect of ecological systems, from population-

346 level and up (Schmidt-Nielsen, 1984; Anderson-Teixeira et al., 2012). Individuals of each species
347 will require more energy to maintain normal maintenance, growth, and reproductive function and
348 therefore use a greater proportion of resources. Assuming resource availability remains the same,
349 this will increase intraspecific competition, resulting in lower species abundances and higher
350 extinction probabilities (MacArthur & Wilson, 1963; Hurlbert & Stegen, 2014) that will shift
351 community composition, potentially changing the dominant species, trophic structure, and
352 interspecific interactions. This would ultimately affect ecosystem-level energy fluxes (Allen et
353 al., 2005; Yvon-Durocher & Allen, 2012). Like metabolic rate, size itself impacts many aspects
354 of population, community, and ecosystem ecology (e.g., cascading effects on foraging and
355 interspecific competition in woodrats in Smith et al., 1998) independently of its impact through
356 metabolic rate. The shifts in size that ectotherms may experience with warming are likely to
357 compound many of these cascading impacts as well. Incorporating the effects of temperature
358 change through its coordinated impacts on metabolism and size will be challenging, but previous
359 work on changing body size (Woodward et al., 2005; Ohlberger, 2013) is a potential guide.
360 Particularly informative is an extensive study by O'Gorman et al. (2012) which showed
361 significant effects of body size on individuals, populations, communities, and ecosystem
362 processes in Icelandic streams with a temperature gradient.

363 Understanding how climate change will impact species and ecosystems is difficult
364 because ecological systems are complex. Temperature does not impact one aspect of ecology, but
365 influences dynamics at almost every level, from the physiology of organisms to the rates of
366 ecosystem fluxes. We often reduce this complexity by studying the direct effects of temperature
367 change on some particular component of ecology, such as the effect on metabolic rate, and then
368 sometimes additionally the direct effect of the changed ecological component on some other

369 ecological process. Our results highlight the need to consider the coordinated impact of multiple
370 pathways of effects when making predictions about how species will respond to climate change.
371 While we focused here on the body size response of ectotherms to temperature as an indirect
372 effect on metabolic rate, this is by no means the only indirect pathway by which temperature can
373 impact metabolic rate. Temperature can impact size through a variety of other environmental
374 pathways besides the temperature-size response, including through resource availability, which
375 could then consequently affect body size in various ways (McNab, 2010; Bickford et al., 2011).
376 Designing studies to assess the relative importance of direct and indirect effects of temperature
377 on species, communities, and ecosystem properties of interest is an important next step for our
378 ability to predict the impacts of climate change.

379

380 **ACKNOWLEDGEMENTS**

381 This research was supported by the Gordon and Betty Moore Foundation Data-Driven Discovery
382 Grant and the NSF CAREER grant, both to Ethan White. Thanks to Ellen Bledsoe for feedback
383 on data visualization.

384

385 **SUPPLEMENTARY MATERIALS LIST**

386 **Appendix S1** Methods for converting non-mass measurements to mass

387

388 **DATA ACCESSIBILITY**

389 All temperature-mass data, along with associated cleaning and analysis R scripts, are available
390 on Dryad.

391

392 **BIOSKETCH**

393 The Weecology group, in conjunction with collaborators, works on diverse ecological questions
394 by linking empirical and quantitative approaches, with a focus on macroecology and
395 computational techniques.

396 Author contributions: K.A.T., F.S., and S.K.M.E conceived the project and collected data, K.R.,
397 D.J.H., and S.K.M.E. analyzed data, and K.R. and S.K.M.E. primarily completed the writing
398 with contributions from all co-authors.

399

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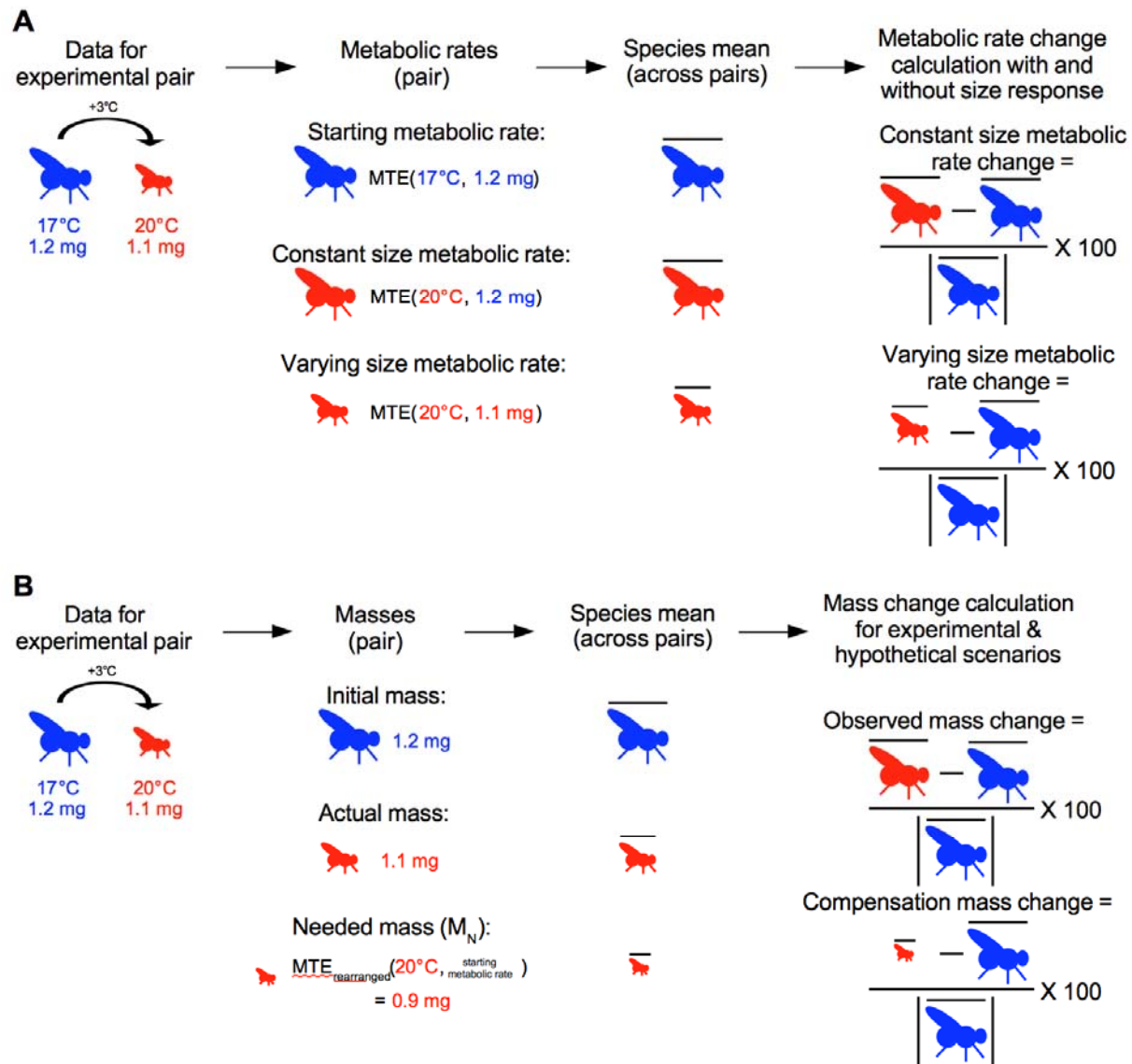
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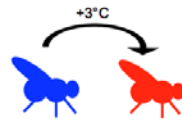
547 **FIGURES**
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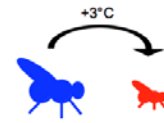
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550 Figure 1. Diagrams showing how the experimental data from the pairs were used to calculate
551 constant size and varying size metabolic rate changes for each species (A), and how the data
552 were used to calculate observed and compensation mass change for each species (B). The
553 example data is from the species *Aedes aegypti*.

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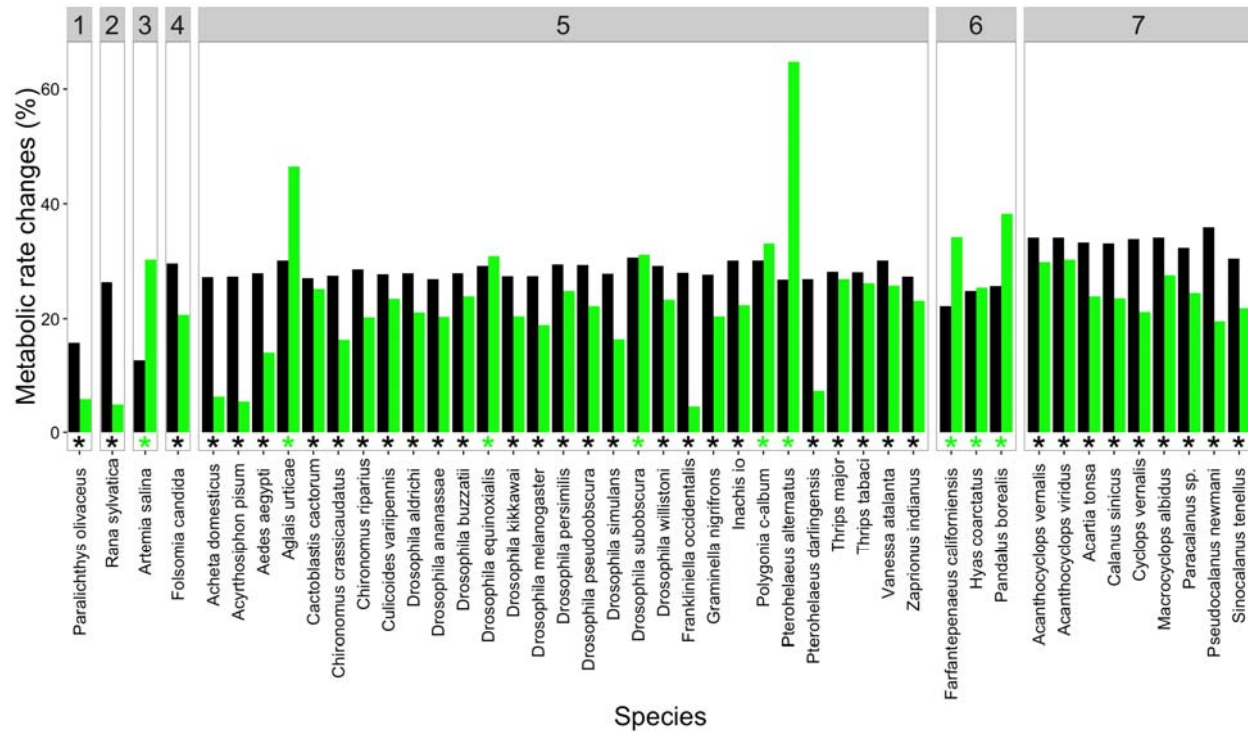
Constant size metabolic rate change



Varying size metabolic rate change



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562 Figure 2. Constant size metabolic rate change (black bar) and varying size metabolic rate change
 563 (green bar) for all species, represented as percent change from starting metabolic rate to
 564 metabolic rate without the indirect effect of size response and to metabolic rate with indirect
 565 effect, respectively. A positive percent difference indicates an increase from starting metabolic
 566 rate. Asterisks are colored according to whether constant size metabolic rate (black asterisk) or
 567 varying size metabolic rate (green asterisk) is larger for each species. Species are grouped by
 568 class, with classes labelled at the top of the figure as follows: 1 = Actinoperygii, 2 = Amphibia, 3
 569 = Branchiopoda, 4 = Entognatha, 5 = Insecta, 6 = Malacostraca, 7 = Maxillopoda.

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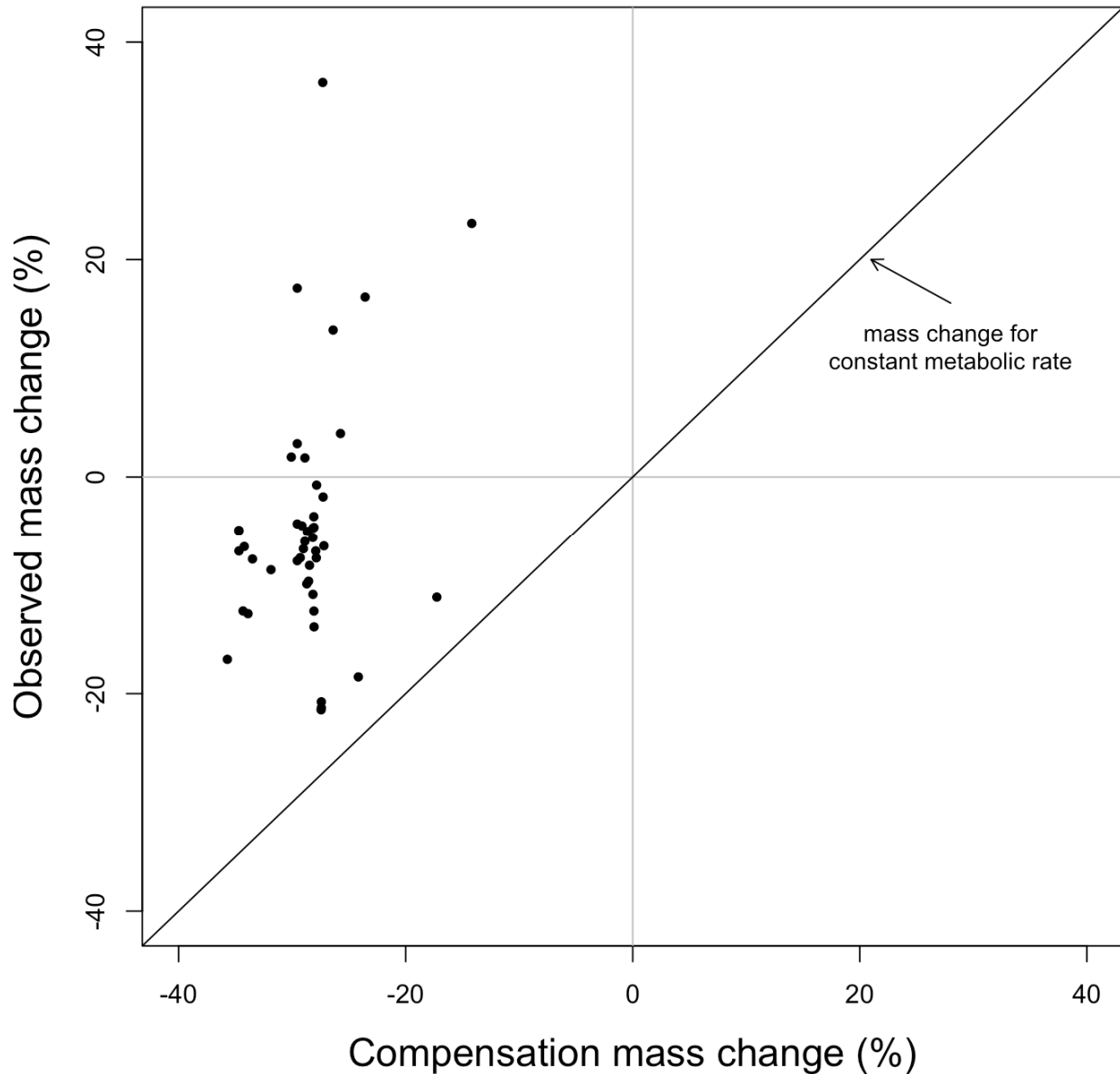
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580 Figure 3. Comparison between compensation mass change and observed mass change for each
581 species. Compensation mass change is the percent change from initial mass to needed mass (i.e.,
582 mass change needed to maintain metabolic rate with increased temperature), while observed
583 mass change is the percent change from initial mass to actual mass (i.e., observed mass change
584 of individuals of each species raised experimentally). No change in mass and no change needed
585 in mass are indicated by grey lines. Equivalence between needed mass and actual mass shown by
586 black line.

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