Drastic growth effect explains sympatric cannibalistic polymorphism

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Joe Yuichiro Wakano

Department of Biological Sciences
The University of Tokyo

Agenda

- Basic introduction to evolutionary game theory
- Cannibalistic polymorphism
  - cost/benefit of cannibal morph
  - food web structure
- Model 1
  - without drastic growth effect
- Model 2
  - with drastic growth effect
- Conclusion

Basic introduction to Evolutionary Game Theory

- The frequency of a gene that gives higher fitness to its carrier will increase (Darwinian theory of evolution).
- If animal behavior is determined by a gene, the best behavior will evolve.
- The best behavior often depends on behavior of other animals.
- If there are only two types of behavior (A & B), fitness of each behavior depends on the frequency of A (frequency-dependent selection).
- Such a situation is studied by evolutionary game theory.

Basic introduction to Evolutionary Game Theory

- Terminology
  - player = animal / individual
  - strategy = behavior (genetically determined)
  - payoff = fitness
  - equilibrium
  - stability
- Classic game theory
  - rational players with full knowledge of payoff matrix
  - rational decision making
- Evolutionary game theory
  - blind players
  - natural selection

Basic introduction to Evolutionary Game Theory

	p	*1-p*	
	Hawk	Dove	
Hawk	-1	2	$-p+2(1-p)$
Dove	0	1	$1-p$

$$F(Hawk) = -3p + 2$$

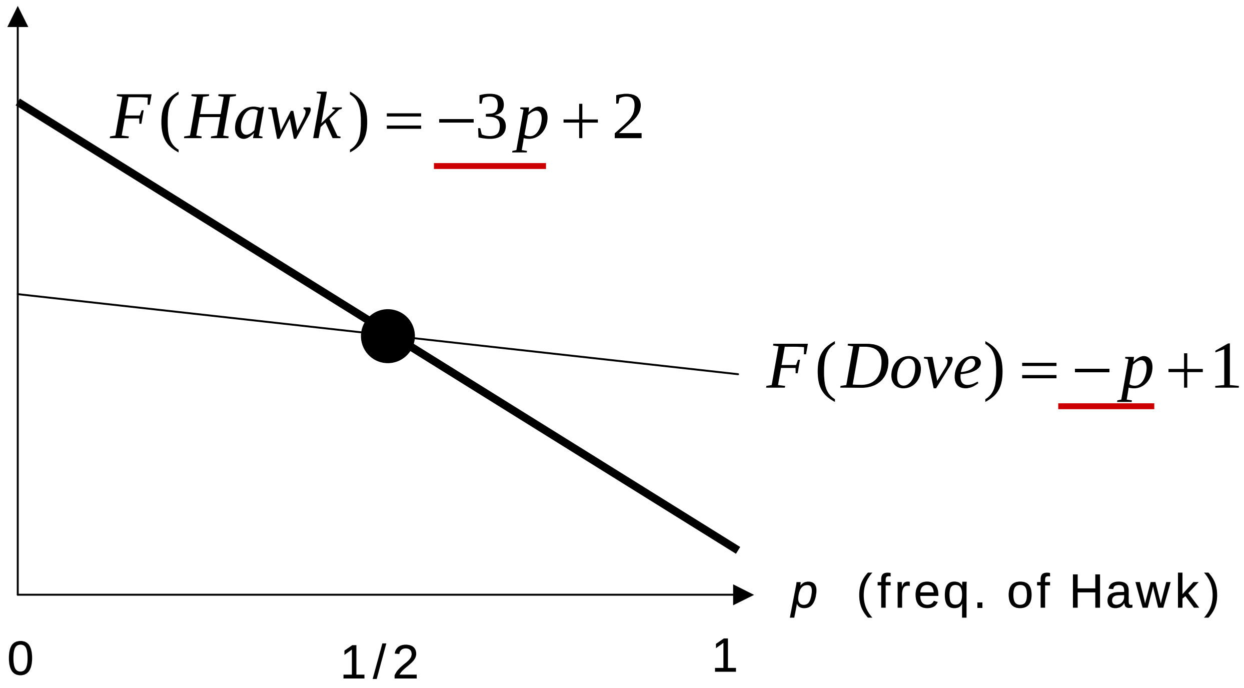
$$F(Dove) = -p + 1$$

If $p=1/2$, both strategies are equally successful.

$p=1/2$ is **equilibrium**.

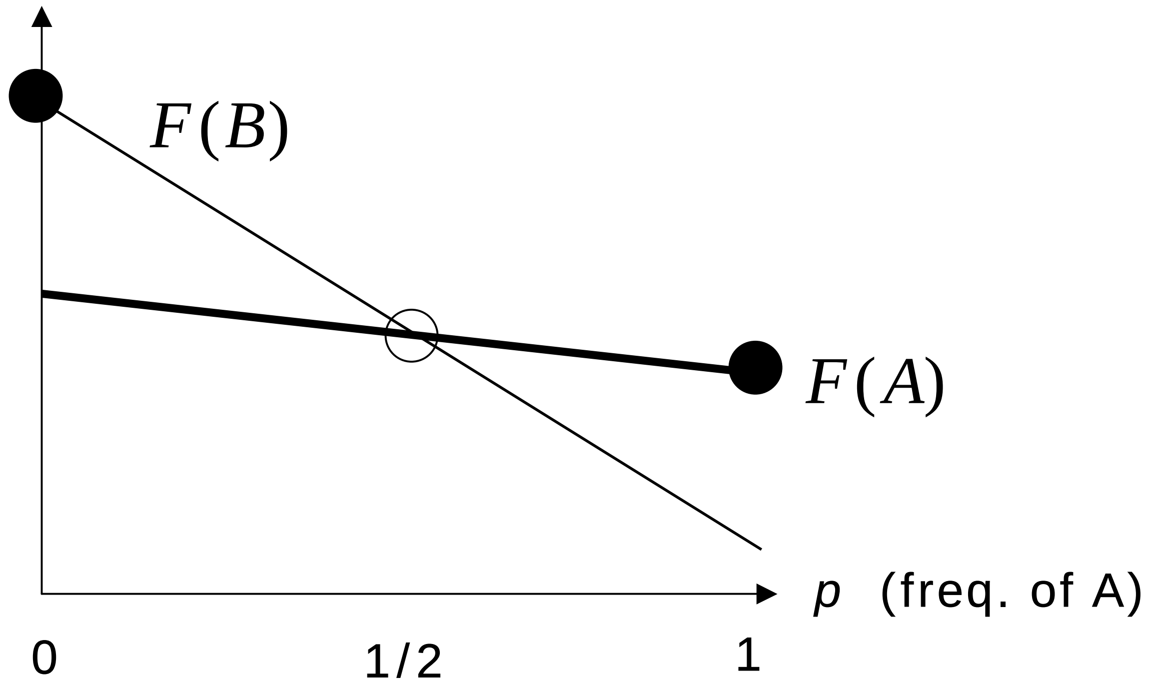
Basic introduction to Evolutionary Game Theory

- Stable Equilibrium



Basic introduction to Evolutionary Game Theory

- Unstable Equilibrium



Cannibalistic polymorphism

Hynobius retardatus salamander larvae

cannibal morph

typical morph

Photo by Y. Kohmatsu

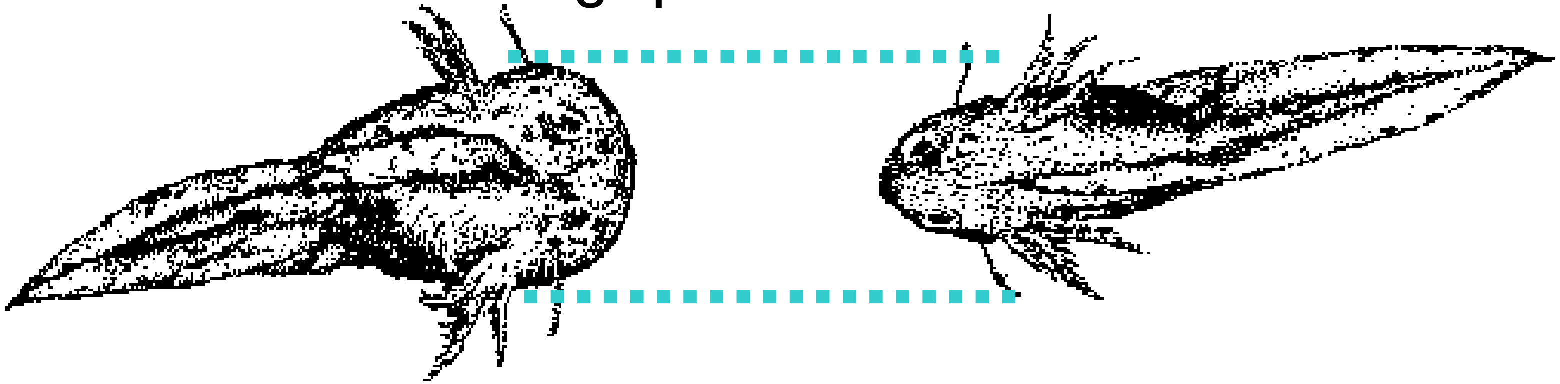
Cannibalistic polymorphism

- Sympatric coexistence of cannibal morphs and typical morphs
  - *Ambystoma* salamanders
  - *Hynobius* salamanders
  - *Scaphiopus* toads

Benefit of cannibal morph

- Advantage in cannibalism

gape limited



cannibal morph

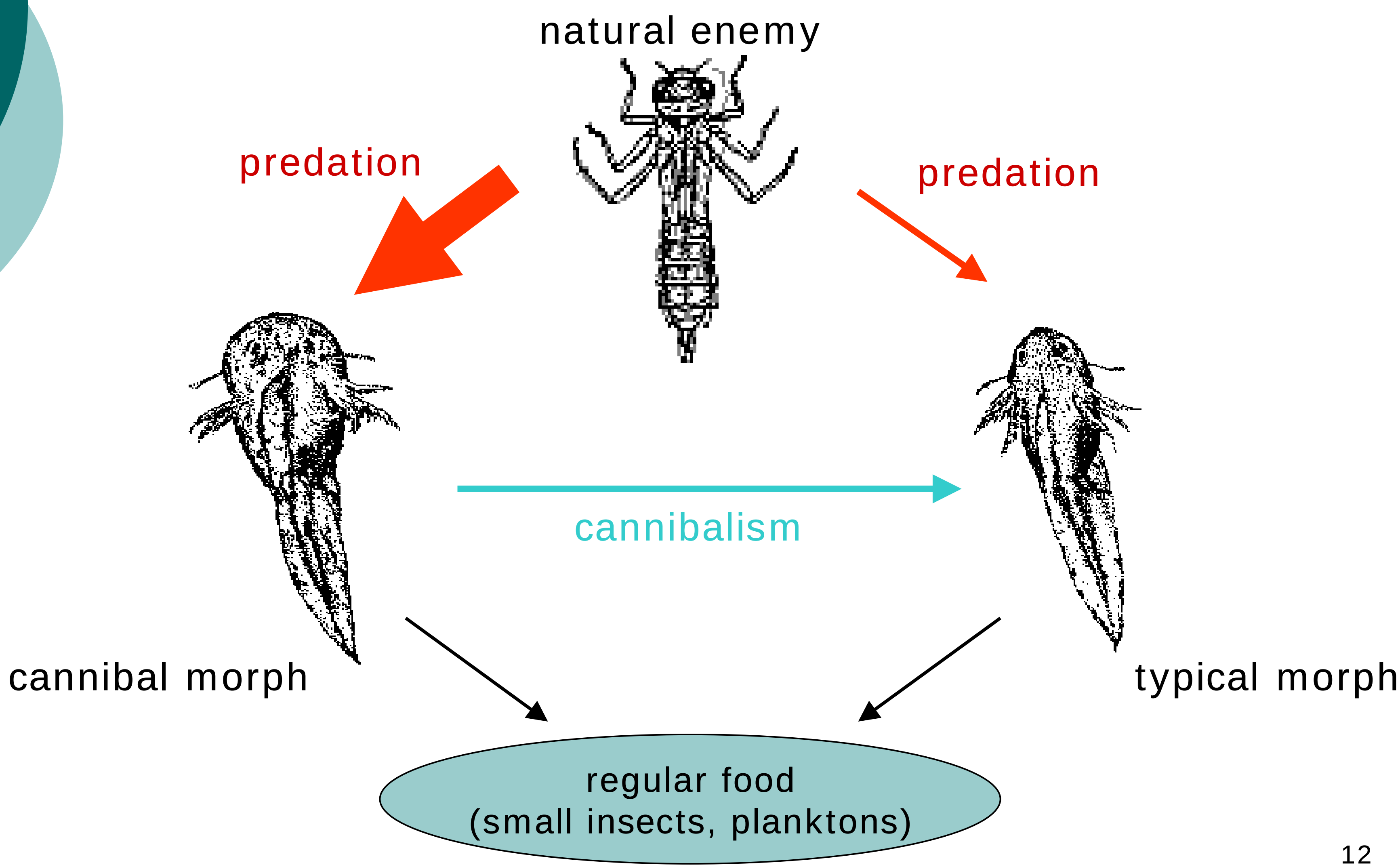
typical morph

Cost of cannibal morph

- not very clear
  - Costs such as eating relatives, pathogen infection or handling time are the cost of cannibalism.

- Larger mortality
  (due to decreased swimming speed)

Food web


natural enemy
predation
predation
cannibalism
cannibal morph
typical morph
regular food
(small insects, planktons)

Assumptions

- Two distinct strategies:
  cannibal and typical morphs
- The strategy is genetically determined
  - experimental studies shows both genetic basis and phenotypic plasticity
- Only cannibal morphs can perform cannibalism

Goal of the study

- Explain the cannibalistic polymorphism as the stable coexistence solution in an evolutionary game model
- Determine the condition under which such a polymorphic solution exists

Model 1: parameters

Freq. of cannibal morph	p
Freq. of typical morph	$1-p$
Intensity of cannibalism	γ
Freq. of cannibalism	$\Gamma = \gamma p(1-p)$

(Population size is normalized to unity.)

Model 1:
Body size at the end of growth period

Typical morph A

Cannibal morph $kA\dfrac{\Gamma}{p} + B$

growth by regular food consumption

size of victim

probability with which each cannibal morph can eat a typical morph

k : Energy conversion factor (<1)

(the efficiency of digestion)

Model 1: Fitness

(fitness) = (body size) X (survival rate)

Cannibal morph

$$F_C = \left(kA\frac{\Gamma}{p} + B \right) \cdot m$$

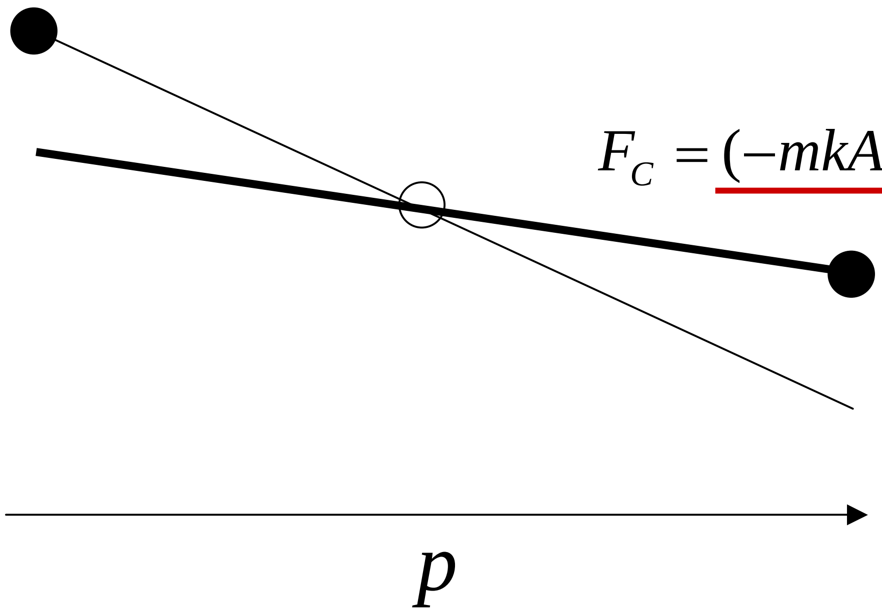
Typical morph

$$F_T = A \cdot \frac{1 - p - \Gamma}{1 - p}$$

Relative survival rate of cannibal morph
(cost of cannibal morph is 1-*m*)

$$m\,(<1)$$

Model 1:
The result



$$F_C = (-mkA\gamma)p + (mB - mkA\gamma)$$

$$F_T = (-A\gamma)p + A$$

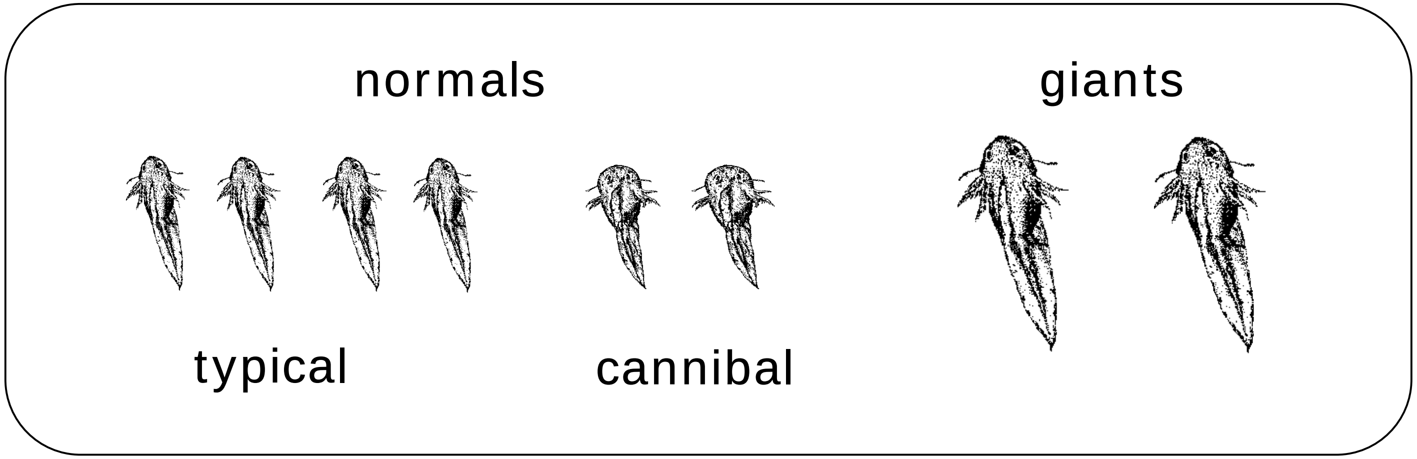
Since $mk<1$, even if the intersection exists,
it is always unstable equilibrium.

Coexistence will not evolve.

Drastic growth effect

- Larvae initially have similar body size.
- A cannibalism promotes the cannibal to outstanding size (a giant)
- Once giants appear, they monopolize most cannibalisms

(Difference between typical/cannibal morphs becomes negligible.)



Drastic growth effect

Fitness of a giant is naturally expected to be very high.

The aim of taking cannibal morph strategy might be to increase the probability of becoming a giant by developing a slightly larger organ (cf. head width).

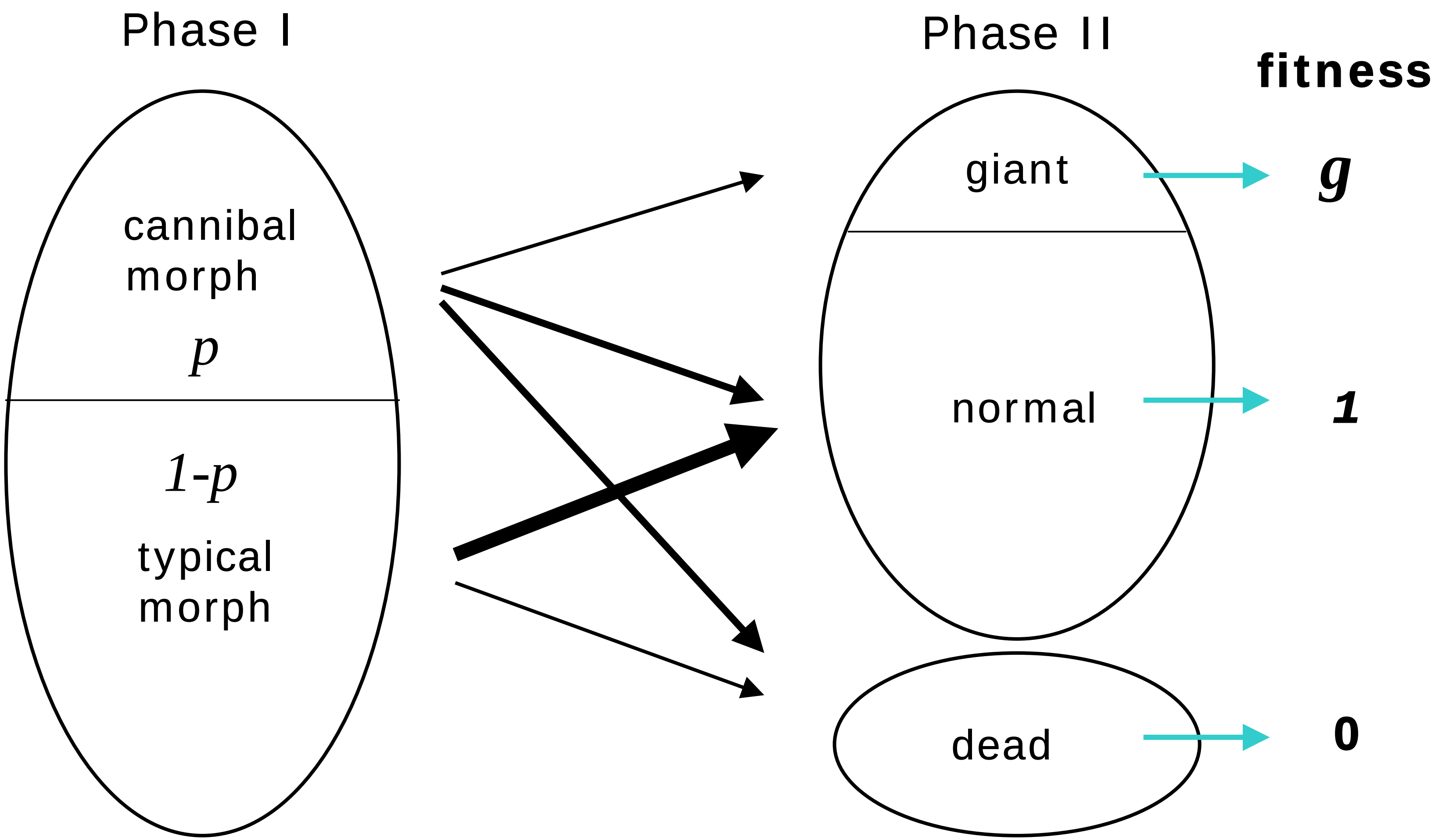
Model 2: Assumptions

- consider only normal individuals and level 1 giants
- Fitness of a giant is constant

A level 1 giant will proceed to level 2 by performing successful cannibalism. For simplicity, however, we neglect such a chain. The most important point is how many cannibal morphs become giants.

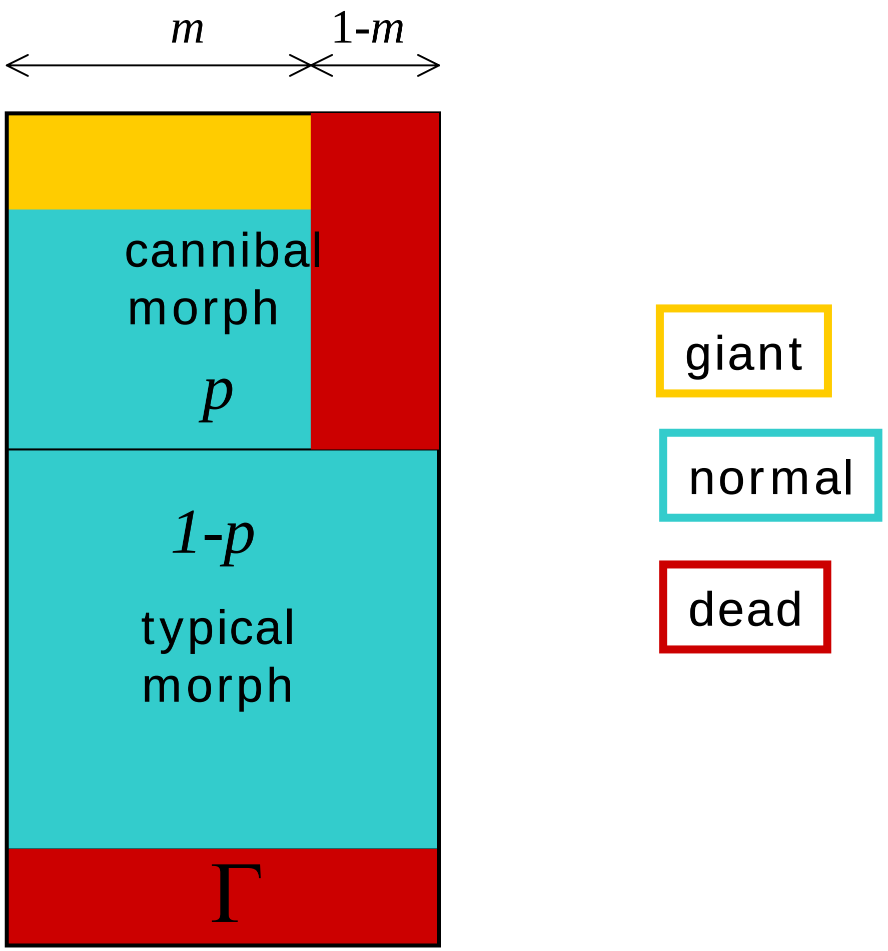
In real salamanders, almost all occurrences of cannibalism are monopolized by a few giants. However,
rare occurrences among normal larvae, which produces a giant, are important.

Model 2



Phase I
Phase II
fitness
cannibal morph
p
1-p
typical morph
giant
normal
dead
g
1
0

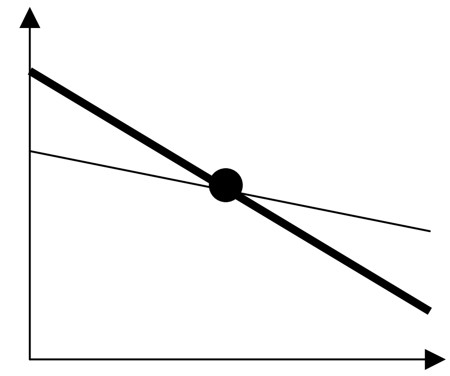
Model 2



Model 2: Analysis

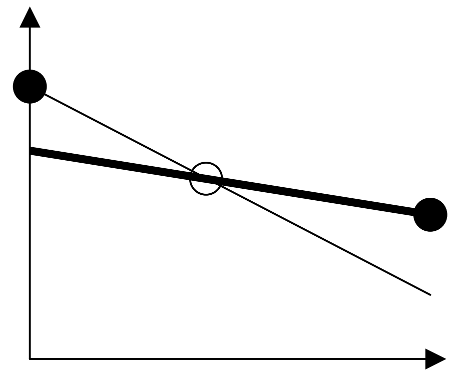
$$F_C = \frac{1}{p}\left[\Gamma g + (p - \Gamma)\right] \cdot m$$

$$F_T = \frac{1 - p - \Gamma}{1 - p}$$



$$F_C = \underline{-2m\gamma(g-1)}\, p + m\{2\gamma(g-1)+1\}$$

$$F_T = \underline{-2\gamma}\, p + 1$$



$$p^* = \frac{m\{2\gamma(g-1)+1\}-1}{2\gamma\{m(g-1)-1\}}$$

Model 2: Analysis

If

$$m > \frac{1}{g-1} \quad \text{(stability condition)}$$

$$m > \frac{1}{2\gamma(g-1)+1}$$

$$m < 1 - 2\gamma$$

(existence condition of an equilibrium)

then, there is a globally stable interior equilibrium, that is,

stable coexistence solution

Model 2:
Necessary condition for stability

$$m > \frac{1}{g-1}$$ (stability condition)

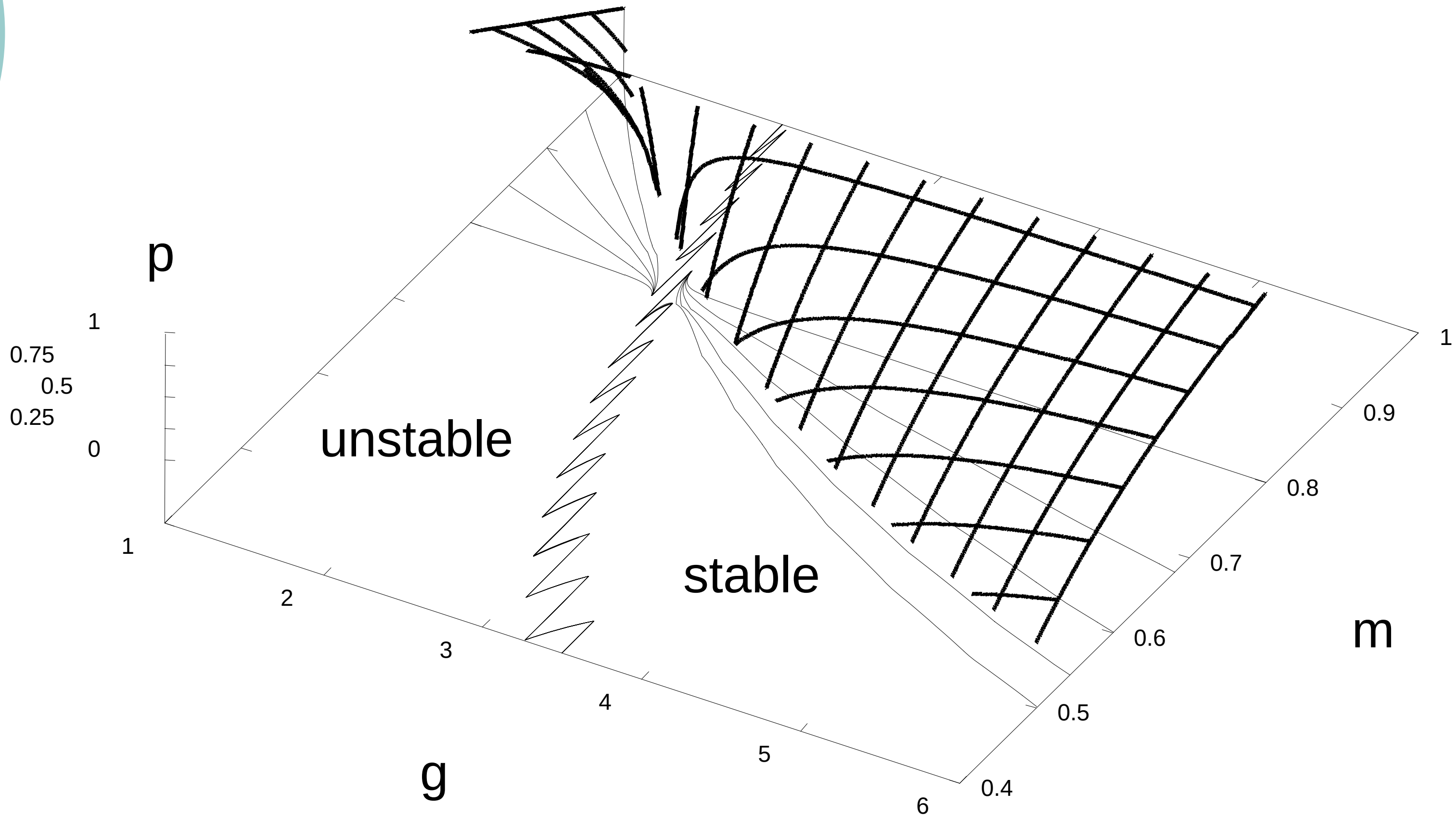
$$\Updownarrow$$

$$g > 1 + \frac{1}{m}$$

$$\Downarrow$$

$$g > 2$$

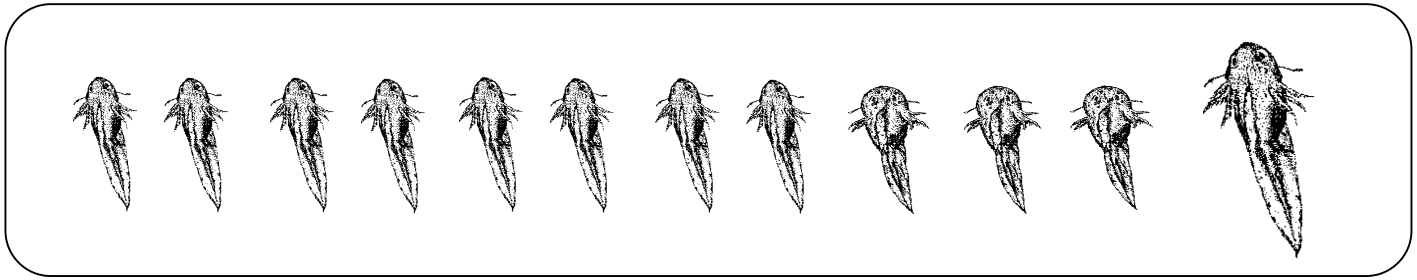
Evolutionarily stable frequency of cannibal morphs



Summary of the analysis

- Evolutionary outcome is one of
  - i) domination of typical morph
  - ii) domination of cannibal morph
  - iii) stable coexistence
- Coexistence evolves when g is large and m is intermediate.
- For coexistence, $g > 2$ is necessary

Is *g* >2 realistic ?
Experimental data



Ambystoma tigrinum salamander’s case:

No more than one cannibal (=giant) appeared per aquarium containing 16 larvae (Pfennig & Collins 1993).

Fitness of a giant is **much larger** than two times fitness of non-giants.

This promotes the stable coexistence of typical/cannibal morphs or **polymorphism**.

Conclusion

- Evolutionary game models of cannibalistic polymorphism are proposed
- The condition of stable coexistence of typical/cannibal morphs is studied

- Considering drastic growth effect, large fitness of a giant (>2) promotes evolution of cannibalistic polymorphism.

Thank you for your attention.