A critical review of the use and performance of different function types for modeling temperature-dependent development of arthropod larvae

Brady K. Quinn*

Department of Biological Sciences, University of New Brunswick, 100 Tucker Park Road, Saint John, NB, Canada E2L 4L5

*Corresponding author: bk.quinn@unb.ca, 1-506-343-7676

Highlights:

- Temperature-dependent development functions of arthropod larvae were reviewed
- Data from published studies were re-tested and fit with eight different function types
- 86.5 % of published studies did not fit their data with the best function of those tested
- Performance differed among functions and was related to taxon and temperature range tested
- Function type impacted predicted development times, so using the best function matters

ABSTRACT

Temperature-dependent development influences production rates of economically- and ecologically-important arthropod species, including crustaceans important to fisheries and agricultural pests. Numerous candidate equation types (development functions) exist to describe the effect of temperature on development time, yet most studies use only a single type of equation and there is no consensus as to which, if any model predicts development rates better than the others, nor what the consequences of selecting a potentially incorrect model equation are on predicted development times. In this study, a literature search was performed of studies fitting development functions to development of arthropod larvae (87 species). The published data of some (52) of these species were then fit with eight commonly-used development functions. Overall performance of each function type and consequences of using a function other than the best one to model data were assessed. Performance was also related to taxonomy and the range of temperatures examined. The majority (86.5 %) of studies were found to not use the best function out of those tested. Using the incorrect model lead to significantly less accurate (e.g., mean difference ± SE 7.9 ± 1.7 %, range: 1-18 %) predictions of development times than the best function. Overall, Heip Power, Quadratic, Bělehrádek, and Modified Arrhenius functions performed well, Linear Rate and Tauti Exponential were intermediate, and the Linear Sum and Brière-2 functions performed poorly. More complex functions only performed well when wide temperature ranges were tested, which tended to be confined to studies of insects or arachnids compared with those of crustaceans. Results indicate the biological significance of choosing the best-fitting model to describe temperature-dependent development time data.

Key Words: Temperature; arthropod; larval development; development functions; molting rate

1. Introduction:

Temperature affects biota at all levels, ranging from effects at the fundamental biochemical and physiological levels (Bělehrádek, 1935; Coutant and Talmage 1976; Somero, 2004) to effects on individual organisms (Brière et al., 1999; MacKenzie, 1988), populations (Aiken and Waddy, 1986; Cooper et al., 2012; McLaren et al., 1969), communities, and ecosystems (Menge, 1978; McQuaid and Branch, 1985). Through its effects on the physical and chemical properties of biologically active molecules, such as enzymes, temperature affects the rate at which numerous life processes occur, including metabolism, oxygen consumption, photosynthesis, movement, survival, growth, and embryonic development (Bělehrádek, 1935; Brière et al. 1999; Corkett, 1972; Coutant and Talmage 1976; Du et al., 2007; Geffen and Nash, 2012; Herzig, 1983; McLaren et al., 1969). Temperature also significantly affects larval development rate of poikilothermic animals, including some vertebrate larvae (Lind and Johansson, 2007; Kang et al., 2009; Miller et al., 2006) and those of invertebrates (e.g., de Severyn et al., 2000; Jenkins et al. 2006; Singh and Sharma, 1994). Temperature has particularly strong impacts on moulting and development of arthropods (Anger, 1984; Corkett and McLaren, 1970; Easterbrook et al., 2003; Hamasaki et al., 2009; Koda and Nakamura, 2010; MacKenzie, 1988; Marchioro and Forester, 2011; McLaren, 1963).

Within certain tolerance limits (Bělehrádek, 1935; Brière et al., 1999; Campbell et al., 1974; Shi and Ge, 2010) rates of biological processes of poikilotherms, including larval development, are positively correlated with temperature; thus, higher temperatures generally result in more rapid development than lower temperatures. This has important ecological implications, as environmental temperatures can influence generation times, production cycles, and population dynamics of such organisms. Higher or lower temperatures could, for example,

lead to changes in the amount and/or timing of peak secondary marine production of copepods (Huntley and López, 1992; McLaren, 1963), outbreaks of agricultural pests (Easterbrook et al., 2003) or vector-borne diseases (Bayoh and Lindsay, 2003), or introduction and establishment of invasive species into new areas (de Rivera et al., 2007). Water temperatures could also influence patterns of recruitment to populations of marine invertebrates, including crustaceans such as lobsters and crabs, on which human fisheries depend (Aiken and Waddy, 1986; Anger, 1984; Caddy, 1986; MacKenzie, 1988; Rothlisberg, 1979).

When modeling ecology and population dynamics of arthropods, equations are used to represent the functional relationship between environmental temperature and development rate or time of larvae. These equations, hereafter referred to as development functions, are derived by rearing larvae at different controlled temperatures in a lab or hatchery setting, observing development times of multiple larvae at each temperature, and then using regression analyses to fit an equation relating temperature to development time (or its inverse, rate) to the data obtained. There are countless potential forms of equation that can be used to fit such data, including various linear, simple curvilinear, and complex non-linear functions (e.g., see reviews by Anger, 2001; Angilleta Jr., 2006; Blanco et al. 1995; Guerrero et al., 1994; Heip, 1974; McLaren, 1995; Shi and Ge, 2010; Smits et al. 2003). These functions differ in form, assumptions, procedures used to derive their parameters, and most importantly in terms of the development times predicted. For example, development times of American lobster, *Homarus americanus* (H. Milne Edwards, 1837), larvae predicted with these eight different development function types can differ from each other and the data used to derive them by ≥ 40 days at the same temperatures (see Fig. 1; Table S1). However, this is no clear standard rule or consensus as to what is the "best" type of development function to apply to these kinds of data. Researchers

93 are generally left to choose the type of development function to use on their own, and will often
94 select one or a very few forms that have the best apparent match to their characters of their data
95 or has been used by other studies on the same or related species (e.g., Edgar and Andrew, 1990;
96 McLaren et al., 1969). Given the potential for different functions to make very different
97 predictions of development times (e.g., Fig. 1), however, development function choice should be
98 given more consideration in studies on these species.

99 It is possible that certain function types may in general be better representations of the
100 relationship between temperature and development of arthropod larvae, or specific sub-groups
101 within the Arthropoda (e.g., arachnids vs. crustaceans vs. insects), for example because they
102 come closer to capturing thermal performance relations of enzymes and other biomolecules
103 mediating moulting and development cycles in these taxa (Brière et al., 1999; Huey and
104 Stevenson, 1979; Somero, 2004). As a result, such functions might also achieve better fit to
105 development data, be able to more-closely match real observed development times, and make
106 better predictions of development in nature. Differences in methodologies used in studies on
107 different taxa, for example the fact that the range of temperatures tested is generally wider for
108 insects and arachnids than crustaceans; (reviewed by Hartnoll, 1982; Quinn and Rochette, 2015),
109 might also lead to apparent taxonomic differences in function performance and should be
110 investigated. Several previous studies have compared the characteristics of different
111 development function types in general (Anger, 2001; Blanco et al., 1995; Guerrero et al., 1994;
112 McLaren, 1995), while others have attempted to fit multiple function types to data for one or two
113 specific species under study in order to select the best function for their data (e.g., Angilletta Jr.,
114 2006; Heip, 1974; Shi and Ge, 2010; Smits et al., 2003). Many other studies seem to choose one
115 or very few function(s) semi-arbitrarily, without discussing alternatives (e.g., de Oliveria et al.,

2009; Thompson 1982; see also Results). However, no previous study has attempted to assess the degree to which one versus multiple types of development functions are used in published studies, compared performance of different types of development functions across multiple species, or assessed the overall impact of function choice to predictions made with such functions. Such a large-scale analysis is needed, though, because it could potentially allow functions that tend to better represent development data in general to be identified, which can then allow for more informed decisions by future studies on arthropod larval development.

In this study, a critical literature review was conducted to assess whether and to what extent studies of temperature-dependent development of arthropod larvae attempt to represent their data with more than one development function type, and also which specific types of functions tend to be used. Then, data from previously published studies were extracted and retested to derive multiple different development functions for the same datasets. The best model type for each dataset was determined, and whether or not published studies actually used the best function type for their data was recorded. Overall performance of different function types were assessed by comparing overall function rankings, proportion of variance explained, and information loss across datasets. Any taxonomic patterns (e.g., whether particular function types performed better for arachnids than for crustaceans and/or insects) and whether performance was related to the range of temperatures tested were also noted. The consequences of using different function types were then tested by comparing the difference of predicted versus observed development times, fit, and information loss of the function type used in original studies versus that of the best function for the data.

2. Materials and methods:

2.1. Literature review:

A literature search was conducted through Web of Science (Thompson Reuters, 2015) for the terms "temperature" AND "development". An initial search was carried out on 12 September 2012, through which the majority of the data in the present study were obtained; this search yielded 1,052 results. A second search was carried out on 19 November 2014, which returned 35 additional results not available or published online at the time of the initial search. These 1,087 total search results were them further examined, and several criteria were used to remove non-relevant results. Accessible peer-reviewed studies that reported larval development rates or times of arthropods at different temperatures and derived a regression equation(s) (i.e., development function) from their data were sought out. Studies that looked exclusively at at growth (size increase), which is a distinct process from development (Forster et al., 2011), were excluded.

After applying these criteria, 73 studies of 87 different arthropod species were obtained for subsequent examination and analyses (Table S2). Several specific types of development function were frequently utilized in these studies (Table S2); a sub-sample of these functions are presented in Table 1 and discussed in the next section (2.2.1, below). Studies were published between 1970 and 2014, and conducted in several different countries on marine, freshwater, and terrestrial species (Table S2) of various taxa within the Arachnida (Phylum Arthropoda: Subphylum Chelicerata), Crustacea, and Insecta (Table S2). To assess whether published studies tested multiple development functions on their data, each study was carefully read and the number and types of development functions used to fit the data for each study species were noted. Even if results from multiple functions were not reported, if alternative functions than reported were at least mentioned in the Methods sections of studies they were counted as having

considered > 1 function. Also if any study tested multiple development functions on their data and concluded one of these to be the "best" function for their data this was also noted. The percent (%) of the 87 species datasets from the literature search on which one, two, or more functions were tested, and the % of datasets on which different types of functions were tested, were then calculated.

2.2. Meta-analysis:

2.2.1. Development functions considered in this study:

In the present study, eight development function types were examined (Table 1; Figure 1). These included two functions derived by simple linear fitting to development data (the Linear Rate and Linear Sum functions), three simplistic curvilinear (non-linear) functions (Heip Power, Tauti Exponential, and Quadratic functions), two more-complex curvilinear functions including a nonzero minimum temperature (T_{min}) for development (Bělehrádek and Modified Arrhenius functions) and one very complex, asymmetrical non-linear function including both a minimum (T_{min}) and maximum (T_{max}) temperature for development (Brière-2) (Table 1). These functions were found in the literature review in the present study (see section 2.1 and Results) to be used quite frequently in studies of arthropod larvae. Additional development functions also exist, including several functions resembling the Brière-2 one (i.e., including T_{min} and T_{max} parameters) but with very complex structures requiring specialized fitting procedures not readily applicable in many statistical software packages (e.g., Huey and Stevenson, 1979; Ikemoto and Takai, 2000; Lactin et al., 1995; Logan, 1988; Schoolfield et al., 1981; Wang et al., 1982; see review by Shi and Ge, 2010); as such, these additional functions were not considered further in this study.

The Linear Rate function is fit to development rate (d) data and becomes a hyperbola after transformation back to development time (D) (d= 1/D; Campbell et al., 1974; Table 1). The Linear Sum function is a true linear model that is simply fit to D (Winberg, 1971; Table 1). Both of these linear functions can be used to derive starting estimates for the values of T_{min} and T_{max} (Campbell et al., 1974; Table 1) to be used in deriving Bělehrádek, Modified Arrhenius, and Brière-2 functions (see below). The Heip function is a simple Power fit of D versus temperature with an implicit minimum threshold for development of 0°C (Heip, 1974). The Tauti function is likewise a simple exponential curve fit to time data, which is equivalent to the Exponential function often fit to rates (Guerrero et al., 1994; Tauti, 1925). The Quadratic function is a second-order symmetrical polynomial function with positive curvature, in which above a particular temperature D begins to increase with temperature beyond a minimum value (e.g., de Oliveira et al., 2009; Quinn and Rochette, 2015). The Bělehrádek (Bělehrádek, 1936; McLaren, 1963) and Modified Arrhenius (Guerrero et al., 1994) functions are based on power and modified exponential curves, respectively, but with an added parameter (a nonzero minimum temperature, T_{min}) included at which development rate approaches zero (Modified Arrhenius) while time approaches infinity (Bělehrádek) at a vertical asymptote; if biologically-realistic values of T_{min} cannot be obtained, then this parameter can be set to 0°C, making these functions equivalent in this case to the Heip Power and regular Arrhenius functions (Guerrero et al., 1994). It should be noted that both the regular and Modified Arrhenius functions relate development rate to the inverse of temperature, rather than directly to temperature itself (see Table 1), and are thus distinct from typical exponential curves. Lastly, the Brière-2 function is normally fit to rate and has two vertical asymptotes at T_{min} and T_{max}, at which development time approaches infinity (rate approaches 0) (Brière et al., 1999). The Brière-2 development curve is left-skewed, with

207 T_{max} occurring at temperatures very close to that at which minimum development times occur
208 (Brière et al., 1999). There is also a Brière-1 function, in which the value of the b-parameter (see
209 Table 1) is constrained to a value of 2 (Brière et al., 1999), but because during preliminary
210 analyses far-better fits were obtained when allowing this parameter to vary than when
211 constraining it (results not shown), the more-limited Brière-1 version of this function was not
212 considered further in the present study.
213
214 *2.2.2. Re-analysis of species datasets from published studies:*
215 To assess whether the function(s) used in published studies were actually the "best"
216 functions for these published datasets, data were extracted for re-analysis from as many of the
217 studies obtained through the literature search described above as possible. Studies or datasets
218 from the literature search that did not examine at least one of the eight development function
219 types described in the Introduction (Table 1; Figure 1) and previous section (2.2.1) or did not
220 present their data in a way that allowed it to be extracted for retesting (e.g., only mean
221 development times resented, without any measure of error), had to be excluded. Therefore, only
222 52 species datasets out of the 87 studies from the literature search could be retested (Table S2);
223 these included 7 arachnids (all mites, in the Subclass Acari), 20 Crustaceans (9 copepods and 11
224 decapods), and 25 insects in 6 orders (5 Coleoptera, 3 Diptera, 5 Hemiptera, 4 Hymenoptera, 6
225 Lepidoptera, and 2 Thysanoptera) (Table S2). Raw data or means ± error (standard deviation
226 (SD), standard error (SEM), etc.) and sample sizes were extracted from tables or figures in
227 published papers for each of these 52 species and used to generate datasets for reanalysis.
228 Each study dataset was analyzed with linear and nonlinear regressions (Table 1) between
229 temperature and development time or rate, as appropriate. These regression were carried out

using IBM SPSS Statistics 22 (SPSS Inc., 2014). To simplify analyses, only total development times or rates (i.e., summed across multiple larval stages) were examined and data for individual stages were not. For development functions including thermal limits (T_{min} or T_{max}; see Table 1 and section 2.2.1), unconstrained regressions were initially carried out, with starting values for these parameters set to values estimated from linear functions (see Table 1 and section 2.2.1, above). However, results were not accepted if this yielded biologically unrealistic estimates, such as $T_{min} < 0°C$ in a species not known to survive and develop at sub-zero temperatures, unreasonably low T_{min} (e.g., -100°C) or high T_{max} (e.g., 100°C), or T_{min} or T_{max} within the temperature range for which successful development was reported in the original study. In this case, constrained regressions were carried out (e.g., $T_{min} \geq 0°C$, T_{min} < minimum T with successful development, T_{max} > maximum T with successful development, etc.) until satisfactory values were obtained.

Once a regression equation corresponding to each development function was obtained for each dataset, AIC_C values (Akaike's Information Criterion (AIC) corrected for finite sample size; Akaike, 1973; Anderson, 2008) were calculated using the residual sum of squares (RSS) between observed development times and those predicted by each function for each study (Anderson, 2008). Development functions were then ranked for each species dataset based on AIC_C-values. The "best" possible rank was 1, corresponding to the lowest AIC_C value, and the "worst" possible rank – if there were no ties – was 8, which corresponded to the highest AIC_C value among the functions tested. For each species dataset, whether or not the function used in its original published study was the same as that determined to be the "best" function for the data in this study was noted. RSS values were also used to calculate R^2-values for each function, on each dataset. These values were used as a measure of function performance (see next section, 2.2.3),

indicating the proportion of the variation in observed development times that was explained by each temperature-dependent development function.

2.2.3. Assessing and comparing the overall performance of different functions:

To determine whether any particular type(s) of function tended to do "better" than others, the overall performance of each development function across species datasets was assessed using three measures: average ranking (determined using AIC_C), R^2, and Δ_i values. These measures of performance were also compared across different taxonomic groups (arachnids, crustaceans, and insects) as it was possible that certain functions might better represent development of animals in a certain group(s) better than animals in others; this could be due to real biological differences among taxa or to different experimental methodologies used for their rearing.

Calculation of function rankings and R^2-values for each function on each dataset was described above (previous section). Δ_i values were calculated once the best function for a given dataset was determined to assess the information potentially lost by using a function other than the best one (Anderson, 2008); a lower Δ_i value is better, and indicates less information loss. The Δ_i value for a given function, "i", is calculated by subtracting the AIC_C value of the best function of those tested from its AIC_C value (Anderson 2008); therefore, the best function will have $\Delta_i = 0$. A function with a lower Δ_i, higher R^2, or lower (better) ranking value on average than other functions was considered to have performed better overall than other functions.

Separate two-way ANOVAs were carried out in IBM SPSS Statistics 22 (SPSS Inc., 2014) to compare each of these three measures of performance (rankings, R^2, and Δ_i) across different development functions (factor with 8 levels; Table 1), as well as among different taxonomic groups (factor with 3 levels: Arachnida, Crustacea, and Insecta). If a statistically-

276 significant ($p \leq 0.05$) interaction between function and taxon was found, the data for that
277 measure were split by taxon and then separate one-way ANOVAs comparing different functions
278 were carried out for each taxon. If significant differences among functions were found, Tukey's
279 Honestly Significant Difference (HSD) test was used to perform post-hoc comparisons among
280 specific function types.
281
282 *2.2.4. Assessing the consequences of development function choice:*
283 The consequences of choosing one function versus another to predict larval development
284 at different temperatures were assessed by comparing whether and how much the best function
285 identified in this study predicted observed development times relative to the function originally
286 used in the study from which each species dataset was obtained (hereafter the "original"
287 function). Three measures, described in detail below, were calculated for each of the 52 species
288 datasets to assess consequences of function choice. These were mean "improvement", R^2
289 increase, and original study function Δ_i.
290 To calculate the first of these, "improvement", the absolute deviance (in days) between
291 predicted (using a development function) and mean observed development time was calculated
292 for both the best and original study functions, at each temperature tested in original studies. The
293 absolute deviance for the original function was then subtracted from that for the best function at
294 each temperature, to determine how much predictions were improved (i.e., became closer to
295 observed values) by using the best versus original function. These differences were then
296 averaged across all temperatures to calculate a mean absolute "improvement" (in days) per each
297 dataset that was due to using the best versus original functions. Mean improvement per dataset
298 was also expressed as a percent improvement by performing the aforementioned calculations, but

299 before averaging differences between deviance of best and original functions across temperatures
300 these differences were divided by the original function's deviance and multiplied by 100 %; this
301 translated the improvement from a "raw" measure (in days) to a percentage (%).

302 R^2 increase was simply calculated for each dataset by subtracting the R^2-value of that
303 dataset's original function from that of its best function. Percent R^2 increase was also calculated
304 for each dataset by dividing the R^2 by the original function's R^2, and then multiplying by 100 %.
305 A large R^2 increase implied that a greater proportion of the variation in development time was
306 explained by the best function than the original one.

307 The Δ_i of the original function for each dataset was also examined to assess the extent of
308 potential information lost by using these, rather than the best functions, to fit the data. As
309 described above, a lower Δ_i (closer to 0 = Δ_i of best function) is better, and implies the function
310 retains more useful information than a function with a higher Δ_i. Generally a function with $\Delta_i < 2$
311 contains some useful information, even if it is not the "best" function, whereas a function with Δ_i
312 > 14 is highly unlikely to be informative (Anderson 2008). A high original function Δ_i value
313 would imply that the original function was considerably less informative than the best function.

314 If the best function for a given dataset was the same as the original function, all of the
315 measures described above would have a value of zero; if any measure were not significantly
316 different from zero, then, it would imply that using the best versus original function did not result
317 in meaningfully different predicted development times. Therefore, the distributions of mean
318 "improvement" and R^2 increase when best versus original functions were used to predict
319 development times, as well as original function Δ_i values, across all species datasets were
320 compared to zero (null hypothesis of no differences) using analysis of confidence intervals
321 (Cummings et al., 2007). Mean values ± 95 % confidence intervals (95 % C.I.) of each

322 measurement were calculated across all datasets. If the 95% C.I.s did not overlap with zero the
323 null hypothesis could be rejected and a significant ($p < 0.05$) impact of function choice
324 concluded.
325
326 2.3. Potential relationship between thermal range and function performance:
327 One interesting pattern noted during the literature review in this study was that studies of
328 temperature-dependent development differed considerably in their methodology, particularly
329 regarding the range of temperatures tested. Thermal ranges varied considerably among studies in
330 general, from as narrow as 6°C to as wide as 35°C (Table S2). Differences also appeared to exist
331 between studies of different taxonomic groups, particularly between studies of crustaceans
332 versus those of arachnids and insects (Hartnoll, 1982; Quinn and Rochette, 2015; Table S2). To
333 confirm whether such taxonomic differences were significant, the thermal range for each species
334 dataset subjected to detailed re-analysis (n =52 total) was calculated as the maximum
335 temperature tested in its original study minus the minimum temperature tested; this included any
336 temperatures at which successful development was not observed (i.e., survival = 0 %), as this
337 implies a developmental threshold (like T_{min} and T_{max} in the Brière-2 function, for example).
338 One-way ANOVA was then used to compare thermal ranges among taxonomic groups.
339 More complex functions have lower power to model smaller datasets (Shi and Ge, 2010).
340 This is especially true for complex development functions containing threshold temperatures
341 (T_{min} and T_{max}) if these are fit to data recorded over narrow thermal ranges not approaching a
342 species' real thermal limits (Shi and Ge, 2010). In such cases, thermal thresholds have to be
343 extrapolated too far beyond actual observations, resulting in excessively extreme estimates for
344 these parameters. One could thus expect that complex functions like Brière-2 may perform better

345 when wider thermal ranges are tested, potentially approaching or encompassing real thermal
346 limits. To test whether or not more complex functions would be selected as better functions when
347 wider thermal ranges were tested, Pearson's correlation coefficients (R) were calculated between
348 the thermal ranges calculated for each dataset and the ranking of each function per dataset. Thus,
349 eight separate correlation analyses were carried out (one for each type of development function),
350 each consisting of 52 thermal range-ranking pairs (one pair per dataset). Whether correlations
351 were significant ($p \leq 0.05$), and if significant R-coefficients were positive or negative was
352 examined. As lower ranking values implied better function performance (see above), a positive
353 correlation for a given function implied that the function did worse when a wider range of
354 temperatures was tested, whereas a negative correlation meant that the function did better when a
355 wider thermal range was tested.
356
357 **3. Results:**
358
359 3.1. Results of literature review – usage of different functions:
360 Out of 87 different species datasets, over half (56.5 %, or 49 datasets) were reported to
361 have been fit with only one development function and the majority (89.2 %, or 78 datasets) were
362 fitted with four or fewer functions (Fig. 2A). In most cases studies that used 2-4 functions
363 examined insects or arachnids (Fig. 2A) and used 1-3 complex functions (like the Brière-2
364 function) plus the Linear Rate function to derive starting values for T_{min} and T_{max} parameters in
365 these complex functions (Fig. 2B; Table S2). The only taxonomic group for which > 4 different
366 functions were tested was Insecta, for which 10.6 % of all species datasets (9 in total,
367 representing 18.1 % of insects) were tested with 5-17 different development functions (Fig. 2A).

368 The most frequently-used development functions overall, and particularly among studies
369 of the Insecta and Arachnida, were the Linear Rate (34.9 % of all datasets, 48.7 % of insect
370 datasets, 29.5 % of arachnids) and Brière-2 functions (7.6 % of all datasets, 5.0 % of insects,
371 35.3 % of Arachnida), in addition to various other complex functions (30.2 % of all datasets,
372 37.5 % of Insecta, 35.3 % of arachnids) not examined in detail in this study (Fig. 2B; Table S2;
373 see Methods, section 2.2.1.). No other function types were used for arachnids, and the only other
374 functions used for insects were the Heip Power and Quadratic functions, and these were only
375 used rarely (5.0 and 3.8 % of insect datasets, respectively; Fig. 2B). All eight development
376 functions examined in this study – in addition to a few other types - were used in previous
377 studies of Crustacea (Fig. 2B; Table S2), with the most common being the Heip Power and
378 Bělehrádek functions in 6.8 and 8.3 % of all datasets, respectively (Fig. 2B), representing 25.7
379 and 31.3 % of Crustacean datasets.
380
381 3.2. Results of meta-analysis – did previous studies use the "best" function for their data?
382 The development function(s) used to fit species datasets and/or concluded to have been
383 the "best" function for these data in their original studies were found, in the vast majority of
384 cases, not to be the best function for the data out of the eight functions examined (Fig. 3). When
385 AIC_C was used to rank functions, the best function for 86.5 % of 52 study datasets was
386 concluded to be a different one than that selected in previous studies (Fig. 3). For all three
387 taxonomic groups, a considerable majority of datasets (75.0 % for Crustacea, 92.1 % for Insecta,
388 and 100 % for Arachnida) were found to be best fit using a different function than that used in
389 original studies of these species (Fig. 3).
390

391 3.3. Overall performance of different functions:

392 There was a significant interaction ($F_{14, 392} = 4.180$, $p < 0.001$) between the effects of
393 taxonomic group and development function type on overall performance of the eight different
394 development functions as assessed by ranking functions with AIC_C. Therefore differences in
395 rankings among functions were compared for each taxonomic group separately. In all three
396 taxonomic groups, ranking did significantly differ among different development functions
397 (Arachnida: $F_{7, 48} = 22.061$, $p < 0.001$; Crustacea: $F_{7, 48} = 11.103$, $p < 0.001$; Insecta: $F_{7, 48} =$
398 32.833, $p < 0.001$). Differences in rankings among functions were actually very similar across
399 the different taxonomic groups (Fig. 4). There were some differences among taxa in terms of the
400 placement of functions of more intermediate mean rankings; for instance, the Tauti Exponential
401 function was ranked well among Crustacea (Fig. 4C) but not for the other taxa (for Arachnida it
402 had one of the poorest ranks (Fig. 4A) and it was intermediate for Insecta (Fig. 4B)) and the
403 Linear Rate and Brière-2 functions were ranked poorly for the Arachnida and Crustacea (Fig.
404 4A, C) but intermediately for Insecta (Fig. 4B). However, the functions with the "best" (lowest
405 values, closest to 1) and "worst" (highest values, furthest from 1) mean rankings were mostly
406 consistent among groups. The best-ranked functions included the Heip Power, Quadratic, and
407 Bělehrádek functions for all three taxonomic groups, as well as the Modified Arrhenius function
408 in both Arachnida and Insecta (Fig. 4). The worst functions included the Linear Sum function in
409 all three taxa and the Brière-2 function in both Arachnida and Crustacea (Fig. 4).
410
411 3.4. Consequences of function choice:

412 R^2-values differed among the eight development functions ($F_{7, 392} = 7.973$, $p < 0.001$;
413 Fig. 5A) but not among taxonomic groups ($F_{2, 392} = 1.635$, $p = 0.196$); there was no significant

414 interaction between function and taxonomy ($F_{14, 392} = 1.138$, $p = 0.323$). Mean R^2-values were
415 fairly high for all development functions and ranged between 0.7 and 0.9 (Fig. 5A), meaning
416 that, on average, all temperature-dependent development functions tested were able to explain
417 the majority of variation in observed development times. Significant differences were found
418 among functions, however. The Heip Power, Quadratic, Bělehrádek, and Modified Arrhenius
419 functions had the highest overall R^2-values (approximately 0.9) and explained significantly more
420 variation in development time than the Tauti Exponential and Linear Rate functions, which had
421 intermediate R^2-values (approximately 0.8) (Fig. 5A). The Linear Sum and Brière-2 functions
422 had the lowest R^2-values, of 0.7 on average and explained significantly less variation in
423 development time than all other functions except the Linear Rate function (Tukey's HSD test, p
424 < 0.001; Fig. 5A). The explanatory power of development functions therefore differed by as
425 much as 10-20% on average depending on which was used (Fig. 5A).

426 Δ_i values also differed among functions ($F_{7, 392} = 6.178$, $p < 0.001$) but not among taxa (F
427 $_{2, 392} = 1.766$, $p = 0.172$; non-significant interaction: $F_{14, 392} = 0.812$, $p = 0.656$; Fig. 5B). All
428 mean Δ_i values were high (mean $\Delta_i \geq 44.5$) because each function was not selected as the best
429 function by AIC_C at least once, and in many cases the difference between the AIC_C values of the
430 best function and the 2nd best function (Δ_i) were quite large (as evidenced by the variance in Fig.
431 5B). The lowest average Δ_i values of 44.5 and 47.5 were calculated for the Bělehrádek and
432 Modified Arrhenius functions, and the highest value (mean $\Delta_i = 451.2$) for the Linear Sum
433 function (Fig. 5B). There were therefore large differences in the amount of information attained
434 depending on which function was used.

435 Mean improvement ± 95 % C.I. in how well predicted development times matched
436 observed time when the best versus the originally-used function were utilized was 1.9 ± 0.4 days,

437 and mean improvement per dataset ranged from < 1 to > 5 days (Fig. 6A). These improvements
438 could be fairly large in terms of percent improvement over predictions using original function,
439 which ranged from 1 to 18 % or greater, with an average value ± 95 % C.I. s of 7.9 ± 1.7 % (Fig.
440 6B). When the best function was found in this study to not be the same as the function used in
441 the original studies from which datasets were obtained (n = 42/52 datasets), the R^2 increased by
442 an average ± 95 % C.I.s of 0.105 ± 0.045 (Fig. 6C), which is significantly greater than zero ($p <$
443 0.05) meaning that ~10 % of the variation in the data was better explained using the best
444 function. The difference in R^2-values between originally-used and best functions could be much
445 greater in many cases, though, as percent increase in R^2 by using the best function ranged from
446 as low as 1% to as high as 80% for certain study datasets (Fig. 6C); mean percent increase in R^2
447 ± 95 % C.I. was 5.935 ± 4.340 % (Fig. 6C). Additionally the mean Δ_i of the originally-used
448 functions was 261.9 ± 99.0 (Fig. 6D), indicating a substantial loss of information relative to the
449 actual best function, at least as determined in the present study. All measures of improvement
450 resulting from using the best rather than original functions on species datasets were significantly
451 different from zero (analysis of confidence intervals, $p \leq 0.05$; Fig. 6).
452
453 3.5. Range of temperature tested in studies versus function performance:
454 Thermal ranges tested in original studies differed significantly among studies of different
455 taxonomic groups ($F_{2, 49} = 12.607$, $p < 0.001$; see also Table S2). Interestingly, studies of
456 crustaceans tended to be carried out over significantly smaller thermal ranges (mean ± 95% C.I.
457 = 10.7 ± 1.4 °C) than those of arachnids (17.5 ± 3.0 °C' Tukey's HSD test, p =0.003) or insects
458 (16.82 ± 2.0 °C; Tukey's HSD test, $p < 0.001$) implying notable differences in the way thermal

459 effects are investigated in these taxa; thermal ranges studied for Insects and Arachnids did not
460 differ, however (Tukey's HSD test, $p = 0.937$).

461 The range of temperatures examined in previous studies was significantly correlated with
462 performance (ranking) of several of the development functions tested in this study (Table 2).
463 Rankings of the Linear Sum, Heip Power, and Tauti Exponential functions by AIC_C were
464 weakly, but significantly and positively correlated with temperature range (Table 2), meaning
465 that these functions tended to do more poorly (higher value = poorer rank, further from 1) when
466 larger thermal ranges were tested. Conversely, rankings of the Modified Arrhenius, Bělehrádek,
467 and Brière-2 functions ranked by AIC_C were negatively correlated with temperature range (Table
468 2), meaning that these functions performed better (lower value = better rank, closer to 1) when
469 studies tested a wider range of temperatures.

470

471 **4. Discussion:**

472

473 4.1. Use and performance of different development functions in previous studies:

474 Modeling functional relationships between temperature and life history characters is an
475 essential component of studying the biology of poikilothermic organisms (Angilletta Jr., 2006;
476 Bělehrádek, 1935; Shi and Ge, 2010). Predictions of generation times (Huntley and Lopez,1992),
477 timing of seasonal events (Bayoh and Lindsay, 2003), dispersal potential (de Rivera et al., 2007),
478 and recruitment to adult populations of Arthropoda (Aiken and Waddy, 1986; Caddy, 1986)
479 produced by such modeling efforts are thus sensitive to the types of temperature-dependent
480 larval development functions incorporated in these. Development times of arthropod larvae
481 predicted for the same species and temperatures by different function types can differ

482 substantially, which has important impacts on predictions made. Using the best possible function
483 to represent a given species' and/or study's dataset should thus be a crucial component of the
484 study of temperature-dependent arthropod larval development, which should precede reporting
485 and use of the results of such studies in models. However, in the present study this important step
486 was found to be largely bypassed by the majority of studies. Particular function types tended to
487 be used more often than others for particular taxonomic groups with little or no clear justification
488 for the choice made, while consideration of alternative function types was rarely reported in
489 published papers. In most cases the function used in original published studies was not actually
490 the best one for the datasets presented. Further, fitting these data with the best model resulted in
491 better fit, less disagreement between predicted and observed development times, decreased
492 information loss, and presumably also better predictive ability. These results demonstrate that
493 development function choice is an important but often-ignored step in research on arthropod
494 larval development, which should be given greater consideration in future studies.

495 Choosing one particular development function might have some justification if any
496 function(s) could be said to be better overall than others. In the present study, no single function
497 type was found to be the best or worst, but the Heip Power, Quadratic, Bělehrádek, and Modified
498 Arrhenius functions tended to perform quite well overall, while the Linear Sum and Brière-2
499 functions tended to perform quite poorly. Functions that performed well overall might be
500 recommended as good starting points for fitting development data, and those that did poorly
501 overall could conversely be used with caution. However, even these functions were not
502 universally found to be the best or worst for all datasets. For example, the Linear Sum function
503 was actually found to be the best for American lobster (*Homarus americanus* (H. Milne
504 Edwards, 1837)) data from Quinn et al. (2013), while the Heip Power, Bělehrádek, and other

overall "good" functions performed more poorly on these data (Table S1). Also, the Brière-2 function, which performed poorly overall, did somewhat better on insect data than for other taxa and actually was among the best models for some insect species datasets (Table S2). Therefore, it is difficult to make general statements about which function is always best to use; this must rather be assessed on a case-by-case basis, for each species and study. Results in this study showed that not using the best function for a given dataset can result in very different predicted development times, which could lead to very different (and potentially erroneous) inferences and predictions of species biology by modeling studies (Miller et al., 1998; Miller et al., 2006; Quinn, 2014; Reitzel et al., 2004). The practice among many fields of study has been to fit data with a development function type that has been used in previous studies on similar species; for example, the frequent use of the Bělehrádek function on copepod crustaceans (Anger, 2001; Corkett and McLaren, 1970; Hamasaki et al. 2009) or Linear Rate + complex function(s) on insects and arachnids (Golizadeh and Zalucki, 2012; Shi and Ge, 2010; Smits et al., 2003; Table S2). However, based on results of the present study this practice should be discontinued.

4.2. Importance of temperature range tested to function performance:

An interesting finding in the present study was that overall performance of several function types was correlated with the range of temperatures tested in original published studies. Specifically, as the range of temperatures tested increased performance (i.e., likelihood to be ranked as the best model) of the simplest functions examined (Linear Sum, Heip Power, and Tauti Exponential) decreased while that of the most complex functions (Bělehrádek, Modified Arrhenius, and Brière-2) increased. This result does make sense, however, if one considers the "real" nature of temperature-biological rate relationships. Because the actual performance of the

528 enzymes mediating larval development most certainly have upper and lower functional threshold
529 temperatures, beyond which development cannot progress (Brière et al., 1999; Quinn and
530 Rochette, 2015; Somero, 2004), one can assume that for most species the "true" relationship
531 between temperature and development time resembles the Brière-2 function, or similar complex
532 asymmetrical curves (e.g., Huey and Stevenson, 1979; Shi and Ge, 2010). A study carried out
533 over a very wide range of temperatures should be able to approach or exceed thermal thresholds
534 and therefore identify these limiting temperatures, and thus be best explained by a complex,
535 Brière-2-type function. However, if one carries out their study over a more narrow thermal
536 range, they will only be able to "observe" a certain section of the development curve, which
537 could be located relatively far from one or both threshold temperatures. This could result in the
538 observed temperature-development data having a distinctly Linear, Quadratic, or Power
539 function-like shape, such that one of these alternative, simpler functions would be identified as
540 the "best" function for the data over this specific range. Indeed, this seems to have been the case
541 in several of the datasets examined, in which thermal ranges and/or sample sizes were relatively
542 small (e.g., Quinn et al., 2013; Corkett and McLaren, 1970; Hamasaki et al., 2009; Carlotti et al.,
543 2007; Table S1, S2) and the best function was determined to be one of the simpler functions,
544 such as the Linear Sum or Heip function, even though these should be the least-realistic
545 (Bělehrádek, 1935; Brière et al., 1999; Somero, 2004). Importantly, when this occurs the best
546 function will be the one that provides the most informative description of development times
547 over a very specific range of temperatures, but its performance is likely to degrade if
548 extrapolation beyond this range is attempted. Ultimately the "best" function should be of a
549 complex form resembling a Brière-2-type function, but most studies, especially of Crustacea, are

not conducted over sufficiently wide temperature ranges to be allow good estimates of such functions' parameters to be derived.

The vast majority of insects and arachnids have terrestrial and/or freshwater aquatic habitats, in which temporal variability in air and water temperatures can be very large (Pakyari et al., 2011; Sanchez-Ramos et al., 2007; Stavrinides et al. 2010). As a result, the likelihood of these organisms and their larvae being exposed to extreme temperatures exceeding thresholds for moulting, development, and/or survival can be high. Conversely, many crustaceans (and all of those examined in the present review; Table S2) inhabit the marine realm as larvae and/or adults (Paul and Paul, 1999; Roberts et al., 2012; Thompson, 1982). While it is not impossible that marine crustacean larvae could encounter temperatures too high for development or survival (e.g., such warm extremes could occur in shallow coastal areas, highly-stratified water columns, intertidal zones at low tide, or more generally due to future climate change; Caffara et al., 2012; Quinn and Rochette, 2015), they are thought to be far more likely to encounter lower limiting temperatures, especially in the deeper ocean or temperate regions (Hartnoll, 1982; MacKenzie, 1988). This perceived difference in limiting temperatures appears to have lead studies on temperature-dependent development in these groups along different paths. Studies of insects and arachnids often use very wide temperature ranges with the intent of capturing lower and upper limiting temperatures for development in their species because these physiological limits are known to be essential to modeling these species in their natural environments (Shi and Ge, 2010; Smits et al., 2003). Studies of crustaceans, to the contrary, tend to be limited to more narrow thermal ranges deemed "ecologically-relevant" (i.e., likely to be encountered by the species in nature); occasionally these include lower limits, but in general physiological limits, especially upper ones, are rarely sought (Hartnoll, 1982).

573 While there is certainly logic behind the use of narrower, more-relevant thermal ranges in
574 studies of Crustacea, this approach still has potential to result in errors for two main, related
575 reasons. First, the type of development function used changes predicted development times both
576 at and between (interpolation) observed temperatures and especially outside of these
577 (extrapolation) (Angilletta Jr., 2006; Campbell et al., 1974; Quinn and Rochette, 2015). Second,
578 thermal development limits actually change the shape of the "real" and estimated (i.e., fitted by
579 regression) development curve, for example by decreasing its curvature when lower and upper
580 limits are further apart and increasing curvature when these are closer together (Bělehrádek,
581 1935; Brière et al., 1999; Shi and Ge, 2010; personal observations by author). All else being
582 equal, these difference in curvature can result in very different development times at the same
583 temperatures. As a result, it is important to know the physiological limits of a given species when
584 modeling its development. Even if a species rarely encounters temperatures close to these limits,
585 development times calculated at intermediate temperatures will be impacted by the values of
586 these limits; if one ignores these limits and uses a different function type, or attempts to estimate
587 limits by extrapolation from a narrow thermal range, there is great potential for erroneous
588 predictions of development times to be made.
589
590 4.3. Discussion of potential limitations and next steps:
591 In the present review, published studies on arthropod larvae were obtained through
592 literature searches through Web of Science (Thompson Reuters, 2015). These searches were by
593 no means comprehensive – many other studies of temperature-dependent development of
594 arthropod larvae exist that were not indexed in this search engine – but it was extensive and did
595 provide a good sample of such studies encompassing many different years, regions, and

596 arthropod taxa (Table S2). This sample of the relevant literature was thus appropriate and useful
597 for the purposes of the present review of development function usage and performance. An
598 expanded search using additional search tools in a future study could obtained data for other
599 taxonomic groups within the Arthropoda (e.g, myriapods, more non-Acari arachnids (spiders),
600 other orders of Crustacea and Insecta, etc.), or even outside of this phylum (e.g., molluscs: de
601 Severyn et al., 2000; nematodes: Jenkins et al., 2006; Singh and Sharma, 1994; urochorates:
602 Kang et al., 2009; vertebrates: McLaren and Cooley, 1972; Miller et al. 2006), which may reveal
603 additional patterns in study design, taxonomy, and function usage of interest. However, overall
604 patterns and conclusions of the present study would likely hold true. To simplify analyses, this
605 study conducted analyses on total larval development time data rather than on individual larval
606 stages. However, in most species development time of each larval stages has a distinct response
607 to temperature, requiring different developmental equations to be derived for each stage (Corkett
608 and McLaren, 1970; Hartnoll, 1982). Often survival to and through later larval stages is very
609 low, so power to fit more complex functions to later-stage development data can be limited. As a
610 result, the best function can potentially differ among larval stages of the same species, in the
611 same study; indeed, this was noted for American lobster data in the present study (Table S1). A
612 future study should investigate stage-specific changes in the "best" development function(s), to
613 confirm whether such patterns could impact the overall performance of different function types,
614 prediction error, and so on. However, it would make mathematical sense for similar patterns to
615 be found through such a detailed review to those noted in the present study, given that similar
616 factors (e.g., sample sizes and thermal ranges tested) would impact function performance.
617 As noted in the Introduction and Methods (2.2.1), numerous development function types
618 exist in addition to the eight examined in detail in this study. Many of these are extremely

619 complex (e.g., Angilletta Jr., 2006; Huey and Stevenson, 1979; Logan, 1988; Schoolfied et al.,
620 1981; Shi and Ge, 2010) and used very frequently in studies of arthropod (mainly non-Crustacea)
621 larvae (Golizadeh and Zalucki, 2012; Huang et al., 2008; Mobarakian et al., 2014; Table S2). It
622 is possible that one or more of the functions not examined herein could actually be the closest to
623 "real" development relationships and/or perform better overall than all others. For example, Shi
624 and Ge (2010) concluded that the Performance function (Huey and Stevenson, 1979) was best
625 out of the 12 functions they tested on development data for diamondback moth, *Plutella*
626 *xylostella* (L.). This and other additional functions should thus be investigated in a future,
627 expanded review. However, findings of this review that one or few functions are used by most
628 studies, the best function was not the one used in most original published studies, and that using
629 the non-best function results in poorer predictions would not change through consideration of
630 such additional functions. In fact, more complex functions are unlikely to achieve much higher
631 performance on many of the datasets obtained in the present study, particularly those for
632 Crustacea reared over narrow, non-extreme thermal ranges; if anything, functions with greater
633 complexity than the Brière-2 one are most likely to do worse on many of these datasets due
634 smaller sample sizes (Shi and Ge, 2010).

635 In this study function performance was assessed mainly in terms of fit (R^2 and observed
636 versus predicted values) and information loss (AIC_C and Δ_i). These gave good indications of how
637 appropriate each function and its parameter estimates were for particular datasets (e.g., how well
638 sample sizes supported estimation of more complex functions). However, future studies could
639 take more thorough approaches to assessing predictive ability of different functions. One
640 approach to be used in the future to assess function performance could be cross-validation
641 (Picard and Cook, 1984; Anderson, 2008). Even better would be actually testing development

642 functions on new data, for example by predicting development times for a particular species at
643 different temperatures using different functions derived in a prior study, and then measuring new
644 development times and comparing these to predictions. If future studies attempted this, very
645 thorough tests and new evidence in favour of one function or another might be obtained.
646
647 4.4. Implications of development time predictions based on different functions:
648 Differences in development times predicted for the same species and temperature among
649 development functions have potential to impact various types of predictions relevant to arthropod
650 biology and ecology. Larval survival is usually inversely related to larval duration, such that
651 slower development results in fewer potential recruits to adult populations (Reitzel et al., 2004;
652 Roberts et al., 2012). Most life history and bio-physical models account for this by reducing
653 larval numbers in simulated cohorts by a certain percentage at each model time step, resulting in
654 substantial, exponential losses per each additional step spend in larval development (e.g., Miller
655 et al., 1998; Quinn, 2014). In many crustaceans, the larval phase of the life cycle is the main
656 dispersive phase (Anger, 1984; de Rivera et al., 2007; MacKenzie, 1988). Lengthening the larval
657 developmental period of such larvae can dramatically alter how far and to where larvae drift in
658 simulations with ocean currents; for example, simulations by Quinn (2014) showed that slowing
659 larval development (and thus lengthening drift time) of American lobster larvae by 60 % could
660 result in increased drift distances of larvae by up to ca. 500 km. If drift were overestimated in
661 such models, for instance due to use of inappropriate development functions, then the degree of
662 population mixing would be overestimated and an incorrect estimate of population structure
663 obtained; underestimation by the same means could also lead to considerable errors. Likewise if
664 dispersal ability of larvae of an invasive species, such as the green crab *Carcinus maenas* (L.) (de

665 Rivera et al., 2007), were underestimated in this way potential invasions to new regions that
666 could be predicted may be missed. Using development functions to estimate the timing of
667 seasonal peaks in abundance of disease vectors (Bayoh and Lindsay, 2003), agricultural pests
668 (Campbell et al., 1994; Easterbrook et al., 2003; Stavrinides et al., 2010), or species that serve as
669 important food sources to others (e.g., copepod secondary productivity in the ocean: Carlotti et
670 al., 2007) also depends on being able to make good estimates of larval development. For many
671 species very small differences in development time similar to the difference in "errors" of best
672 and original studies' functions are enough to dramatically alter the nature and implications of
673 modeled predictions (e.g., ≤ 1-5 days; Gadino and Walton, 2012). The type of development
674 function used can thus have large impacts on predictions, so it is important that studies attempt to
675 find the best model for their data. Importantly, much research is now being initiated to assess
676 how future climate change will impact many species, including arthropods and their larvae
677 (Caffara et al., 2012; Quinn and Rochette, 2015). Use of non-best development functions within
678 such research clearly could result in erroneous predictions as well and so should be avoided.
679
680 4.5. Recommendations and conclusions:
681 Based on results of this study, it is recommended that future studies examining effects of
682 temperature on development of arthropod larvae consider and attempt to fit multiple alternative
683 development function types to their data to determine the best way to model their results and
684 report that this was attempted. No one function type is better or worse overall, but the range of
685 temperatures to be considered and potential use of results (e.g., for extrapolation to temperatures
686 not observed) can be used as a guide when deciding which functions are most likely to provide
687 good representations of data. In general simpler functions (Heip Power, Tauti Exponential) could

688 provide better descriptions of development observed over relatively narrow thermal ranges (but
689 provide poor extrapolation ability). Conversely, wider ranges encompassing lower (Bělehrádek,
690 Modified Arrhenius) and/or upper (Brière-2 and similar functions) limiting temperatures for
691 development can support more complex functions, which potentially resemble more closely true
692 enzymatic and biological thermal performance curves (Brière et al., 1999; Somero, 2004) and
693 may allow modeling over all temperatures potentially encountered. Studies on crustaceans in
694 particular should be conducted over wider thermal ranges in the future so that limiting
695 temperatures of these species can be identified and more complex, presumably realistic
696 development functions reliably fit to data for these organisms. Considering different potential
697 function types to find the best for each dataset should lead to better predictions of larval
698 development times in support of subsequent research on these important species.
699

700 **Acknowledgements:**

701

702 Thanks are due to Rémy Rochette, Joël Chassé, Jeff Houlahan, and Heather Hunt for advice and
703 guidance during this project, and the University of New Brunswick, Saint John Campus, for
704 providing resources that made the review and analyses possible.
705

706 **References:**

707 Aiken, D.E., Waddy, S.L., 1986. Environmental influence on recruitment of the American
708 lobster, *Homarus americanus*: a perspective. Can. J. Fish. Aquat. Sci. 43, 2258-2270.

709 Akaike, H., 1973. Information theory as an extension of the maximum likelihood principle, in:
710 Petrov, B.N., Csaki, F. (Eds.), Second International Symposium on Information Theory.
711 Akademiai Kiado, Budapest, pp. 267-281.
712 Al-Saffar, Z.Y., Grainger, J.N.R., Aldrich, J., 1996. Temperature and humidity affecting
713 development, survival and weight loss of the pupal stage of *Drosophila melanogaster*,
714 and the influence of alternating temperature on the larvae. J. Therm. Biol. 21, 389-396.
715 Anderson, D.R., 2008. Model Based Inference in the Life Sciences: A Primer on Evidence.
716 Springer Science+Business Media, LLC, New York.
717 Anger, K., 1984. Development and growth in larval and juvenile *Hyas coarctatus* (Decapoda,
718 Majidae) reared in the laboratory. Mar. Ecol. Prog. Ser. 19, 115-123.
719 Anger, K., 2001. Crustacean Issues 12: The Biology of Decapod Crustacean Larvae. A.A.
720 Balkema, Rotterdam.
721 Angilletta, Jr., M.J., 2006. Estimating and comparing thermal performance curves. J. Therm.
722 Biol. 31, 541-545.
723 Bayoh, M.N., Lindsay, S.W., 2003. Effect of temperature on the development of the aquatic
724 stages of *Anopheles gambiae* sensu stricto (Diptera: Culicidae). Bull. Entomol. Res. 93,
725 375-381.
726 Bělehrádek, J., 1935. Temperature and living matter. Protoplasma Monographia, No. 8.
727 Borntraeger, Berlin.
728 Blanckenhorn, W.U., 1997. Effects of temperature on growth, development and diapause in the
729 yellow dung fly – against all the rules? Oecologia 111, 318-324.

730 Blanco, J. M., Guerrero, F., Rodríguez, V., 1995. The fate of comparisons of models in
731 temperature-dependent growth of copepods: a reply to the comments by McLaren. J.
732 Plankton Res. 17, 1391-1394.
733 Brière, J.F., Pracross, P., Rioux, A.Y., Pierre, J.S., 1999. A novel rate model of temperature-
734 dependent development for arthropods. Environ. Entomol. 28, 22-29.
735 Caddy, J.F., 1986. Modelling stock-recruitment processes in Crustacea: some practical and
736 theoretical perspectives. Can. J. Fish. Aquat. Sci. 43, 2330-2344.
737 Caffara, A., Rinaldi, M., Eccel, E., Rossi, V., Pertot, I., 2012. Modelling the impact of climate
738 change on the interaction between grapevine and its pests and pathogens: European
739 grapevine moth and powdery mildew. Agr. Ecosyst. Environ. 148, 89-101.
740 Campbell, A., Frazer, B.D., Gilbert, N., Gutierrez, A.P., Mackauer, M., 1974. Temperature
741 requirements of some aphids and their parasites. J. Appl. Ecol. 11, 431-438.
742 Carlotti, F., Bonnet, D., Halsband-Lenk, C., 2007. Development and growth rates of
743 *Centropages typicus*. Progress in Oceanography 72, 164-194.
744 Cave, R.D., Schiacchetano, C., Diaz, R., 2009. Temperature-dependent development of the
745 cycad Aulacapsis scale, *Aulacapsis yasumatsui* (Hemiptera: Diaspididae). Florida
746 Entomol. 92, 578-581.
747 Choy, S., 1991. Embryonic and larval biology of *Liocarcinus holsatus* and *Necora puber*
748 (Crustacea: Brachyura: Portunidae). J. Exp. Mar. Biol. Ecol. 148, 77-92.
749 Compolo, O., Malacrinò, A., Laudani, F., Maione, V., Zappalà, L., Palmeri, V., 2014. Population
750 dynamics and temperature-dependent development of *Chrysomphalus aonidum* (L.) to
751 aid sustainable pest management decisions. Neotrop. Entomol. 43, 453-464.

752 Cooper, B.S., Tharp II, J.M., Jernberg, I.I., Angilletta Jr., M.J., 2012. Developmental plasticity of
753 thermal tolerances in temperate and subtropical populations of *Drosophila melanogaster*.
754 J. Therm. Biol. 37, 211-216.
755 Corkett, C.J., 1972. Development rate of copepod eggs of the genus *Calanus*. J. Exp. Mar. Biol.
756 Ecol. 10, 171-175.
757 Corkett, C.J., McLaren, I.A., 1970. Relationships between development rate of eggs and older
758 stages of copepods. J. Mar. Biol. Assoc. U.K. 50, 161-168.
759 Coutant, C.C., Talmage, S.S., 1976. Thermal effects. J. Wat. Poll. Contr. Fed. 48, 1486-1544.
760 Cummings, G., Fiddler, F., Vaux, D.L., 2007. Error bars in experimental biology. J. Cell Biol.
761 177, 7–11.
762 de Oliveira, S.A., Souza, B., Auad, A.M., da Silva, D.M., Souza, L.S., Carvalho, C.A., 2009.
763 Desenvolvimento e reprodução de *Sipha flava* (Forbes) (Hemiptera: Aphididae) em
764 diferentes temperaturas. Neotrop. Entomol. 38, 311-316.
765 de Rivera, C.E., Hitchcock, N.G., Teck, S.J., Steves, B.P., Hines, A.H., Ruiz, G.M., 2007. Larval
766 development rate predicts range expansion of an introduced crab. Mar. Biol. 150, 1275-
767 1288.
768 de Severeyn, Y. G., Severeyn, H., Grant, W., Reverol, Y., 2000. Effect of water temperature on
769 larval development of the bivalve mollusk *Tivela mactroides*: evaluation in the laboratory
770 and via simulation. Ecol. Model. 129, 143-151.
771 Du, W.-G., Hu, L.-J., Lu, J.-L., Zhu, L.-J., 2007. Effects of incubation temperature on embryonic
772 development rate, sex ratio and post-hatching growth in the Chinese three-keeled pond
773 turtle, *Chinemys reevesii*. Aquaculture 272, 747-753.

774 Easterbrook, M.A., Fitzgerald, J.D., Pinch, C., Tooley, J., Xu, X.-M., 2003. Development time
775 and fecundity of three important arthropod pests of strawberry in the United Kingdom.
776 Ann. Appl. Biol. 143, 325-331.
777 Edgar, A.J., Andrew, T.E., 1990. A simple method for fitting Bělehrádek's equation to
778 embryonic development data of zooplankton. Hydrobiologia 194, 177-181.
779 Eliopoulos, P.A., Kontodimas, D.C., Stathas, G.J., 2010. Temperature-dependent development of
780 *Chilocorus bipustulatus* (Coleoptera: Coccinellidae). Mol. Ecol. Evol. 39, 1352-1358.
781 Emmert, C.J., Mitzell III, R.F., Andersen, P.C., Frank, J.H., Stimac, J.L., 2008. Effects of
782 contrasting diets and temperatures on reproduction and prey consumption by
783 *Proprioseiopsis asetus* (Acari: Phytoseiidae). Exp. Appl. Acarol. 44, 11-26.
784 Forster, J., Hirst, A.G., 2012. The temperature-size rule emerges from ontogenetic difference
785 between growth and development rates. Functional Ecol. 26, 483-492.
786 Forster, J., Hirst, A.G., Woodward, G., 2011. Growth and development rates have different
787 thermal responses. Am. Nat. 178, 668-678.
788 Gadino, A.N., Walton, V.M., 2012. Temperature-related development and population parameters
789 for *Typhlodromus pyri* (Acari: Phytoseiidae) found in Oregon vineyards. Exp. Appl.
790 Acarol. 58, 1-10.
791 Gao, G.-Z., Perkins, L.E., Zalucki, M.P., Lu, Z.-Z., Ma, J.-H., 2013. Effect of temperature on the
792 biology of *Acyrthosiphon gossypii* Mordvilko (Homoptera: Aphididae) on cotton. J. Pest.
793 Sci. 86, 167-172.
794 Geffen, A.J., Nash, R.D.M., 2012. Egg development rates for use in egg production methods
795 (EPMs) and beyond. Fish. Res. 117-118, 48-62.

796 Golizadeh, A., Zalucki, M.P., 2012. Estimating temperature-dependent developmental rates of
797 potato tuberworm, *Phthorimaea operculella* (Lepidoptera: Gelechiidae). Insect Sci. 19,
798 609-620.
799 Gonzàlez, L., Carvajal, J., 2003. Life cycle of *Caligus rogercresseyi* (Copepoda: Caligidae)
800 parasite of Chilean reared salmonids. Aquaculture 220, 101-117.
801 Greenberg, S.M., Sétamou, M., Sappington, T.W., Liu, T.-X., Coleman, R.J., Armstrong, J.S.,
802 2005. Temperature-dependent development and reproduction of the boll weevil
803 (Coleoptera: Curculionidae). Insect Sci. 12, 449-459.
804 Guerrero, F., Blanco, J.M., Rodríguez, V., 1994. Temperature-dependent development in marine
805 copepods: a comparative analysis of models. J. Plankton Res. 16, 95-103.
806 Haghani, M., Fathipour, Y., Talebi, A.A., Baniameri, V., 2007. Temperature-dependent
807 development of *Diglyphus isaea* (Hymenoptera: Eulophidae) on *Liriomyza sativae*
808 (Diptera: Agromyzidae) on cucumber. J. Pest Sci. 80, 71-77.
809 Hamasaki, K., Sugizaki, M., Dan, S., Kitada, S., 2009. Effect of temperature on survival and
810 developmental period of coconut crab (*Birgus latro*) reared in the laboratory. Aquaculture
811 292, 259-263.
812 Hartnoll, R.G., 1982. Growth, in: The Biology of the Crustacea, Vol. 2: Embryology,
813 Morphology, and Genetics. Abele, L.G. (Ed.). Academic Press, New York, pp. 111-196.
814 Heip, C., 1974. A comparison between models describing the influence of temperature on the
815 development rate of copepods. Biologisch Jaarboek Dodonaea 42, 121-125.
816 Herzig, A., 1983. The ecological significance of the relationship between temperature and
817 duration of embryonic development in planktonic freshwater copepods. Hydrobiologia
818 100, 65-91.

819 Huang, Z., Ren, S., Musa, P.D., 2008. Effects of temperature on development, survival,
820 longevity, and fecundity of the *Bemisia tabaci* Gennadius (Homoptera: Aleyrodidae)
821 predator, *Axinoscymnus cardilobus* (Coleoptera: Coccinellidae). Biol. Control 46, 209-
822 215.
823 Huey, R.b., Svenson. R.D., 1979. Integrating thermal physiology and ecology of ectotherms: a
824 discussion of approaches. Am. Zool. 19, 357-366.
825 Huntley, M.E., López, M.D.G., 1992. Temperature-dependent production of marine copepods: a
826 global synthesis. Am. Nat. 140, 201-242.
827 Ikemoto, T., Takai, K., 2000. A new linearized formula for the law of total effective temperature
828 and the evaluation of line-fitting methods with both variables subject to error. Environ.
829 Entomol. 29, 671-682.
830 Jacas, J.A., Peña, J.E., Duncan, R.E., Ulmer, B.J., 2008. Thermal requirements of *Fidiobia*
831 *dominica* (Hymenoptera: Platygastridae) and *Haeckeliania sperata* (Hymenoptera:
832 Trichogrammatidae), two exotic egg parasitoids of *Diaprepes abbreviatus* (Coleoptera:
833 Curculionidae). BioControl 53, 451-460.
834 Jaffari, S., Fathipour, Y., Faraji, F., 2012. Temperature-dependent development of *Neoseiulus*
835 *barkeri* (Acari: Phytoseiidae) on *Tetranychus urticae* (Acari: Tetranychidae) at seven
836 constant temperatures. Insect Sci. 19, 220-228.
837 Jenkins, E. J., Kutz, S.J., Hoberg, E.P., Polley, L., 2006. Bionomics of larvae of
838 *Parelaphostronglyus odocoilei* (Nematoda: Protostrongylidae) in experimentally infected
839 gastropod intermediate hosts. J. Parasitol. 92, 298-305.
840 Kamps, D.M., 1978. The effect of temperature on the development time and brood size of
841 *Diaptomus pallidus* Herrick. Hydrobiologia 61, 75-80.

842 Kang, K.H., Zhang, Z.F., Bao, Z.M., Zhou, B., Han, C.B., 2009. Influence of water temperature
843 on spawning induction and larval development of the sea squirt *Halocynthia ritteri* (Oka,
844 1906). Aquaculture Res. 40, 513-518.
845 Karimi-Malati, A., Fathipour, Y., Talebi, A.A., 2014. Development response of *Spodoptera*
846 *exigua* to eight constant temperatures: Linear and nonlinear modeling. J. Asia-Pac.
847 Entomol. 17, 349-354.
848 Khan, M., Gregg, P., Mensah, R., 2009. Effect of temperature on the biology of *Creontiades*
849 *dilutus* (Heteroptera: Miridae). Austral. J. Entomol. 48, 210-216.
850 Kim, D.-S., Riedhl, H., 2005. Effect of temperature on development and fecundity of the
851 predaceous plant bug *Deraeocoris brevis* reared on *Ephestia kuehniella* eggs. BioControl
852 50, 881-897.
853 Kim, S.C., Song, J.-H., Kim, D.-S., 2008. Effect of temperature on the development and
854 fecundity of the Cryptic Mealybug, *Pseudococcus cryptus*, in the laboratory. J. Asia-Pac.
855 Entomol. 11, 149-153.
856 Klein Breteler, W.C.M., Gonzalez, S.R., Schogt, N., 1995. Development of *Pseudocalanus*
857 *elongatus* (Copepoda, Calanoida) cultured at different temperatures and food conditions.
858 Mar. Ecol. Prog. Ser. 119, 99-110.
859 Koda, K., Nakamura, H., 2010. Effects of temperature on the development and survival of an
860 endangered butterfly, *Shijimiaeoides divinus barine* (Leech) (Lepidoptera: Lycaenidae).
861 Entomol. Sci. 13, 29-34.
862 Krüger, R.F., Kirst, F.D., de Souza, A.S.B., 2010. Rate of development of forensically-important
863 Diptera in southern Brazil. Revista Brasileira de Entomologia 54, 624-629.

Lactin, D.J., Holliday, N.J., Johnson, D.L., Craigen, R., 1995. Improved rate model of temperature-dependent development by arthropod. Environ. Entomol. 24, 68-75.

Lavagnini, T.C., de Freitas, S., Bezerra, A.L., 2009. Aspectos biológicos de *Chrysoperla raimundoi* Freitas & Penny (Neuroptera, Chrysopidae). Revista Brasileira de Entomologia 53, 629-634.

Lefebvre, F., Pasquerault, T., 2004. Temperature-dependent development of *Ophyra aenescens* (Wiedemann, 1830) and *Ophyra capensis* (Wiedemann, 1818) (Diptera, Muscidae). Forensic Sci. Int. 139, 75-79.

Li, D., 2002. The combined effects of temperature and diet on development and survival of a crab spider, *Misumenops tricuspidatus* (Fabricius) (Araneae: Thomisidae). J. Therm. Biol. 27, 83-93.

Lind, M.I., Johansson, F., 2007. The degree of adaptive phenotypic plasticity is correlated with the spatial environmental heterogeneity experienced by island populations of *Rana temporaria*. J. Evo. Biol. 20, 1288-1297.

Liu, S.-S., Meng, X.-D., 1999. Modelling development time of *Myzus persicae* (Hemiptera: Aphididae) at constant and natural temperatures. Bull. Entomol. Res. 89, 53-63.

Logan, D.P., Kettle, C.G., 2007. Temperature-dependent development and distribution in the soil profile of pupae of greyback canegrub *Dermolepida albohirtum* (Waterhouse) (Coleoptera: Scarabaeidae) in Queensland sugarcane. Austral. J. Entomol. 46, 17-22.

Logan, J.A., 1988. Toward an expert system for development of pest simulation models. Environ. Entomol. 17, 359-376.

885 Luypaert, G., Witters, J., Huylenbroeck, J.V., Maes, M., De Riek, J., De Clercq, P., 2014.
886 Temperature-dependent development of the broad mite *Polyphagotarsonemus latus*
887 (Acari: Tarsonemidae) on *Rhododendron simsii*. Exp. Appl. Acarol. 63, 389-400.
888 MacKenzie, B.R., 1988. Assessment of temperature effects on interrelationships between stage
889 durations, mortality, and growth in laboratory-reared *Homarus americanus* Milne
890 Edwards larvae. J. Exp. Mar. Biol. Ecol. 116, 87-98.
891 Marchioro, C.A., Forester, L.A., 2011. Development and survival of the diamondback moth,
892 *Plutella xylostella* (L.) (Lepidoptera: Yponomeutidae) as a function of temperature:
893 effects of number of generations in tropical and subtropical regions. Neotrop. Entomol.
894 40, 533-541.
895 Mazzei, K.C., Newman, R.M., Loos, A., Ragsdale, D.W., 1999. Development rates of the native
896 milfoil weevil, *Eurhychiopsis lecontei*, and damage to Eurasian watermilfoil at constant
897 temperatures. Biol. Control 16, 139-143.
898 McLaren, I.A., 1963. Effects of temperature on growth of zooplankton and the adaptive value of
899 vertical migration. J. Fish. Res. Board Can. 20, 685-727.
900 McLaren, I.A., 1995. Temperature-dependent development in marine copepods: comments on
901 choices of models. J. Plankton Res. 17, 1385-1390.
902 McLaren, I.A., Cooley J.M., 1972. Temperature adaptation of embryonic development rate
903 among frogs. Physiol. Zool. 45, 223-228.
904 McLaren, I.A., Corkett, C.J., Zillioux, E.J., 1969. Temperature adaptations of copepod eggs from
905 the Arctic to the Tropics. Biol. Bull. 137, 486-493.
906 McQuaid, C.D., Branch, G.M., 1985. Trophic structure of rocky intertidal communities: response
907 to wave action and implications for energy flow. Mar. Ecol. Prog. Ser. 22, 153-161.

908 Mehrnejad, M.R., 2012. Biological parameters of *Elasmus nudus* (Hymenoptera, Eulophidae), a
909 parasitoid of the pistachio fruit hull borer moth, *Arimania komaroffi* (Lepidoptera,
910 Pyralidae). Biocontrol Sci. Technol. 22, 659-670.
911 Menge, B.A., 1978. Predation intensity in a rocky intertidal community: effect of an algal
912 canopy, wave action and desiccation on predator feeding rates. Oecologia 34, 17-35.
913 Miller, C.B., Lynch, D.R., Carlotti, F., Gentleman, W., Lewis, C.V.W., 1998. Coupling of an
914 individual-based population dynamic model of *Calanus finmarchicus* to a cricualtion
915 model for the Georges Bank region. Fish. Oceanogr. 7, 219-234.
916 Miller, D.C.M., Moloney, C.L., van der Lingen, C.D., Lett, C., Mullon, C., Field, J.G., 2006.
917 Modelling the effects of physical–biological interactions and spatial variability in
918 spawning and nursery areas on transport and retention of sardine *Sardinops sagax* eggs
919 and larvae in the southern Benguela ecosystem. J. Mar. Syst. 61, 212-229.
920 Milne Edwards, H., 1837. Histoire naturelle des Crustacés, comprenant l'anatomie, la
921 physiologie et la classification de ces animaux. Volume 2. Librairie encyclopédique de
922 Roret, Paris.
923 Mironidis, G.K., Savopoulou-Soultani, M., 2009. Development, survival and growth rate of the
924 *Hyposoter didymator-Helicoverpa armigera* parasitoid-host system: effect of host instar
925 at parasitism. Biol. Control 49, 58-67.
926 Mobarakian, M., Zamani, A.A., Karmizadeh, J., Naghadeh, N.M., Emami, M.S., 2014.
927 Modelling development of *Callosobruchus maculatus* and *Anisopteromalus calandrae* at
928 various constant temperatures using linear and non-linear models. Biocontrol Sci. Tech.
929 24, 1308-1320.

930 Mochizuki, S., Kayaba, Y., Tanida, K., 2006. Larval growth and development in the caddisfly
931 *Cheumatopsyche brevilineata* under natural thermal regimes. Entomol. Sci. 9, 129-136.
932 Mols, P.J.M., van de Ende, E., Blommers, L.H.M., 1998. Embryonic and larval development of
933 *Orthosia* (Lep., Noctuidae) species used for optimizing timing of monitoring and control
934 in apple orchards. J. Appl. Entomol. 122, 431-439.
935 Morimoto, S., Imamura, T., Visarathanonth, P., Miyanoshita, A., 2007. Effects of temperature on
936 the development and reproduction of the predatory bug *Joppeicus paradoxus* Puton
937 (Hemiptera: Joppeicidae) reared on *Tribolium confusum* eggs. Biol. Control 40, 136-141.
938 Newman, B.K., Papadopoulos, I., Vorsatz, J., Woolridge, T.H., 2006. Influence of temperature
939 on the larval development of *Upogebia africana* and *U. capensis* (Decapoda:
940 Thalassinidae: Upogebiidae) in the laboratory. Mar. Ecol. Prog. Ser. 325, 165-180.
941 Nondillo, A., Redaelli, L.R., Botton, M., Pinent, S.M.J., Gitz, R., 2008. Exigências Térmicas e
942 Estimativa do Número de Gerações Anuais de *Frankliniella occidentalis* (Pergande)
943 (Thysanoptera: Thripidae) em Morangueiro [Thermal Requirements and Estimate of the
944 Annual Number of Generations of *Frankliniella occidentalis* (Pergande) (Thysanoptera:
945 Thripidae) on Strawberry Crop]. Neotrop. Entomol. 37, 646-650.
946 Pakyari, H., Fathipour, Y., Enkegaard, A., 2011. Estimating development and temperature
947 thresholds of *Scholothrips longicornis* (Thysanoptera: Thripidae) on eggs of two-spotted
948 spider mite using linear and nonlinear models. J. Pest Sci. 84, 153-163.
949 Palmer, M.A., Coull, B.C., 1980. The prediction of development rate and the effect of
950 temperature for the meiobenthic copepod, *Microarthridion littorale* (Poppe). J. Exp. Mar.
951 Biol. Ecol. 48, 73-83.

952 Park, H.-H., Ahn, J.-J., Park, C.-G., 2014. Temperature-dependent development of
953 *Cnaphalocrocis medianalis* Guenée (Lepidoptera: Pyralidae) and their validation in semi-
954 field conditions. J. Asia-Pac. Entomol. 17, 83-91.
955 Paul, A.J., Paul, J.M., 1999. Development of larvae of the golden king crab *Lithodes aequispinus*
956 (Anomura: Lithodidae) reared at different temperatures. J. Crustac. Biol. 19, 42-45.
957 Picard, R., Cook, D., 1984. Cross-validation of regression models. J. Am. Stat. Assoc.79, 575-
958 583.
959 Prasad, Y.G., Prabhakar, M., Sreedevi, G., Rao, G.R., Venkateswarlu, B., 2012. Effect of
960 temperature on development, survival and reproduction of mealybug, *Phenacoccus*
961 *solenopsis* Tinsley (Hemiptera: Pseudococcidae) on cotton. Crop Protect. 39, 81-88.
962 Quinn, B.K., 2014. Assessing potential influence of larval development time and drift on large-
963 scale spatial connectivity of American lobster (*Homarus americanus*). M.Sc. Thesis,
964 University of New Brunswick, Saint John, NB.
965 Quinn, B.K., Rochette, R., 2015. Potential effect of variation of water temperature on
966 development time of American lobster larvae. ICES J. Mar. Sci. 72 (Supplement 1), i79-
967 i90.
968 Quinn, B.K., Rochette, R., Ouellet, P., Sainte-Marie, B., 2013. Effect of temperature on
969 development rate of larvae from cold-water American lobster (*Homarus americanus*). J.
970 Crustac. Biol. 33, 527-536.
971 Reitzel, A.M., Miner, B.G., McEdward, L.R., 2004. Relationships between spawning date and
972 larval development time for benthic marine invertebrates: a modeling approach. Mar.
973 Ecol. Prog. Ser. 280, 13-23.

974 Roberts, S.D., Dixon, C.D., Andreacchio, L., 2012. Temperature dependent larval duration and
975 survival of western king prawn, *Penaeus (Melicertus) latisulcatus* Kishinouye, from
976 Spencer Gulf, South Australia. J. Exp. Mar. Biol. Ecol. 411, 14-22.
977 Romalho, F.S., Wanderley, P.A., Malaquias, J.B., Rodrigues, K.C.V., Souza, J.V.S., Zanuncio,
978 J.C., 2009. Temperature-dependent development rates of *Bracon vulgaris*, a parasitoid of
979 boll weevil. Phytoparasitica 37, 17-25.
980 Rothlisberg, P.C., 1979. Combined effects of temperature and salinity on the survival and growth
981 of the larvae of *Pandalus jordani* (Decapoda: Pandalidae). Mar. Biol. 54, 125-134.
982 Sànchez-Ramos, I., Àlvarez-Alfageme, F., Castañera, P., 2007. Development and survival of the
983 cheese mites, *Acarus farris* and *Tyrophagus neiswanderi* (Acari: Acaridae), at constant
984 temperatures and 90% relative humidity. J. Stored Products Res. 43, 64-72.
985 Schoolfield, R.M., Sharpe, P.J.H., Magnuson, C.E., 1981. Non-linear regression of biological
986 temperature-depednent rate models based on absolute reaction-rate theory. J. Theor. Biol.
987 88, 719-731.
988 Shi, P., Ge, F., 2010. A comparison of different thermal performance functions describing
989 temperature-dependent development rates. J. Therm. Biol. 35, 225-231.
990 Singh, M., Sharma, S.B., 1994. Temperature effects on development and reproduction of
991 *Heterodera cajani* on Pigeonpea. J. Nematol. 26, 241-248.
992 Smits, N., Brière, J.-F., Fargues, J., 2003. Comparison of non-linear temperature-depednent
993 development rate models applied to *in vitro* growth of entomopathogenic fungi. Mycol.
994 Res. 107, 1476-1484.
995 Somero, G.N., 2004. Adaptation of enzymes to temperature: searching for basic “strategies”.
996 Comp. Biochem. Phys. B 139, 321-333.

997 Son, Y., Lewis, E.E., 2005. Modelling temperature-dependent development and survival of
998 *Otiorhynchus sulcatus* (Coleoptera: Curculinonidae). Agr. Forest Entomol. 7, 201-209.
999 Stavrinides, M.E., Lara, J.R., Mills, N.J., 2010. Comparative influence of temperature on
1000 development and biological control of two common vineyard pests (Acari:
1001 Tetranychidae). Biol. Control 55, 126-131.
1002 Tauti, M., 1925. J. Imp. Fish Inst. Tokyo, 21, (cited in Winberg, 1971 and Guerrero et al., 1994).
1003 Taveras, R., Hilje, L., Carballo, M., 2004. Development of *Hypsipyla grandella* (Zeller)
1004 (Lepidoptera: Pyralidae) in response to constant temperatures [Desenvolvimento de
1005 *Hypsipyla grandella* (Zeller) (Lepidoptera: Pyralidae) em diferentes temperaturas
1006 constants]. Neotrop. Entomol. 33, 1-6.
1007 Thessalou-Legaki, M., 1990. Advanced larval development of *Callianassa tyrrhena* (Decapoda:
1008 Thalassinidea) and the effect of environmental factors. J. Crustac. Biol. 10, 659-666.
1009 Thompson, B.M., 1982. Growth and development of *Pseudocalanus elongatus* and *Calanus* sp.
1010 In the laboratory. J. Mar. Biol. Assoc. U.K. 62, 359-372.
1011 Tofangsazi, N., Buss, E.A., Meagher, R., Mascarin, G.M., Arthurs, S.P., 2012. Thermal
1012 requirements and development of *Herpetogramma phaeopteralis* (Lepidoptera:
1013 Crambidae: Spilomelinae). J. Econ. Entomol. 105, 1573-1580.
1014 Tun-Lin, W., Burkot, T.R., Kay, B.H., 2000. Effects of temperature and larval diet on
1015 development rates and survival of the dengue vector *Aedes aegypti* in north Queensland,
1016 Australia. Medical and Vet. Entomol. 14, 31-37.
1017 Ulmer, B.J., Jacas, J.A., Peña, J.E., Duncan, R.E., Castillo, J., 2006. Effect of temperature on life
1018 history of *Aprostocetus vaquitarum* (Hymenoptera: Eulophidae), an egg parasitoid of
1019 *Diaprepes abbreviatus* (Coleoptera: Curculionidae). Biol. Control 39, 19-25.

1020 Voss, S.C., Cook, D.F., Hung, W.-F., Dadour, I.R., 2012. Survival and development of the
1021 forensically important blow fly, *Calliphora varifrons* (Diptera: Calliphoridae) at constant
1022 temperatures. Forensic Sci. Med. Pathol. 10, 314-321.
1023 Wang, R.-S., Lan, Z.-X., Ding, Y.-Q., 1982. Studies on mathematical models of the relationship
1024 between insect development and temperature. Acta. Ecol. Sin. 2, 47-57. [In Chinese]
1025 Winberg, G.G., 1971. Methods for the Estimation of Production of Aquatic Animals. Academic
1026 Press, London.
1027 Yao, S., Huang, Z., Ren, S., Mandour, N., Ali, S., 2011. Effects of temperature on development,
1028 survival, longevity, and fecundity of *Serangium japonicum* (Coleoptera: Coccinellidae), a
1029 predator of *Bemisia tabaci* Gennadius (Homoptera: Aleyrodidae). Biocontrol Sci.
1030 Technol. 21, 23-34.
1031 Zhao, F., Zhang, W., Hoffman, A.A., Ma, C.-S., 2014. Night warming on hot days produces
1032 novel impacts on development, survival and reproduction in a small arthropod. J. Anim.
1033 Ecol. 83, 769-778.
1034
1035 **Electronic Supplementary Material:**
1036
1037 **Table S1.** Development function parameter estimates, R^2, and AIC_C for American lobster data
1038 plotted in Figure 1.
1039
1040 **Table S2.** List of studies and species obtained for the literature review and meta-analyses,
1041 including taxonomic grouping, function type(s) used, best function, whether the best and used
1042 function were the same, and temperature range tested.

Tables and Figures:

Table 1. Names and forms of the 8 different development functions examined in this study. Functions ranged in complexity from linear [2] to simple curvilinear [1, 3, 4, 5], to complex curvilinear (including a "biological minimum temperature" parameter, T_{min}) [6, 7], to complex asymmetrical (including both T_{min} and a "biological maximum temperature", T_{max}) [8]. If a T_{min} ("biological minimum temperature") or T_{max} ("biological maximum temperature") value is implied within or estimable from a given function, this is indicated in the "Notes" column. In all equations D is development time (in days), T is temperature (°C), A, B, C, a, and b are fitted constants, and e is the Euler number. See section 2.2.1 for other details of these functions.

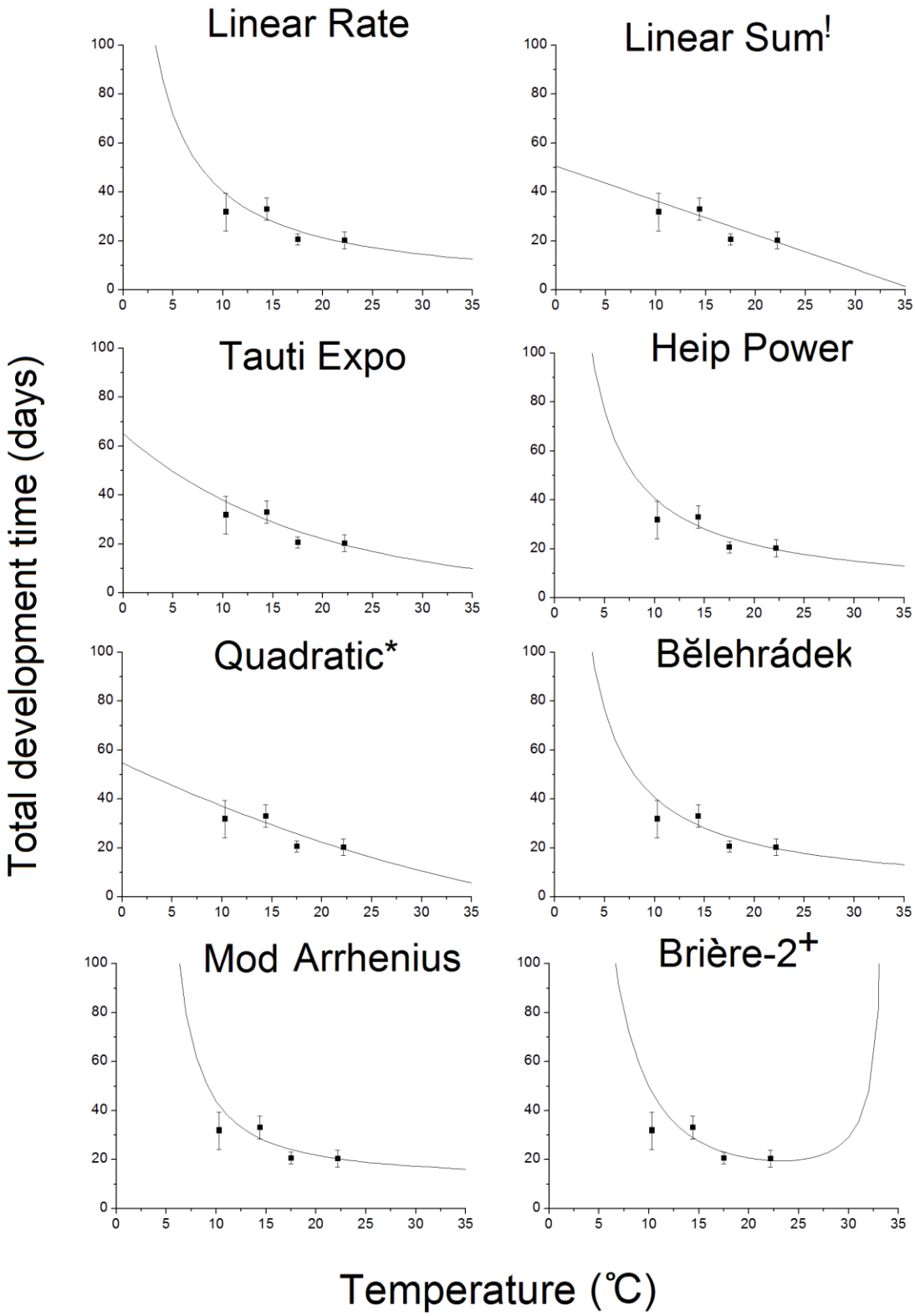
Function [a]	Equation [b, c]	Notes
[1] Linear Rate[1]	$D = 1/(a + bT)$	$T_{min\ est} = -a/b$
[2] Linear Sum[2]	$D = A + BT$	$T_{max\ est} = -A/B$
[3] Heip Power[3]	$D = AT^B$	$T_{min} = 0°C$
[4] Tauti [d] Exponential[4]	$D = Ae^{BT}$	No T_{min}
[5] Quadratic[5]	$D = AT^2 + BT + C$	No T_{min}, $D_{min} = C$
[6] Bělehrádek[6, 7]	$D = A(T-T_{min})^B$	
[7] Modified Arrhenius[8]	$D = 1/[ae^{b(1/(T-Tmin))}]$	
[8] Brière-2[9]	$D = 1/[aT(T-T_{min})(T_{max}-T)^{(1/b)}]$	

[a] References for development functions are as follows: [1]Campbell et al. 1974; [2]Winberg (1971); [3]Heip (1974); [4]Tauti (1925); [5]de Oliveira et al. (2009); [6]Bělehrádek (1935); [7]McLaren (1963); [8]Guerrero et al. (1994); [9]Brière et al. (1999); [b] Functions that are usually fitted to development rate (d = 1/D) are here represented in their inverted form, from which D can be directly calculated; [c] For clarity lowercase letters (a, b) are used for functions fitted to d, and uppercase letters (A, B, C) are used for functions fitted directly to D;. [d] The Exponential function as presented here [4] is mathematically equivalent to the Tauti function, $D = 1/[ae^{bT}]$, such that a = 1/A and b = -B, so the two are treated interchangeably.

1061 **Table 2.** Correlations between the ranges of temperatures (°C) tested in original studies and rank
1062 (out of 8) of development functions based on AIC_C for each species dataset. Pearson's
1063 correlation coefficient values (R) and their associated p-values (evaluated for n = 52 pairs) are
1064 presented; statistically-significant p-values ($p \leq 0.05$) are indicated in bold text.

Function	R	p
Linear Rate	+0.067	0.637
Linear Sum	+0.387	**0.005**
Heip Power	+0.425	**0.002**
Tauti Exponential	+0.427	< **0.001**
Quadratic	+0.056	0.696
Bělehrádek	-0.356	**0.010**
Modified Arrhenius	-0.510	< **0.001**
Brière-2	-0.324	**0.019**

1065
1066
1067



1068

Figure 1. (*Preceding page*) Examples of the curves formed by different development functions, when these are used to calculate development time (y-axes, days) at different temperatures (x-axes, °C). Types of functions plotted here are those presented in Table 1. Actual functions (see Table S1) were derived from and fitted to data for total development times (combined time to complete larval stages I-III) of American lobster (*Homarus americanus* (H. Milne Edwards, 1837)) larvae, as reported by Quinn et al. (2013); mean observed development times ± 95 % C.I.s are plotted (squares) along with predictions of development functions (lines). Coefficients, R^2, AIC_C, and Δ_i values for these functions are presented in Table S1. '*' = function used by Quinn et al. (2013) to fit the data, '!' = actual "best" function for these data, and '+' = worst function for these data.

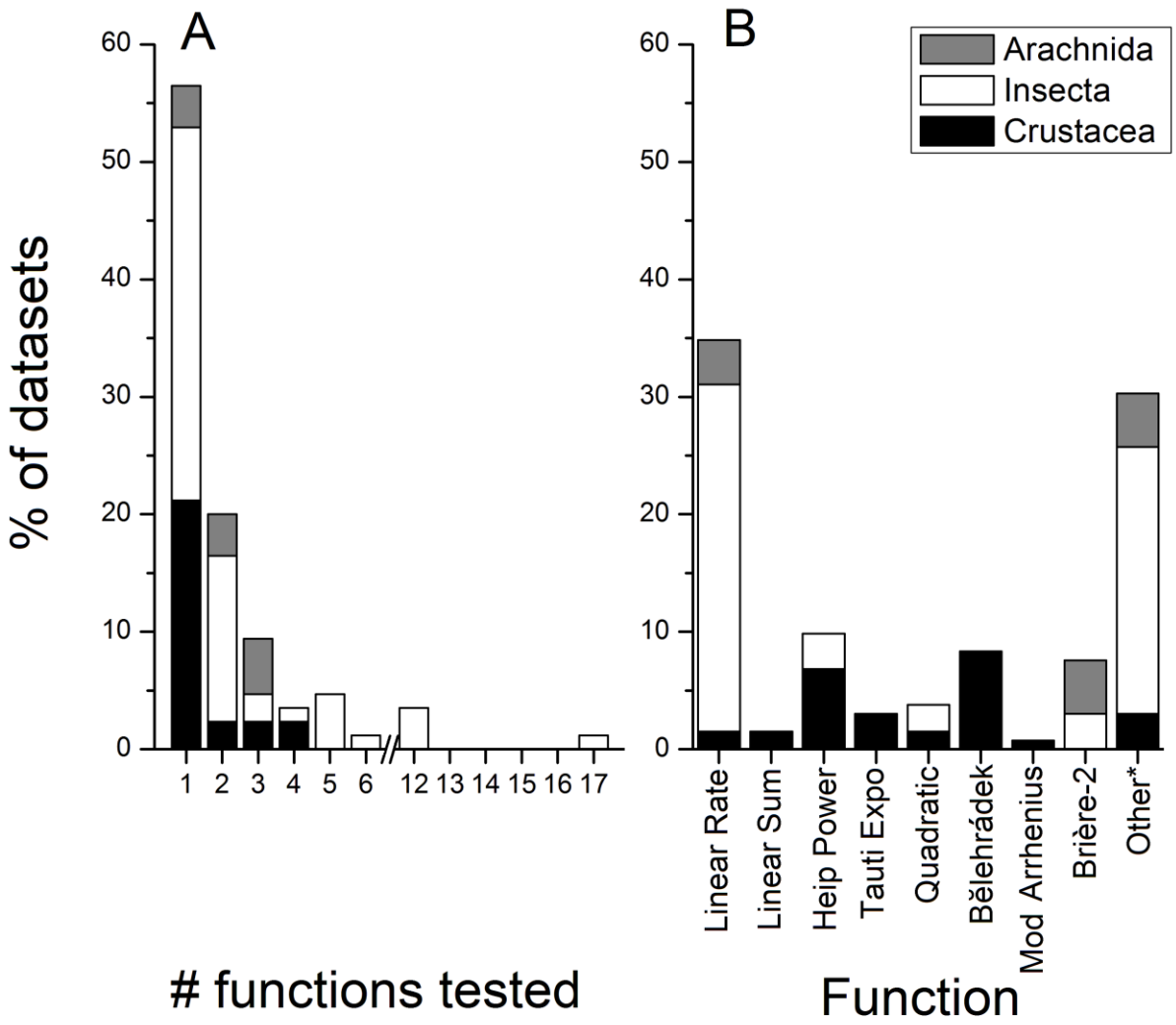


Figure 2. Usage in each development study reviewed of (A) one or more different types of development function and (B) specific development function types. The percentage (%) of species datasets obtained in initial literature review (n = 87 total, see Table S2) that were tested with each number and type of functions is plotted on the y-axes and broken down by taxa (gray bars = arachnids, black = insects, and white = crustaceans). Tauti Expo = Tauti Exponential function, and "Mod Arrhenius" = Modified Arrhenius function. *The "Other" category in (B) includes all function types not otherwise listed; for clarity, if more than one "Other" function was tested by original studies per dataset (see Table S2) it is not counted toward the total shown here.

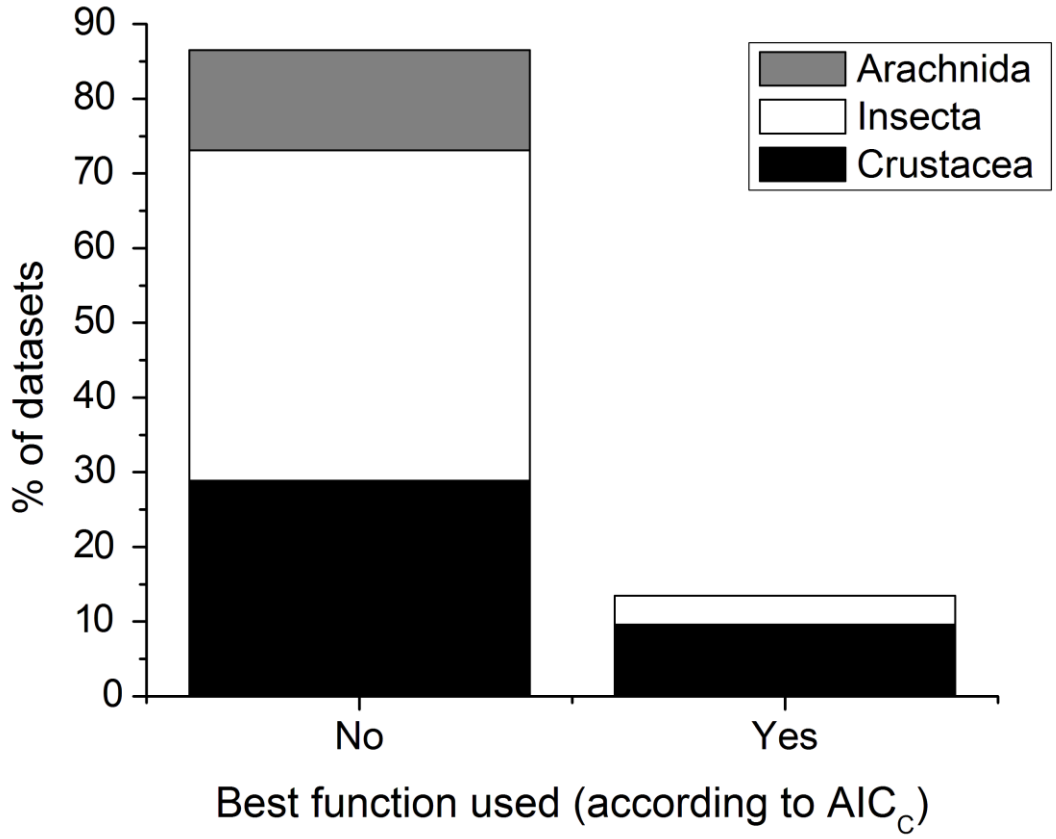
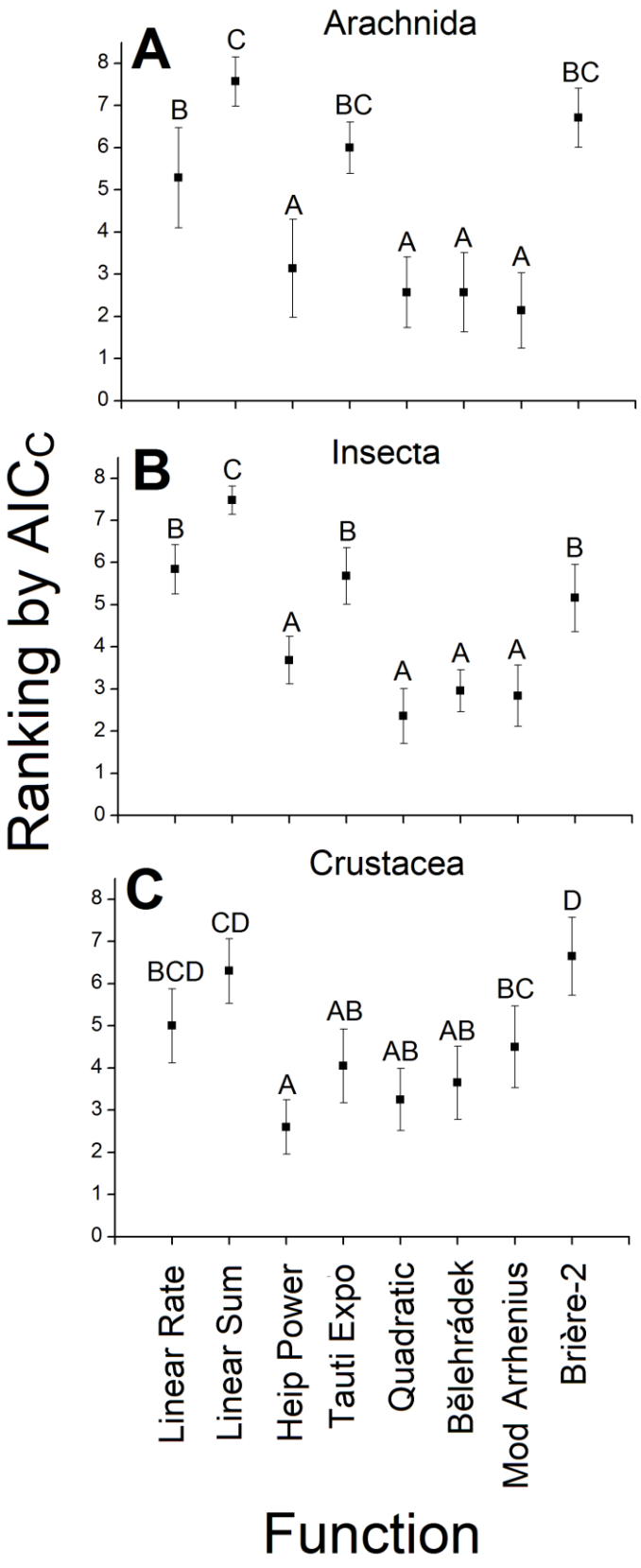


Figure 3. Percentage (%) of species datasets re-analyzed for meta-analysis (n = 52) for which the development function found to be best for the data (lowest AIC_C value, ranking based on AIC_C = 1) in this study agreed with the best function as used in its original published study (Best function used = Yes) or not (Best function used = No). Results are also broken down by taxonomic group, as in Fig. 2.



1095

Figure 4. (*Preceding page*) Overall performance (assessed as ranking based on AIC_C values, y-axes) of each development function (x-axes). Function performance was assessed separately for each taxon: (A) arachnids (n = 7 species for each function), (B) insects (n = 25), and (C) crustaceans (n = 20). Possible rankings ranged from 1 ("best" model) to 8 ("worst"). Values plotted are mean rankings per function and taxonomic group taken across all species datasets within that group ± 95 % C.I.s. Different letters above each mean indicate functions that ranked significantly differently for each taxon (Tukey's HSD test, $p \leq 0.05$).

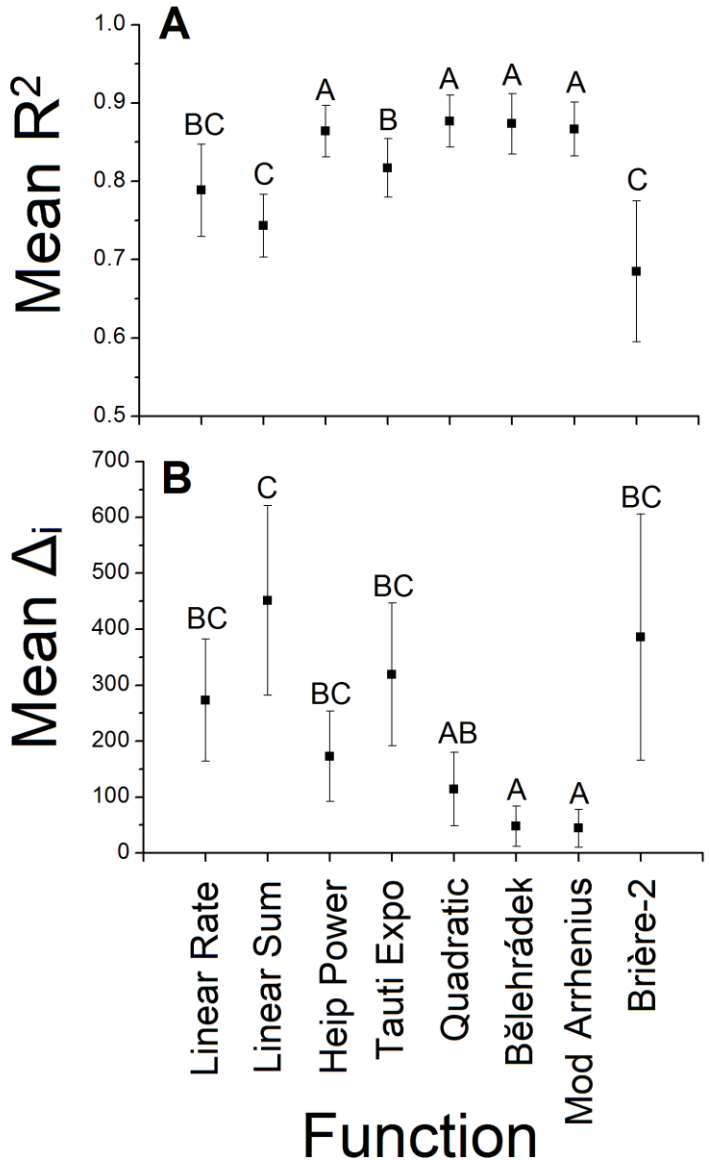


Figure 5. Overall performance of different development functions (x-axes) assessed based on (A) R^2 values and (B) Δ_i values. Values are means ± 95% C.I.s calculated across all species datasets (n = 52), in all taxa for each function. Different letters above each mean indicate functions whose performance differed significantly (Tukey's HSD test, $p \leq 0.05$).

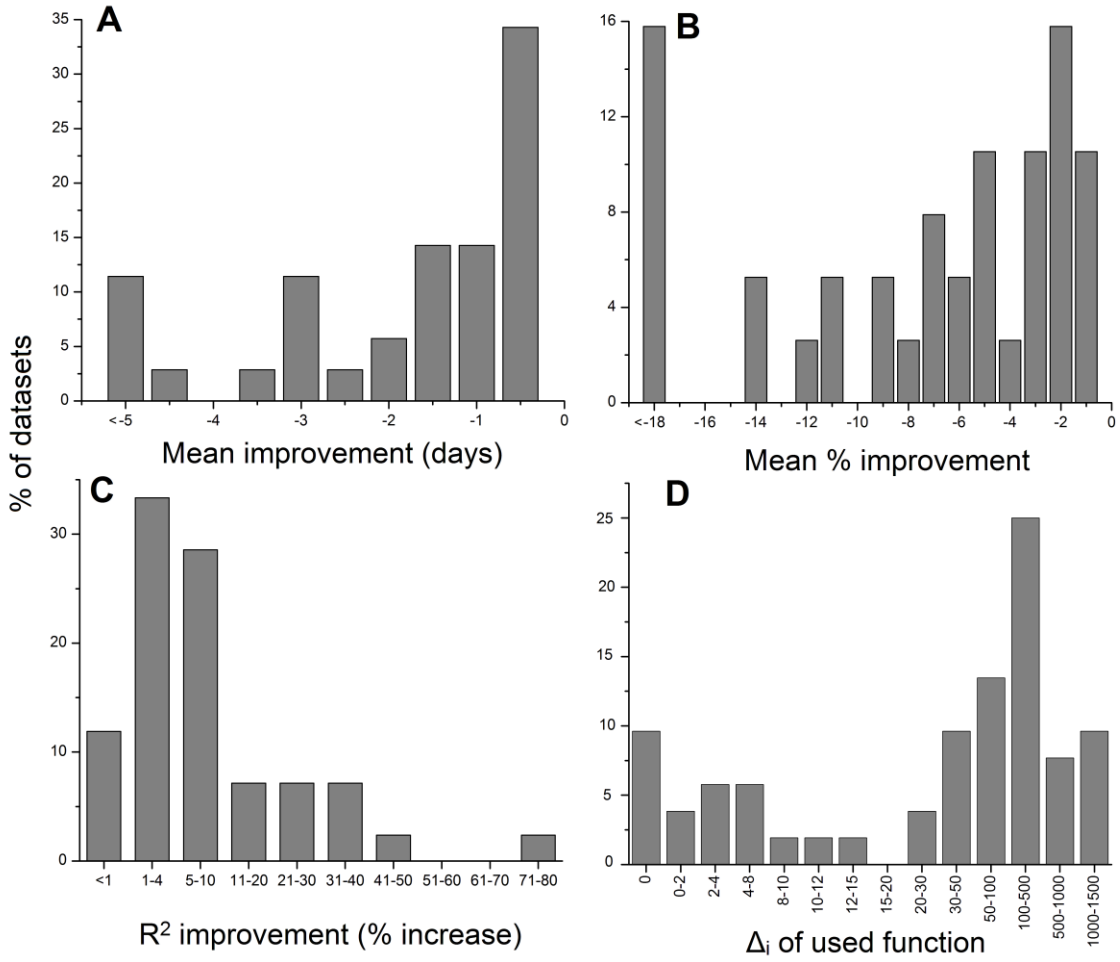


Figure 6. Improvement in terms of (A) reduced mean error (absolute, in days) between observed and predicted development times, (B) reduced percent (%) prediction error, or (C) improved fit (R^2) resulting from using the best function for each species dataset (as determined in this study) as opposed to the function used or found to be best in original published studies. The percentage (%) of species datasets reanalyzed (n = 52, see Table S2) that showed different levels of improvement is plotted on the y-axes. Also shown are the consequences of using the non-best function in terms of (D) information loss (Δ_i of used models); note that $\Delta_i = 0$ is the best model.