Evolution of Parasite Life Cycles: Marshes, Metaphors, and Models

John Janovy, Jr.
Varner Prof Biol Sci
University of Nebraska-Lincoln
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Topics –

- *Posthodiplostomum minimum* in *Fundulus zebrinus* – Where the ideas came from
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• *Haematoloechus* spp. in various anurans – life cycle diversity in congeneric flukes
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• *Haematoloechus* spp. in various anurans – life cycle diversity in congeneric flukes
• The life cycle metaphor – running bases
Topics –

- *Posthodiplostomum minimum* in *Fundulus zebrinus* – Where the ideas came from
- *Haematoloechus* spp. in various anurans – life cycle diversity in congeneric flukes
- The metaphor – running bases
- An embarrassingly simple simulation model – Investments for evolving worms
Posthodiplostomum minimum in Fundulus zebrinus – Where the ideas came from
The South Platte River near Roscoe, Nebraska
Front Range SWE and South Platte River Streamflow

Rocky Mountain snowpack and streamflow in the South Platte River
South Platte River Streamflow and *P. minimum* prevalence

What’s really regulating parasite “success” in this system is Rocky Mountain snowpack.
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Host-Parasite Association

- Host immunity or resistance
- Co-occurring parasites
- Intermediate host populations
- Definitive host use of the river

Distant Planetary Events

The combination of atmospheric phenomena that produces snow in the Rocky Mountains on an annual basis.
What factors actually dictate the flow of parasites through an ecosystem? The case of congeneric frog lung flukes.

Matthew Bolek’s signature image; I have no idea where he got it.
Archetypical and Paradigmatic Life of a Frog Lung Fluke
Real World Lives of North American Frog Lung Flukes

- 511 spp.
- 6 spp.
- 21 spp.
- 12 spp.
The problem of parasite flow through an ecosystem actually looks something like this:
Take each phase of the life cycle separately and examine it comparatively.
What is the role of second intermediate odonate hosts and their parasite interactions in the transmission of frog lung flukes?
The Situation: 2nd Intermediate Host Specificity

(1) *Haematoloechus medioplexus* and *H. varioplexus* are specialists only infecting dragonflies as second intermediate hosts.
The Situation: 2\textsuperscript{nd} Intermediate Host Specificity

(1) *Haematoloechus medioplexus* and *H. varioplexus* are specialists only infecting dragonflies.

(2) *Haematoloechus longiplexus* can infect dragonflies and damselflies.
The Situation: 2\textsuperscript{nd} Intermediate Host Specificity

(1) *Haematoloechus medioplexus* and *H. varioplexus* are specialists only infecting dragonflies.

(2) *Haematoloechus longiplexus* can infect dragonflies and damselflies.

(3) *Haematoloechus complexus* is a generalist infecting dragonflies, damselflies, and other aquatic arthropods.
Cercarial structure:

M. Bolek
142 young of the year Northern Leopard frogs *Rana pipiens* (SVL 4.3 cm) were collected, and examined for *Haematoloechus* species and stomach content data.

75/142 (53%) were infected.

530 worms were recovered (491 immature and 39 mature).

Another 62 frogs young of the year were maintained in the laboratory for 4-6 wk. 30/62 (48%) were infected with 4 immature and 60 mature *Haematoloechus complexus*. 

Cedar Creek; north of Patxon, NE
Really Little Amphibians Had Adult Trematodes!

M. Bolek
Stomach Contents Data for 142 Young of the Year *Rana pipiens* Collected from Cedar Creek

N = 576 Invertebrates
AVE Length = 6.8 mm

Potential intermediate hosts
Stomach Content Data for 142 Rana pipiens Collected from Cedar Creek

- **T. Coleoptera**
- **Gastropoda**
- **Diptera**
- **Lepidoptera**
- **Hymenoptera**
- **Arachnids**
- **Homoptera**
- **A. Coleoptera**
- **A. Hemiptera**
- **Unid. Insects**
- **T. Hemiptera**
- **Amphipoda**
- **Earthworms**
- **Odonata**
- **Orthoptera**
- **Ephemeroptera**

**Other Invertebrates**

**Potential Intermediate Hosts**
**Haematoloechus complexus** recovered from 320 aquatic and semi-aquatic Arthropods from Cedar Creek

<table>
<thead>
<tr>
<th>Arthropod/Ave. Size</th>
<th>Prevalence</th>
<th>No. of Worms Recovered</th>
</tr>
</thead>
<tbody>
<tr>
<td>Larval Dragonflies/30mm</td>
<td>94% (15/16)</td>
<td>300</td>
</tr>
<tr>
<td>Larval Damselflies/15-20mm</td>
<td>67% (10/15)</td>
<td>38</td>
</tr>
<tr>
<td>Adult Damselflies/43mm</td>
<td>48% (13/27)</td>
<td>31</td>
</tr>
<tr>
<td>Coleoptera/10mm</td>
<td>11% (3/27)</td>
<td>6</td>
</tr>
<tr>
<td>Ephemeroptera/8mm</td>
<td>10% (4/42)</td>
<td>14</td>
</tr>
<tr>
<td>Hemiptera/8mm</td>
<td>9% (3/33)</td>
<td>3</td>
</tr>
<tr>
<td>Adult Dragonflies/35mm</td>
<td>7% (6/81)</td>
<td>25</td>
</tr>
<tr>
<td>Amphipoda/6mm</td>
<td>4% (3/70)</td>
<td>5</td>
</tr>
<tr>
<td>Diptera/15mm</td>
<td>0% (0/9)</td>
<td>0</td>
</tr>
</tbody>
</table>

= available prey, limited by gape width in Y-o-Y leopard frogs
**H. complexus**: penetration ability provides and avenue for colonization of y-o-y leopard frogs.

**H. longiplexus**: penetration ability is highly restricted.

**H. medioplexus and H. varioplexus**: lack of penetration ability constrains parasite to large predators.
Adult North American Bullfrog and Northern Leopard Frog
11 European and North American Species from 18 populations

Snyder and Tkach, 2001, JP 87:1433
Second Intermediate Host Specificity

- Damselflies
- Damselflies and Dragonflies
- Dragonflies
- Odonate and Non-odonate Arthropods

Snyder and Tkach, 2001, JP 87:1433
Bolek and Janovy, 2007, JP 93:593
Second Intermediate Host Specificity

- **P. maculosus**
- **P. vespertilionis**
- **P. koreanus**
- **H. similis**
- **H. asper**
- **H. longiplexus**
- **H. breviplexus**
- **H. medioplexus**
- **H. parviplexus**
- **H. complexus**
- **H. coloradensis**
- **H. varioplexus**
- **H. abbreviatus**
- **H. variegatus**

**Damselflies**
- **Damselflies and Dragonflies**
- **Dragonflies**
- **Odonate and Non-odonate Arthropods**

Second Intermediate Host Specificity

- Damselflies
- Damselflies and Dragonflies
- Dragonflies
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Green frogs retain some “hospitability” that bullfrogs have lost (or never had).
Leopard Frogs can be infected with at least five species, but parasite numbers are associated with cercarial penetration of second intermediate host.
Take-home from frogs:

- The paradigmatic life cycle diagram hides a whole lot of host and parasite biology that is of evolutionary importance.

Bolek and Janovy, 2007
What is the appropriate metaphor for thinking about complex life cycles, especially as exemplified by trematodes?
E.g., what happens if you always try to steal second regardless of the situation?

Or, what happens if every batter tries to hit a home run regardless of the situation?
Host-Parasite Encounter Models: Where should a trematode invest its energies?
Host-Parasite Encounter Models

- Assume encounters are random within 2D space.
- Assume infectivity is a function of proximity.
- Allow host and parasite numbers to be varied.
- Allow infectivity to be varied.
- Allow barriers to be erected between hosts and parasites.
- Allow different parasite reproductive methods.
What happens to the adult worm population if you hold everything constant except for one step, then vary that one step by an order of magnitude?
Definitive host

Adult trematode

Eggs shed
In feces

Predation

Second intermediate host

Snail first intermediate host

(A)

(B)

(C)

(D)

(E)

(F)

(G)

(H)
Points at which selection can occur:

- Adult parasite (A)
- Egg/miracidium (B)
- Sporocyst (C)
- Daughter sporocyst (D)
- Redia (E)
- Cercarial production (F)
- Cercarial survival (G)
- Metacercarial survival (H)
Selective forces acting at these points:

- (A) – Host immunity or resistance, available habitats within host, host physiology and biochemistry (adult worm).
- (B) – Abiotic factors (egg/miracidium)
- (C) – Host immunity or resistance, competing parasite species (sporocyst)
- Etc.
Potential parasite responses:

- (A) – Surface proteins, maturation rate, egg production (adult parasite)
- (B) – Egg shell chemistry, stored energy reserves, hatching cues (egg/miracidium)
- (C) – Numbers and rates of germ ball production, epithelium chemistry (sporocyst)
- Etc.
Start with a set of values that would give a “typical” parasite distribution, then start manipulating the various investments.

Cumulative numbers of hosts per pph classes with successive generations (1 through 10)

\[ \text{w1} = 10, \text{eggs} = 200, \text{dsmult} = 10, \text{rmult} = 10, \text{cercs} = 500, \text{w2} = 10 \]

Data file: PPH106.xls
Egg Production vs. Parasite Population Parameter Values

- **Average Number of Adult Worms**
- **Number of Eggs Introduced**
- **Prevalence and Mean**

- **Graph Legend**:
  - # Adults
  - Mean
  - Prevalence
Adult Worm Population Structures With 200 vs. 2000 Eggs Introduced

With 200 eggs: mean = 0.04; prevalence = 0.05
With 2000 eggs: mean = 0.69; prevalence = 0.37
Adult Worm Population Structures With Different Daughter Sporocyst Multiplying Effects

With 10 daughter sporocysts maximum: mean = 0.04; prevalence = 0.05

With 50 daughter sporocysts maximum: mean = 0.42; prevalence = 0.19
Fig. 9 – Adult Worm Population Structures With Different Cercarial Production Values

- With 500 cercariae maximum: mean = 0.04; prevalence = 0.05
- With 2000 cercariae maximum: mean = 0.27; prevalence = 0.18
Effects of worm longevity on adult worm population distribution

Cumulative numbers of hosts per pph classes with successive generations (1 through 10)

$w_1 = 10$, eggs = 200, dsmult = 10, rmult = 10, cercs = 500, $w_2 = 10$

Data file: PPH106.xls
The Keys to “Success” if You’re a Trematode*:

• The most effective way for prevalence and mean to increase is for successive iterations to overlap.
• Thus parasite longevity is a key factor.
• Predict those parasites that are not long lived as adults end up having metacercariae that are.
• In the baseball metaphor, persistence and choice of when to run are keys to success.

*Or any other organisms with complex lives? College profs? College students?
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Questions?
Thirty Iterations (PPHMM.xls)

Cumulative frequency distributions of thirty iterations.

Parasite/Host Classes

Number of hosts infected

egg# = egg# + rnd (x*10)
W2 = rnd * (40 – x)
X = 1 to 30