Evolutionary dynamics of growth strategy in game-theoretical situation in cannibalistic amphibians

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Empirical Facts

Cannibalism is widely observed in amphibian larvae.

Larvae that cannibalize conspecifics has larger body size at metamorphosis.
Empirical Facts

Cannibalistic polymorphism is known in some species.

cannibal morph → cannibalize → typical morph
Empirical Facts

Larger Head $\rightarrow$ Larger Mouth

$\rightarrow$ Advantageous in cannibalism

Relative head sizes determine occurrence of cannibalism.
Empirical Facts

Cannibal morph is more often predated by natural enemy.

natural enemy
(larvae of dragon fly)

cannibal morph

typical morph
Empirical Facts

Cannibal morph is more often predated by natural enemy.

Why?

Unbalanced body shape is thought to change behavior or decrease swimming speed.

cannibal morph
Empirical Facts: Summary

- Benefits from cannibalism.
- Cannibal morph...

Relative head size

Absolute body shape

Evolutionary game model of optimal growth schedule

...suffers from high predation pressure.
**Model**

Head Size $S$

Growth strategy is a distribution function $u(t)$ of the total energy to growth of head size and body length at given time $t$. 

Body length $l$
Model

\[ \frac{d}{dt} (sl) = E \]  
\text{total incoming energy}

\[ \begin{align*}  
l \frac{ds}{dt} &= uE \quad \text{investment to head size} \\
low \frac{dl}{dt} &= (1-u)E \quad \text{investment to body length} \end{align*} \]
For simplicity, we substitute loss of energy intake for being predated by cannibal or natural enemy.

\[ E = asl + C(s, p(s)) - B(S^2) \]

- regular food
- interaction term due to cannibalism
- predation by natural enemy
Model

- Unbalanced body shape brings higher intensity of predation.

\[ B\left(\frac{S}{l^2}\right) \geq 0 \quad (equation \ holds \ when \ s = kl^2) \]

\[ B(x) = b(x - k)^2 \quad \text{for computer simulations} \]

- **Fitness** is measured by volume at time \( T \).

\[ F = \left(s(T)l(T)\right)^2 \]
For successful metamorphosis, body shape must be balanced at time 0 and T.

\[
s(0) = k \{l(0)\}^2, s(T) = k \{l(T)\}^2
\]

- Initial body shape is uniformly fixed.

- \( 0 \leq u \leq 1 \)
Optimal mutant strategy $u_0(t)$ against wild type strategy $u^*(t)$ is derived by Pontrjagin’s theory.

If a growth function $u^*(t)$ is an ESS, the fitness of mutant strategy with growth function $u(t)$ must be maximum at $u(t) = u^*(t)$.

**Necessary condition for ESS is**

$$u_0(t) = u^*(t)$$
Analytic Result

As mutant is rare, growth trajectory of a wild type individual \((s^*, l^*)\) is independent of mutant strategy. We assume the interaction term of mutant as \(C(s - s^*)\). Necessary condition for ESS is

\[
l^2 C''(0) = 3B'(\frac{s}{l^2})
\]

When we define \(C'(0)=c\) and \(B(x) = b(x-k)^2\),

\[
s = kl^2 + \frac{c}{6b} l^4
\]

\[
\begin{align*}
\text{High predation pressure} & \quad \text{Low cannibalistic interaction} \\
\text{Balanced growth}
\end{align*}
\]
Analytic Result

Head size

$s(0)$

$l(0)$

Body length

Optimal Growth

Balanced growth
Derived analytic solutions are only candidates of ESS.

We perform computer simulation including growth dynamics and evolutionary dynamics.

\[
\begin{align*}
E_i &= a s_i l_i + C - b \left( \frac{s_i}{l_i} - k \right)^2 \\
\dot{s}_i &= u_i \left( \frac{E}{l_i s_i} \right) \\
\frac{\dot{l}_i}{l_i} &= (1 - u_i) \left( \frac{E}{l_i s_i} \right) \\
i : \text{genotype}
\end{align*}
\]
Computer simulation 1

Genetically fixed 15 strategies

strategy

trajectory
Interaction term C has an explicit form as

\[ C = \delta \sum_{j=1}^{15} p_j \varphi(s_i - s_j) \]

\[ \varphi(x) = \eta \left( \frac{2}{1 + \exp\left(\frac{-2x}{\eta}\right)} - 1 \right) \]

\[-\eta < \varphi(x) < \eta, \varphi(0) = 0, \varphi'(0) = \gamma\]

\[ \Gamma \equiv \gamma \delta \] corresponds to \( C'(0) \) in analytic model.
Computer simulation 1

Initial genotype distribution is uniform.

Growth of each genotype is simulated from \( t=0 \) to \( t=T \).

Fitness (squared volume at time \( T \)) is determined by this growth simulation.

Genotype distribution in the next generation is determined so that frequency of each genotype is proportional to its fitness.

Random mutation occurs every 100 generations.
## Computer simulation 1

### Result ($\Omega \equiv \delta\eta \quad \Gamma \equiv \gamma\delta$)

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<th>3</th>
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Genotypes with more than 10% time average frequency are shown.
i+ means corresponding genotype has >90% time average frequency.

Some ESS candidates are **not always** realized.
Computer simulation 1

balanced

unbalanced

generation
Why cyclic?

1. *Slightly* more unbalanced growth than population majority is the most adaptive.

2. Fitness of the most unbalanced strategy is very low and balanced strategy invades.

   \[\downarrow\]

   Endless replacement of the dominating strategies.

   similar to Taxon cycle
Individual based model which directly deals death events of individuals is also analyzed. The model can also represent stochastic effect.

- Encounter rate = population density
- Probability of cannibalism = function of difference of head sizes
- Cannibalized / Predated individuals are killed;
  - population density monotonously decreases (actually observed)
- Cannibal receives 50% of volume of the victim as energy intake;
  - successful cannibal grows very suddenly (actually observed)
- Individual who succeeded in cannibalism by chance has larger probability
  of the next successful cannibalism (actually observed)

Qualitative results remain the same.
Computer simulation 2
Conclusion

Evolution of growth strategy might be either

\[
\begin{align*}
\text{convergence to the single strategy} \\
\text{or} \\
\text{the cyclic evolution}
\end{align*}
\]

This depends on environmental parameters.

Under cyclic evolution, the dominating strategy would be completely different between populations whose environmental factors are the same (but evolutionary phases differ).