The thermal dependence of biological traits

2 Anthony I. Dell^{a,b,c*}, Samraat Pawar^{a,d}, and Van M. Savage^{a,e,f}

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- 4 ^a Department of Biomathematics, UCLA, Los Angeles, CA 90024, USA
- 5 b School of Marine and Tropical Biology, James Cook University, Townsville, QLD 4811, Australia
- 6 ^c Systemic Conservation Biology, Department of Biology, University of Göttingen, Göttingen 37073, Germany
- 7 d Department of Ecology & Evolution, University of Chicago, Chicago, IL 60637 USA
- 9 f Santa Fe Institute, Santa Fe, NM 87501, USA

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* Corresponding author: adell@gwdg.de

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Abstract

Environmental temperature has strong and systematic effects on biological processes at all levels of organization, ranging from cells to ecosystems. The large temporal and spatial variation in earth's temperature creates a complex thermal landscape within which life evolves and operates. Here, we present a dataset on how diverse biological rates and times respond to temperature, which we hope will aid in the search for general mechanisms of thermal dependence. For nearly a century, intraspecific studies (within single species' populations) of thermal responses have been conducted on a wide range of organismal traits. Comparative studies of these data are essential for elucidating mechanisms underlying thermal response curves. However, such comparative intraspecific studies have been limited because of a lack of a comprehensive database that organizes these data with consistent units and trait definitions. Here, we present a database of 2,352 thermal responses for 220 traits for microbes, plants, and animals compiled from 270 published sources. This represents the most diverse and comprehensive thermal response dataset ever compiled. The traits in this database span levels of biological organization from internal physiology to species interactions, and were measured in marine, freshwater, and terrestrial habitats for 411 species. Although we include some physiological rates, most data are for ecological traits, which we define here to mean any organismal trait that directly determines interactions between individuals within or between species. We hope that publication of our dataset will encourage others to compile complementary datasets, especially on individual physiology and life history traits. Intraspecific and interspecific (across species' populations) analyses of our dataset should provide new insights into generalities and deviations in the thermal dependence of biological traits, and thus how biological systems, from cells to ecosystems,

- 34 respond to temperature change. Such insights are essential for understanding how natural biological
- 35 systems function, and for how life is responding to Earth's complex and rapidly changing thermal
- 36 landscape.

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Key words

- 39 Temperature, database, ecoinformatics, trait, environmental driver, thermal response, species,
- 40 intraspecific, interspecific, ecology, evolution

Metadata

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42 INTRODUCTION

Because environmental temperature has pervasive effects across cells, individuals, populations, and ecosystems, elucidating mechanisms by which biological systems respond to temperature is essential for understanding how these systems operate in nature. Given rapid changes to Earth's thermal environment (IPCC 2007), understanding species' thermal responses and their consequences for biodiversity and ecosystem functioning is especially critical (Petchey et al. 2010, Rall et al. 2010, Dell et al. in print).

Body temperature, a major driver of individual physiology from cellular respiration to whole organismal respiration, is strongly affected by environmental temperature in ectotherms (Johnson et al. 1974, Cossins and Bowler 1987, Huey and Kingsolver 1989, Somero, Gillooly et al. 2001, Brown et al. 2004, Angilletta 2009, Dell et al. 2011). These individual-level effects cascade up to affect populations, species interactions, and ecosystems. An understanding of how these effects translate across levels of biological organization requires analysis of a broad suite of functional traits spanning from cells to communities (Angilletta 2009, Dell et al. 2011). For nearly a century, intraspecific studies, which measure a trait within a single species' population across a range of temperatures, have been conducted on a variety of biological traits (e.g., Bennett 1980, Hertz et al. 1982, Cossins and Bowler 1987, Gillooly et al. 2002, Savage et al. 2004, Ratkowsky et al. 2005, Frazier et al. 2006, Angilletta 2009, Irlich et al. 2009b). However, comparative studies of these intraspecific data have tended to focus on small subsets of available data (e.g., Huey and Bennett 1987, Huey and Kingsolver 1989, Bauwens et al. 1995, Huey and Berrigan 2001, Irlich et al. 2009b), probably for two central reasons. First, there is clearly a general lack of empirical data on the thermal response of ecological traits required to address particular ecological and evolutionary questions. This issue must be addressed by a renewed effort by empirical biologists to collect more thermal response data on traits relevant to species interactions. Second, there is a lack of a comprehensive database that compiles existing data, which is required to compare methodologically and taxonomically diverse thermal response data.

In this paper we address the second issue by constructing from published sources a dataset that contains 2,352 intraspecific temperature responses. This dataset is the most comprehensive ever compiled for the thermal responses of physiological and ecological traits. We emphasize that this database focuses mainly on "ecological traits", which we define here to mean any organismal trait that directly determines or measures interactions between individuals within or between species. Our effort was motivated by the fact that understanding effects of global warming on species interactions is one

of the major challenges in contemporary ecology (Harrington et al. 1999, Walther et al. 2002, Helmuth et al. 2005, Vasseur and McCann 2005, Woodward et al. 2010, Dell et al. in print). The resulting global database contains intraspecific thermal responses for 220 traits and 411 species of plants, microbes, and animals that span 16 orders of magnitude in body size. This is also the first compilation of organismal thermal responses wherein all traits have been converted to consistent units and standardized trait definitions.

Analysis of this dataset should reveal how biological systems respond to temperature (Irlich et al. 2009a, Dell et al. 2011, Englund et al. 2011, Nilsson-Örtman et al. 2012). These intraspecific data can also be used to investigate interspecific thermal response curves, which are constructed from trait measurements for multiple species at their optimal temperature and plotted together to construct a single curve (Brown et al. 2004, Angilletta 2009, Dell et al. 2011). Patterns of interspecific thermal response curves are important because they represent underlying constraints on thermal adaptation (Gillooly et al. 2001, Gillooly et al. 2002, Izem 2005, Frazier et al. 2006, Knies et al. 2009, Angilletta et al. 2010, Corkrey et al. 2012). This dataset should also be useful in testing assumptions and predictions of mechanistic models, such as the metabolic theory of ecology (Gillooly et al. 2001, Gillooly et al. 2002, Brown et al. 2004). Ultimately, we hope analysis of this comprehensive dataset will illuminate previously unrecognized generalities and deviations in how biological systems respond to temperature (Dell et al. 2011), and help elucidate the mechanisms by which life responds to Earth's complex and rapidly changing thermal landscape.

A. Dataset identity

Compilation of published intraspecific thermal response curves for physiological and ecological traits.

CLASS I. DATASET DESCRIPTORS

B. Dataset identification code

100 TempTrait 001.txt

C. Dataset description

Summary: Dataset has 19,921 records from 2,352 intraspecific temperature response curves that measure the thermal dependence of physiological and ecological traits from 411 taxa and various marine, terrestrial and freshwater habitats. Each record has 65 fields that detail the trait, taxa, and experimental conditions of each thermal response.

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Principal Investigators: *Anthony I. Dell*, Systemic Conservation Biology, Department of Biology, Georg-August University Göttingen, Göttingen 37073, Germany; *Samraat Pawar*, Department of Ecology & Evolution, University of Chicago, Chicago, IL 60637, USA; *Van M. Savage*, Department of Biomathematics, UCLA School of Medicine, Los Angeles, CA 90024, USA. Queries regarding the dataset should be directed to A.I. Dell (adell@gwdg.de).

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Abstract: Environmental temperature has strong and systematic effects on biological processes at all levels of organization, ranging from cells to ecosystems. The large temporal and spatial variation in earth's temperature creates a complex thermal landscape within which life evolves and operates. Here, we present a dataset on how diverse biological rates and times respond to temperature, which we hope will aid in the search for general mechanisms of thermal dependence. For nearly a century, intraspecific studies (within single species' populations) of thermal responses have been conducted on a wide range of organismal traits. Comparative studies of these data are essential for elucidating mechanisms underlying thermal response curves. However, such comparative intraspecific studies have been limited because of a lack of a comprehensive database that organizes these data with consistent units and trait definitions. Here, we present a database of 2,352 thermal responses for 220 traits for microbes, plants, and animals compiled from 270 published sources. This represents the most diverse and comprehensive thermal response dataset ever compiled. The traits in this database span levels of biological organization from internal physiology to species interactions, and were measured in marine, freshwater, and terrestrial habitats for 411 species. Although we include some physiological rates, most data are for ecological traits, which we define here to mean any organismal trait that directly determines interactions between individuals within or between species. We hope that publication of our dataset will encourage others to compile complementary datasets, especially on individual physiology and life history traits. Intraspecific and interspecific (across species' populations) analyses of our dataset should provide new insights into generalities and deviations in the thermal dependence of biological traits, and thus how biological systems, from cells to ecosystems, respond to temperature change. Such insights are essential for understanding how natural biological systems function, and for how life is responding to Earth's complex and rapidly changing thermal landscape.

138 D. Key words: 139 Temperature, database, ecoinformatics, trait, environmental driver, thermal response, species, 140 intraspecific, interspecific, ecology, evolution 141 **CLASS II. RESEARCH ORIGIN DESCRIPTORS** 142 143 A. Overall project description 144 **Identity:** The thermal dependence of biological traits. 145 146 **Originators:** Anthony I. Dell, Samraat Pawar, and Van M. Savage. 147 **Period of study:** Dates of publications from which data were obtained currently range from 1923 to 148 149 2009. 150 151 **Objectives:** The objective of this project was to construct a comprehensive and consistent dataset of 152 measurements of the thermal dependence of a wide range of physiological and ecological traits from 153 diverse taxa and habitats. Such a single, extensive dataset for multiple traits with consistent 154 measurement units and trait definitions should facilitate novel comparative analyses and hypothesis testing, yielding new insights into generalities and important deviations in thermal responses of 155 156 biological systems. Eventually, these data should help reveal general mechanisms by which life 157 responds to changing thermal landscapes worldwide. 158 159 **Abstract:** As above. 160 Sources of funding: University of California Los Angeles (Biomathematics); National Science 161 162 Foundation Division of Environmental Biology (1021010); James Cook University (Tropical 163 Biology), Australian Research Council. 164 165 **B.** Specific subproject description 166 **Data Acquisition.** We searched the published literature for intraspecific thermal response curves on 167 biological traits, with a primary focus on traits central to species interactions. The temperature response of traits can be strongly influenced by organismal behavior (e.g., Schieffelin and Dequeiroz 168 169 1991, Cooper 2000, Shine et al. 2000, Herrel et al. 2007). Therefore, we focused on rates and times of 170 the execution of biological processes (e.g., attack body velocity, handling rate) and not on decisions

about whether to execute them (e.g., attack probability, defense behavior probability). In total, we found 270 data sources that described intraspecific thermal responses, including journal articles, published reports, and books. We attempted to contact authors directly to obtain raw data, but if this was not possible we extracted data directly from tables and text or from figures using DataThief (Tummers 2006). Our use of DataThief made it impossible to know the true precision of the original data. Also, because we sometimes obtained raw data from the authors, in some cases our dataset will not exactly match that described within the original publication (e.g., replicate thermal responses are not combined). This procedure yielded 2,352 intraspecific temperature responses and 19,921 data points. We primarily selected studies where environmental conditions, such as precipitation, light, and prey density were either controlled or standardized. Consequently, most responses were measured in the laboratory, where ectotherm body temperatures were known to be close to ambient (based on direct measurements and extended acclimation times at test temperatures). The 270 sources from which data were described and analysed in this paper are listed in the Citations field of the data file. Because the number of studies on thermal responses of ecological traits is increasing rapidly, we are currently adding to the dataset, which will be updated periodically.

Unit Conversions. Definitions and measures of many traits are inconsistent throughout the literature, so we identified equivalent traits and converted them to comparable definitions and SI units. Where possible, probabilistic trait data were converted to rates or times.

Taxonomy and systematics. Taxonomic designations were used as stated in the source publication, unless there was clear evidence of a name change in which case the new name was used. Each species' taxonomic hierarchy was determined by using Species 2000 (http://www.sp2000.org), the Encyclopedia of Life (http://eol.org), and Animal Diversity Web (http://animaldiversity.ummz.umich.edu).

Body Size. When available, wet mass of each organism was obtained from the original data source. For studies in which body mass was not provided, we developed an algorithm that assigned a wet mass estimate to species in each data row. This algorithm was based on taxonomic relatedness to published size estimates and length-mass regressions, and allowed us to rapidly obtain estimates of wet body mass that well matched published measurements. Details of the algorithm and its implementation are given in Dell et al. (2011).

204	Permit history: NA.
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206	Legal/organizational requirements: None.
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208	Project personnel: Anthony I. Dell, Samraat Pawar, and Van M. Savage.
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211	CLASS III. DATASET STATUS AND ACCESSIBILITY
212	A. Status
213	Latest update: August 2012. Data compilation is ongoing and will be added as collected and verified
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215	Latest Archive date: August 2012.
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217	Metadata status: Metadata are complete and up to date.
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219	Data verification: A.I. Dell, with assistance from S. Pawar, entered records directly from original
220	sources into MS Access. All values were at minimum triple checked at various stages of data
221	complication and analysis. Plots of each thermal response were automatically produced in MS Access
222	and compared to figures in the original source. In addition, outliers in numeric variables were sorted to
223	examine extreme values. For body size estimates (Class II, Section B) we constructed box plots by
224	taxonomy (Family and Order) and observed outliers for errors. It is important to note that in cases
225	where we obtained raw data directly from authors (see above) our data will not exactly match that
226	described within the original publication, because our data will be more detailed (e.g., replicates are
227	not averaged).
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229	B. Accessibility
230	Storage location and medium: The dataset is available from the Ecological Society of America's
231	data archives. A digital version of the dataset in MS Excel format is held by A.I. Dell, and a beta
232	mySQL version (searchable by trait, taxa and citation) is now available online at
233	www.biotraits.ucla.edu.
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235	Contact person: Anthony I. Dell, Systemic Conservation Biology, Department of Biology, Georg-
236	August University Göttingen, Göttingen 37073, Germany (adell@gwdg de)

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238	Copyright restrictions: None.
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240	Proprietary restrictions: None, except this data paper, NSF Division of Environmental Biology
241	Award 1021010, and the website (www.biotraits.ucla.edu) should be cited when the data are used for a
242	publication. In addition, we would appreciate hearing which research questions or teaching exercises
243	the data are being used for.
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245	Costs: None.
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248	CLASS IV. DATA STRUCTURAL DESCRIPTORS
249	A. Dataset file
250	Identity: TempTrait_001.txt
251	
252	Size: 19,921 records (including header) and 65 fields. Total file size is 17.8 mb.
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254	Format and storage media: Uncompressed UTF-16 text, tab delimited.
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256	Header information: The first row of the file contains variable names (see below).
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258	Row information: Each row represents trait performance at a single ambient or body temperature for
259	a single species, or combination of two species when the trait involves interactions between species
260	(e.g., encounter or consumption rate).
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262	Alphanumeric attributes: Mixed. Note that degree of precision (i.e., number of decimal places) in
263	number fields does not always match the original source for two reasons. First, our data is often more
264	detailed than in the original source because where possible we obtained raw data from the authors
265	(e.g., replicate thermal responses are not combined). Second, our use of DataThief (Class II, Section
266	B) made it impossible to know the true precision of the original data. For consistency all SI number
267	fields were converted to scientific notation floating point (Table 1).
268	
269	Special characters/fields: Missing data denoted as NA.

Authentication procedures: Only data from published literature were obtained, although in a few cases we included other associated data offered by authors that we contacted about their published data. Field sums for all numeric fields are listed in the Authen field (Table 1) and should be used to authenticate the accuracy of the data.

B. Variable information

Variables and their details are provided in Table 1. Further details about variables are given in Dell et al. (2011).

TABLE 1. Summary of variable information. "Authen" represents the sum of that numeric field (i.e., all rows) rounded to closest integer, and should be used to authenticate the contents of the data file.

Variable	Variable definition	Туре	Variable codes	Authen
DataSeriesID	Unique identifier code for each intraspecific thermal response curve	Integer	NA	634618613
Trait	Trait name	Character	NA	NA
TraitDef	Trait definition	Character	NA	NA
TraitOrg	Level of biological organization of the trait	Character	<pre>internal = processes internal to the organism; individual = processes at the level of individual organisms that include mechanical interactions with the external environment; population = processes for a group of conspecific individuals; interaction = processes involving interaction between two or more species</pre>	NA
AmbientTemp	Temperature (°C) of ambient environment (i.e., field or experimental arena).	Floating point	If null (NA) then see ConTemp or ResTemp	404934
TraitValueSI	Value of trait performance in SI units	Floating point	NA	523272551
TraitUnitSI	Units for trait performance in SI units	Character	NA	NA
ErrorPosSI	Positive value of error in SI units (see ErrorUnitSI)	Floating point	NA	26230188
ErrorNegSI	Negative value of error in SI units (see ErrorUnitSI)	Floating point	NA	25702176
ErrorUnitSI	Unit of error	Character	<pre>SD = standard deviation; SE = standard error; 95% CI = 95% confidence interval; interquartile range; range</pre>	NA
Replicates	Number of replicates for each record	Integer	NA	145002
Habitat	Habitat where trait performance was measured	Character	terrestrial; freshwater; marine	NA

Variable	Variable definition	Туре	Variable codes	Authen
LabField	Whether trait performance was measured in the laboratory or field	Character	laboratory; field	NA
ArenaValueSI	SI value of size of arena where trait performance was measured	Floating point	NA	165367
ArenaUnitSI	SI unit of size of arena where trait performance was measured	Character	cubic meter; square meter; meter = when only length of arena was stated	NA
ObsTimeValueSI	SI value of total observation time (i.e., time over which experiment was run for measurement of trait performance)	Floating point	NA	4251168740
ObsTimeUnitSI	SI unit of total observation time (i.e., time over which experiment was run for measurement of trait performance)	Character	<pre>second; prey caught = time taken for ObsTimeValueSI number of prey caught</pre>	NA
ObsTimeNotes	Notes for total observation time (i.e., time over which experiment was run for measurement of trait performance)	Character	NA	NA
ResRepValueSI	SI value for how often resources were replaced over observation time	Floating point	NA	810257360400
ResRepUnitSI	SI value for how often resources were replaced over observation time	Character	not replaced; second; to satiation = resources replaced sufficiently frequently so that consumer always had access to resources	NA
Location	Location (generally town, state, country) of where organisms were collected, or when measurements were taken at a different location then both are listed	Character	NA	NA
Latitude	Approximate latitude of middle of location where animals were collected (e.g., filed station, town, state, country), or when not available then where measurements were taken.	,	NA	616917
Longitude	Approximate longitude of middle of location where animals were collected (e.g., filed station, town, state, country), or when not available then where measurements were taken.		NA	-809413
TaxaPresent	Whether one or two taxa are part of the trait measurement and definition. If only a single organism is involved (e.g., metabolic rate, heart rate), it is always listed as a trait for a consumer.	Character	<pre>consumer = trait involves a single organism; consumer- resource = trait involves two organisms</pre>	NA

Variable	Variable definition	Туре	Variable codes	Authen
ConType	Type of consumer	Character	<pre>alive = organism alive when trait performance measured; dead = organism dead when trait performance measured; artificial = 'organism' simulated by a physical stimulus (e.g., predator model, prodding, gravity)</pre>	NA
Con	Binomial name of consumer or lowest taxonomic identity, or other appropriate name for artificial taxa (see ConType)	Character	NA	NA
ConCommon	Common name of consumer	Character	NA	NA
ConStage	Life stage of consumer, and sex in parenthesis when available	Character	NA	NA
ConIDLevel	Taxonomic level to which the consumer was identified	Character	kingdom, phylum, class, order, family, genus, species	NA
ConKingdom	Taxonomic name of Kingdom of consumer	Character	NA	NA
ConPhylum	Taxonomic name of Phylum of consumer	Character	NA	NA
ConClass	Taxonomic name of Class of consumer	Character	NA	NA
ConOrder	Taxonomic name of Order of consumer	Character	NA	NA
ConFamily	Taxonomic name of Kingdom of consumer	Character	NA	NA
ConTrophic	Broad trophic group of consumer, as determined by published literature and expert opinion	Character	<pre>carnivore; detritivore; herbivore; omnivore, producer, artificial (see ConType); self = energy self-supplied (e.g., pupae, egg); dead (see ConType)</pre>	NA
ConThermy	Thermy of consumer	Character	ectotherm; endotherm	NA
ConTemp	Body temperature (°C) of consumer	Floating point	NA	482173
ConTempMethod	Method of determining body temperature of consumer	Character	direct = measured directly from within or on the organism; inferred (ambient) = estimated from known ambient temperature and generally within arena where organism not able to thermoregulate; inferred (endotherm) = body temperature relatively constant and estimated from published literature; inferred (consumer) = estimated from known consumer body temperature (relevant for ResTempMethod, see below)	NA
ConMassValueSI	Mass of consumer as obtained from original source or estimated from other published literature (see Dell et al. (2011) for further details)	Floating point	NA	196296
ConMassUnitSI	SI unit of consumer mass	Character	kilogram (wet body mass) = wet mass of entire body of consumer; kilogram (wet tissue mass) = wet mass of tissue of consumer (e.g., excluding shell for gastropods)	NA

Variable	Variable definition	Туре	Variable codes	Authen
ConDenValueSI	Value of consumer density standardized to SI units	Floating point	NA	2471839374
ConDenTypeSI	Type of units of consumer density	Character	<pre>individual; kilogram (dry body mass); kilogram (wet body mass); liter; to satiation = resource density above what consumer could fully consume (relevant for ResDenTypeSI, see below)</pre>	NA
ConDenUnitSI	SI units of consumer density	Character	arena; square meter; cubic meter	NA
ResType	Same as for	ConType (see a	bove), but for resource	NA
Res	Same as fo	r Con (see abo	ve), but for resource	NA
ResCommon	Same as for C	onCommon (see	above), but for resource	NA
ResStage	Same as for (ConStage (see a	above), but for resource	NA
ResIDLevel	Same as for Co	Same as for ConIDLevel (see above), but for resource		
ResKingdom	Same as for Co	onKingdom (see	above), but for resource	NA
ResPhylum	Same as for ConPhylum (see above), but for resource			NA
ResClass	Same as for (Same as for ConClass (see above), but for resource		
ResOrder	Same as for (ConOrder (see a	above), but for resource	NA
ResFamily	Same as for ConFamily (see above), but for resource			NA
ResTrophic	Same as for ConTrophic (see above), but for resource			NA
ResThermy	Same as for C	onThermy (see	above), but for resource	NA
ResTemp	Same as for	ConTemp (see a	bove), but for resource	312208
ResTempMethod	Same as for ConTempMethod (see above), but for resource			NA
ResMassValueSI	Same as for Conl	MassValueSI (se	ee above), but for resource	554
ResMassUnitSI	SUnitSI Same as for ConMassUnitSI (see above), but for resource			NA
ResDenValueSI	Same as for ConDenValueSI (see above), but for resource			4231969406743 47
ResDenTypeSI	Same as for Con	nDenTypeSI (see	e above), but for resource	NA
ResDenUnitSI	Same as for ConDenUnitSI (see above), but for resource			NA
CitationID	Unique identification nu for citation	mber Integer	NA	7026820
Citation	Citation from which data obtained	was Character	NA	NA
FigureTable	Figure or table from whi data was obtained within original citation		NA	NA

286 A. Data acquisition

Potential data sources were identified using three methods:

1. Using literature search engines (e.g., Web of Science, JSTOR) to find published literature using keyword combinations that included: 'ecological', 'ecology', 'interaction', 'physiological', 'physiology', 'response', 'temperature', 'thermal', and 'trait'. In many cases,

CLASS V. SUPPLEMENTAL DESCRIPTORS

- the authors of these studies were contacted directly to obtain raw data.
- 2. Contacting known researchers in the field of thermal biology and directly requesting data.
- 3. Looking through citations in the publications found by method 1.

294 Once identified, data were obtained by contacting authors and asking for raw data, otherwise directly 295 from the main text and tables of published literature, and from figures using DataThief (Tummers 296 2006) that allows digitization of data points from a graph. 297 298 B. Quality assurance/quality control procedures 299 See comments on data verification (Class III, Section A). 300 301 C. Related material: 302 NA. 303 304 D. Computer programs and data processing algorithms: Data from figures in published literature were obtained with DataThief (Tummers 2006) (see Class V, 305 Section A). Data were entered into a form within MS Access, where unit conversions to SI units were 306 307 also undertaken. Body size estimates were made using an algorithm we constructed and implemented 308 using MS Access (Class II, Section B) (Dell et al., 2011). 309 310 **E.** Archiving: Data files and metadata will be updated periodically at Ecological Archives, and are available in beta 311 312 version at www.biotraits.ucla.edu. 313 314 F. Literature cited: 315 Publications from which data were obtained are stated in the Citation field of the data file. 316 317 **G.** Publications using the dataset: 318 Dell, A. I., S. Pawar, and V. M. Savage. (2011). Systematic variation in the temperature dependence of 319 physiological and ecological traits. Proceedings of the National Academy of Sciences of the United 320 States of America 108:10591-10596. 321 Dell, A. I., S. Pawar, and V. M. Savage. (In press). A framework for the temperature dependence of 322 trophic interactions and the consequences of asymmetries in consumer and resource responses. 323 Journal of Animal Ecology.

Pawar, S., A. I. Dell, and V. M. Savage. 2012. Dimensionality of consumer search space drives

trophic interaction strengths. *Nature* **486**:485-489.

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327	G. History of dataset usage
328	Data request history: NA
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330	Dataset update history: NA.
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332	Review history: NA.
333	
334	Questions and comments from secondary users: NA.
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337	ACKNOWLEDGMENTS
338	We sincerely thank the many authors who graciously donated their time and data. Without their
339	careful work, the compilation of this dataset would have been either impossible or meaningless. In
340	addition, we would like to thank the many organizations that helped fund each of these projects. We
341	thank Kina Winoto for help in porting the original dataset to mySQL and, together with William King,
342	for helping develop the website where this dataset is currently being made available
343	(www.biotraits.ucla.edu). We thank Mike Angilletta, William King and one anonymous reviewer for
344	their detailed and insightful comments. Support for compiling this dataset was provided by James
345	Cook University, the University of California Los Angeles, and the National Science Foundation
346	Division of Environmental Biology Award (1021010).
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349	LITERATURE CITED
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