A life cycle database for parasitic acanthocephalans, cestodes, and nematodes

Daniel P. Benesh1, Kevin D. Lafferty2, 1, Armand Kuris3, 1

1 *Marine Science Institute, University of California, Santa Barbara, CA 93106, USA*

2 *Western Ecological Research Center, U.S. Geological Survey*

3 *Department of Ecology, Evolution and Marine Biology, University of California, Santa Barbara, CA 93106*

Parasitologists have worked out many complex life cycles over the last ~150 years, yet there have been few efforts to synthesize this information to facilitate comparisons among taxa. Most existing host-parasite databases focus on particular host taxa, do not distinguish final from intermediate hosts, and lack parasite life-history information. We summarized the known life cycles of trophically transmitted parasitic acanthocephalans, cestodes, and nematodes. For 973 parasite species, we gathered information from the literature on the hosts infected at each stage of the parasite life cycle (8510 host-parasite species associations), what parasite stage is in each host, and whether parasites need to infect certain hosts to complete the life cycle. We also collected life-history data for these parasites at each life cycle stage, including 2313 development time measurements and 7660 body size measurements. The result is the most comprehensive data summary available for these parasite taxa. In addition to identifying gaps in our knowledge of parasite life cycles, these data can be used to test hypotheses about life cycle evolution, host specificity, parasite life-history strategies, and the roles of parasites in food webs.

*Key words: body size; comparative analysis; complex life cycle; food web; helminth; life history; niche shift; ontogeny; predator-prey interactions; trophic transmission*

**METADATA**

**CLASS I. DATA SET DESCRIPTORS**

**A. Data set identity**: A life cycle database for parasitic acanthocephalans, cestodes, and nematodes

**B. Data set identification code**:

CLC\_database\_hosts.csv

CLC\_database\_lifehistory.csv

**C. Data set description**

**Originator**: Dan Benesh, University of California Santa Barbara

**Abstract**: Parasitologists have worked out many complex life cycles over the last ~150 years, yet there have been few efforts to synthesize this information to facilitate comparisons among taxa. Most existing host-parasite databases focus on particular host taxa, do not distinguish final from intermediate hosts, and lack parasite life-history information. We summarized the known life cycles of trophically transmitted parasitic acanthocephalans, cestodes, and nematodes. For 973 parasite species, we gathered information from the literature on the hosts infected at each stage of the parasite life cycle (8510 host-parasite species associations), what parasite stage is in each host, and whether parasites need to infect certain hosts to complete the life cycle. We also collected life-history data for these parasites at each life cycle stage, including 2313 development time measurements and 7660 body size measurements. The result is the most comprehensive data summary available for these parasite taxa. In addition to identifying gaps in our knowledge of parasite life cycles, these data can be used to test hypotheses about life cycle evolution, host specificity, parasite life-history strategies, and the roles of parasites in food webs.

**D. *Key words****: body size; comparative analysis; complex life cycle; food web; helminth; life history; niche shift; ontogeny; predator-prey interactions; trophic transmission*

**CLASS II. RESEARCH ORIGIN DESCRIPTORS**

**A. Overall project description**

**Identity:** A life cycle database for parasitic worms

**Originator**: Dan Benesh, University of California Santa Barbara

**Period of study**: The database was compiled between 2014 and 2016.

**Source of funding**:Research fellowship to D. Benesh from the Deutsche Forschungsgemeinschaft (BE 5336/1-1)

**B. Research motivation**

Many parasites infect multiple hosts in succession before sexual reproduction. Such complex life cycles seem paradoxical, because parasites risk not being transmitted between their successive obligate hosts and thus dying before reproducing. Additionally, parasites must adapt to multiple host physiologies and immune systems. Nonetheless, complex life cycles are the norm among parasitic worms (Chubb et al. 2010), suggesting they have clear benefits that can explain their evolutionary origin and persistence. Several population dynamic (Dobson and Merenlender 1991, Choisy et al. 2003) and life-history models (Parker et al. 2003b, 2003a, 2009a, 2009b, Iwasa and Wada 2006, Ball et al. 2008) have explored when a complex cycle may be favored over a simple, one-host cycle. For instance, incorporating a small host at the start of the cycle may reduce propagule mortality and increase transmission (e.g., Morand et al. 1995, Poulin and Leung 2011, Benesh et al. 2014), whereas adding a predator to the end of the cycle could facilitate parasite growth to a large and fecund reproductive size (e.g., Arneberg et al. 1998, Poulin et al. 2003, Poulin and George-Nascimento 2007). Complex life cycles can also be beneficial if they increase parasite mating probability (Brown et al. 2001). To evaluate hypotheses about life cycle evolution, we compiled data on the life cycles and life histories of trophically transmitted acanthocephalans, cestodes, and nematodes. Our database differs from other host-parasite databases in that it is not restricted to a particular host taxon (e.g., Nunn and Altizer 2005, Strona et al. 2013) and it distinguishes between intermediate and definitive hosts (Gibson et al. 2005). These data might also be useful in evaluating ecological hypotheses. For instance, parasites have rarely been integrated into food webs (Marcogliese and Cone 1997, Lafferty et al. 2008), although including them affects web diversity, complexity, motif frequency, and trophic niche breadth and contiguity (Dunne et al. 2013). Information on life cycles could enable adding some parasites into food web topology, while information on parasite life history could inform food web energetics and the impacts on hosts.

**C. Methods**

We started with existing comprehensive studies that listed parasite species with known life cycles (Anderson 2000, Benesh et al. 2011, 2014), and then we searched the primary literature to add species and information. For each species, we used its binomial name as a search term in Google Scholar and examined the first 50-100 hits. We occasionally inspected more search results for well-studied species when life-cycle and life-history studies were not among the top hits. We looked for studies describing the life cycle, host associations at each stage of the life cycle, parasite development (how long a parasite infects a host), and/or parasite morphology (size and shape). For most species, we also searched the Biodiversity Heritage Library (http://www.biodiversitylibrary.org/), which was especially useful for obtaining older species descriptions.

**D. Data limitations and potential enhancements**

**Taxonomic scope**: The data cover three taxa of trophically transmitted metazoan parasites (acanthocephalans, cestodes, and nematodes), but do not include a fourth major group, trematodes. Trematodes are unique in that their cycles usually include an asexually reproducing larval stage that is not trophically transmitted, so their transmission dynamics are only partially dependent on predator-prey interactions. Similarly, the database does not include non-trophically-transmitted nematodes that undergo within-host reproduction, e.g. entomopathogenic nematodes. We focused on trophically transmitted parasites, but comparable datasets could be produced for parasites with other transmission strategies (e.g., penetrators, vector-transmission, sexual-transmission, etc.). We strove to be as comprehensive as possible for the three parasite groups covered, but we acknowledge that known cycles do not represent a random sample. In fact, some parasite clades still lack well-worked-out life cycles. By identifying such knowledge gaps, we hope these data will guide future life cycle studies.

**Data quality**: The 2846 source references varied in quality with respect to methods, sample size, and existing knowledge. We often erred on the side of inclusion over exclusion, because comprehensiveness was a goal of the data compilation. Certain variables in the data may be useful in weighting the quality of different observations, such as the age of the study and/or sample sizes.

**Host associations**: Most parasite species can infect more than one host species at any given life cycle stage. We aimed to make the list of host species for a parasite stage representative, but acknowledge they are not exhaustive. Combining this dataset with existing host-parasite checklists could ameliorate this, though it would not overcome intrinsic sampling biases, i.e. some host species have just been more frequently sampled than others.

**Body size**: Parasite size is almost always reported as lengths and widths, rarely as a mass. Mass is a better measure of body size, because it is not shape- (and thus not taxon-) dependent. Users can decide how to best use parasite shape to convert two-dimensional measures of length and width into a three-dimensional measure like mass (see Benesh et al. 2013 for an example of this in tapeworms).

**CLASS III. DATA SET STATUS AND ACCESSIBILITY**

**A. Status**

**Latest update**: The data set has not been updated since its publication.

**Latest archive date**: The data set has not been updated since its publication.

**Metadata status:** Metadata have not been updated since first publication.

**B. Accessibility**

**Contact person**: Dan Benesh, email: [dbenesh82@gmail.com](mailto:dbenesh82@gmail.com)

**Copyright restrictions**: None.

**Proprietary restrictions**: Data are free to use for any non-commercial purpose, but we ask users to cite this data paper in any scholarly outlets.

**Costs**: None

**CLASS IV. DATA SET STRUCTURAL DESCRIPTORS**

**HOST DATA**

**A. Data Set File**

**Identity**:CLC\_database\_hosts.csv

**Size**: 1.94 MB

**Format and storage mode**: CSV

**Contents**:Contains information on hosts and the role they play in the parasites' life cycle.

**B. Variable Information**

**Parasite.species**: scientific name of the parasite species

**Parasite.genus:** name of the parasite genus

**Parasite.group**: helminth group to which the species belongs (acanthocephalan, cestode, or nematode)

**Host.species**: scientific name of the host of a given parasite. The names of all host and parasite species were screened for typos with the Global Names Resolver (http://resolver.globalnames.org/).

**Host.common.name**: vernacular name for host species

**Missing.info**: a dummy variable indicating whether a given host association is evidence-based (0), i.e. documented by natural or experimental infections, or presumed (1), i.e. based on host trophic ecology and/or parasite phylogeny.

**Typical.host**: if the host is considered typical or atypical for a parasite. Reasons for considering a host atypical included the parasite develops poorly in the host, establishment success is low in experimental infections, and/or the host is rarely infected in nature. This is subjective, as it is based on researcher opinions in the primary literature. Thus, the criteria for categorizing a host as atypical can vary from parasite to parasite.

**Host.no**: whether the host is the first, second, third, etc. in the life cycle

**Def.int**: whether the host is a definitive host or an intermediate host

**Facultative**: whether a host is necessary for completion of the life cycle. Three types of facultative hosts are distinguished. 'Progenetic' indicates the host is unnecessary because the parasite can reproduce precociously in the previous host. If a reproducing parasite can be transferred from one definitive host to another definitive host, the latter host is unnecessary and is called 'postcyclic'. Finally, 'paratenic' indicates an intermediate host that is not obligate for infection of the next host. Often, a host is considered 'paratenic' based solely on the lack of any obvious parasite development within the host, and it has not been established experimentally that the host is indeed facultative.

**Stage**: a taxon-general categorization of parasite stage, specifically whether the parasite is an adult or a larva in the host. Larval stages are numbered based on which successive host they infect, e.g. a larva in the first host is called '1larv'.

**Asexual**: whether a stage undergoes asexual reproduction. This only applies to some larval cestodes; their asexual reproduction is classified as low (tens of clonal individuals produced or less) or high (hundreds or even thousands of clonal individuals produced).

**Site**: where the parasite occurs in the host. This is generally the parasite's final site. Not all occupied tissues are listed for species that undergo elaborate migrations through their host.

**Host.habitat**: habitat in which the life cycle takes place (terrestrial, freshwater, marine). Some cycles do not fit well into this categorization (e.g., parasites in estuaries, in salt lakes, or parasites that have larval stages in aquatic hosts and the adult stage in semi-terrestrial hosts such as waterfowl).

**Vert.group**: if the host is a vertebrate, the vertebrate group it belongs to

**Remark**: miscellaneous remarks about the host and/or parasite

**Author**, **Year**, **Journal**, **Volume**, and **Pages**: the bibliographic reference for the data

**PARASITE LIFE HISTORY**

**A. Data Set File**

**Identity**:CLC\_database\_lifehistory.csv

**Size**: 1.98 MB

**Format and storage mode**: CSV

**Contents**:Contains parasite life-history data.

**B. Variable Information**

**Parasite.species**: scientific name of the parasite species

**Parasite.genus:** name of the parasite genus

**Parasite.group**: helminth group to which the species belongs (acanthocephalan, cestode, or nematode)

**Host.species**: scientific name of the host species in which a parasite was studied. The names of all host and parasite species were screened for typos with the Global Names Resolver (http://resolver.globalnames.org/).

**Host.no**: whether the host is the first, second, third, etc. in the life cycle. Propagule stages such as the egg were assigned a value of 0.

**Stage**: a taxon-general categorization of the stage of the parasite. Three propagule stages are distinguished: eggs, embryos within the eggs, and free larvae that have hatched from eggs. Larval stages within hosts are numbered based on which successive host they infect, e.g. a larva in the first host is called '1larv'.

**Egg.hatch**: whether eggs are ingested by the first host ('eaten'), whether they hatch and are eaten ('hatch, eaten'), whether they hatch, grow, and are then eaten ('hatch, grow, eaten'), or whether they hatch and penetrate the first host ('hatch, penetrate'; many of these species can also infect via the oral route).

**Development.time**: the number of days spent developing in a stage before being capable of moving to the next stage. For eggs, it is the time to hatching or the time to embryonation (stated in the variable 'Development.remarks'). For larval parasites, it is the time to infectivity. And for adults, it is the prepatent period.

**Temp**: temperature in Celsius at which development was studied

**Development.remarks**: miscellaneous remarks about parasite development

**Length**: length of the parasite in mm

**Width**: width of the parasite in mm

**Max.length**: maximum reported length of the parasite in mm

**Max.width**: maximum reported width of the parasite in mm

**n**: number of individuals contributing to size estimate

**Size.reported.as**: categorical variable describing how size was reported, i.e. as an average, a range, in a figure, or as just a point measurement.

**Shape**: approximate shape of the parasite stage

**Asexual**: whether size measurements are for individuals or for clonal aggregates (e.g. a cyst) in species undergoing asexual reproduction as larvae

**Sex**: if applicable, whether size was for male or female parasites

**Size.remarks**: miscellaneous remarks about parasite size

**Author**, **Year**, **Journal**, **Volume**, and **Pages**: the bibliographic reference for the data

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