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

Joe Yuichiro Wakano
(Department of Chemical System Engineering, University of Tokyo)

Yukihiro Kohmatsu
Norio Yamamura
(Center for Ecological Research, Kyoto University)

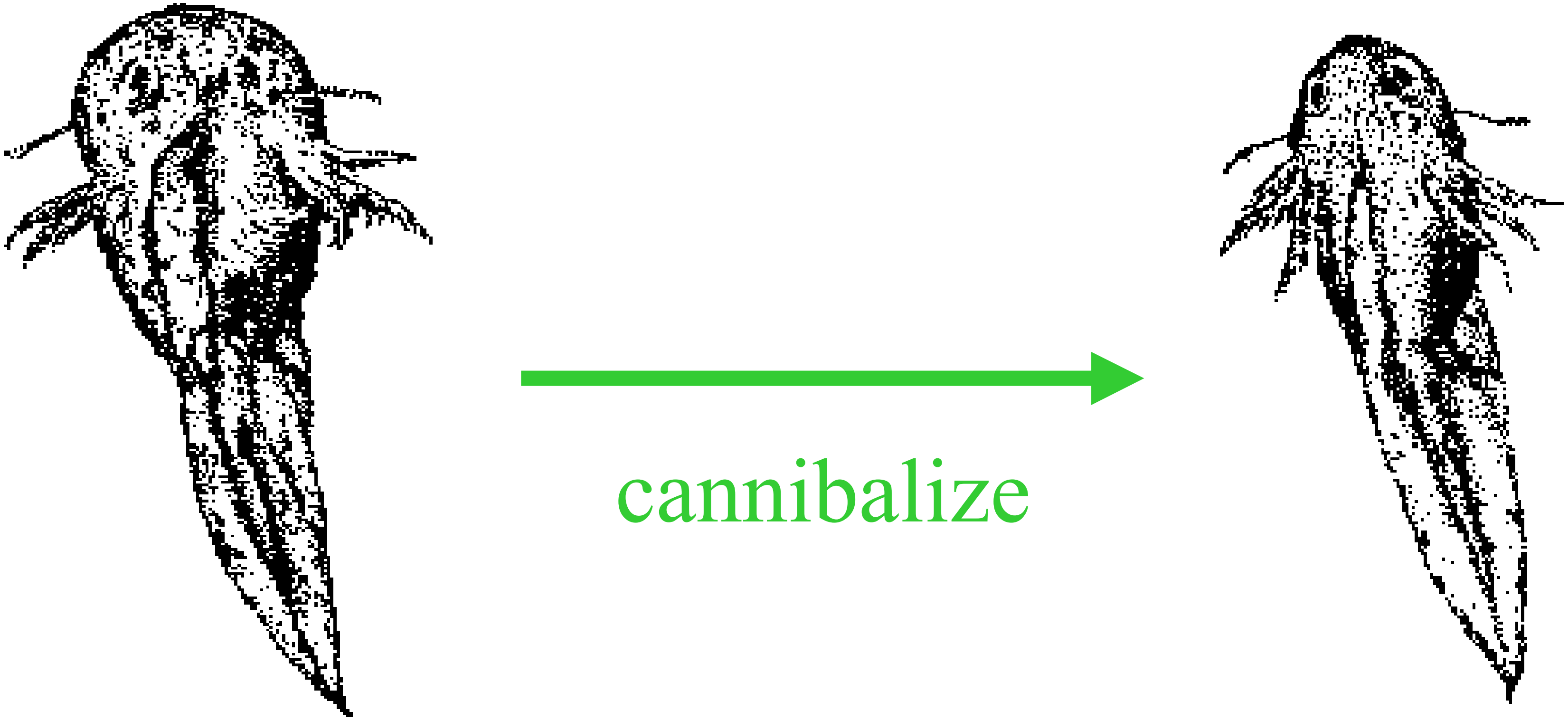
Empirical Facts

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

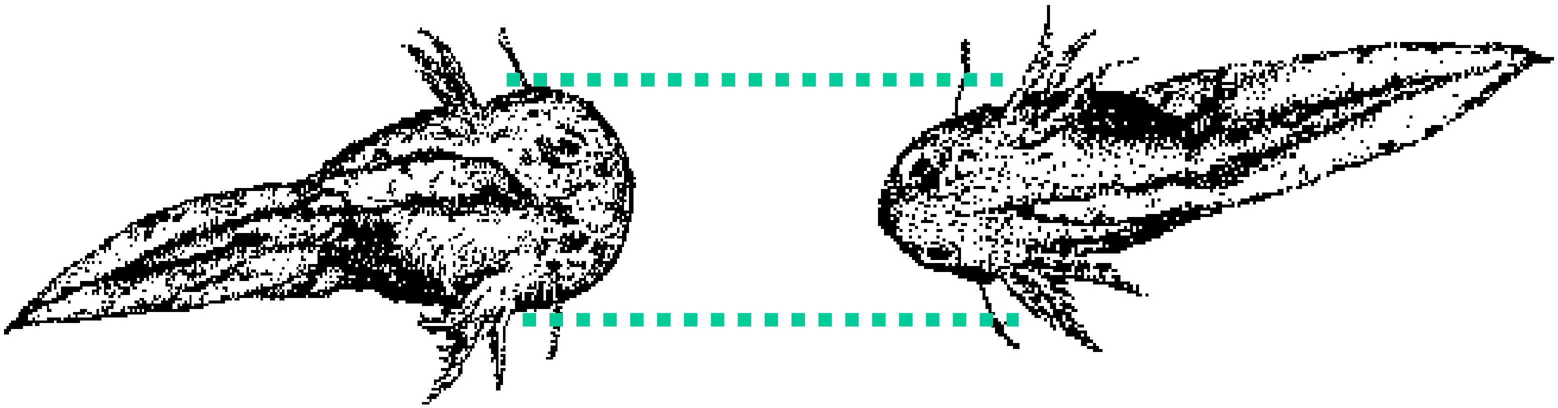
cannibalize

typical morph

Empirical Facts

Larger Head → Larger Mouth

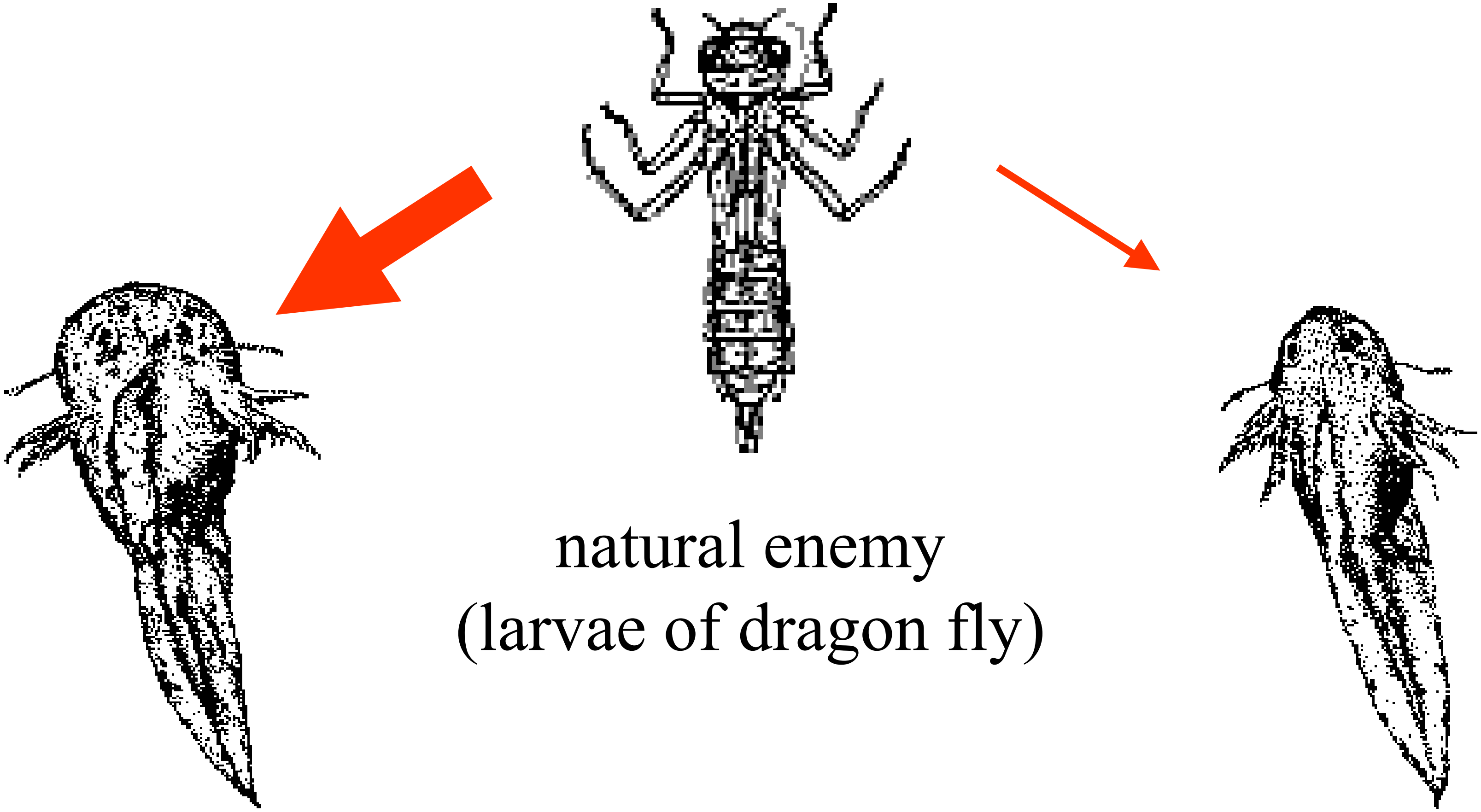
→ **Advantageous in cannibalism**



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.

cannibal morph

Why ?

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

Empirical Facts : Summary

Cannibal morph ...

- benefits from cannibalism.

relative head size

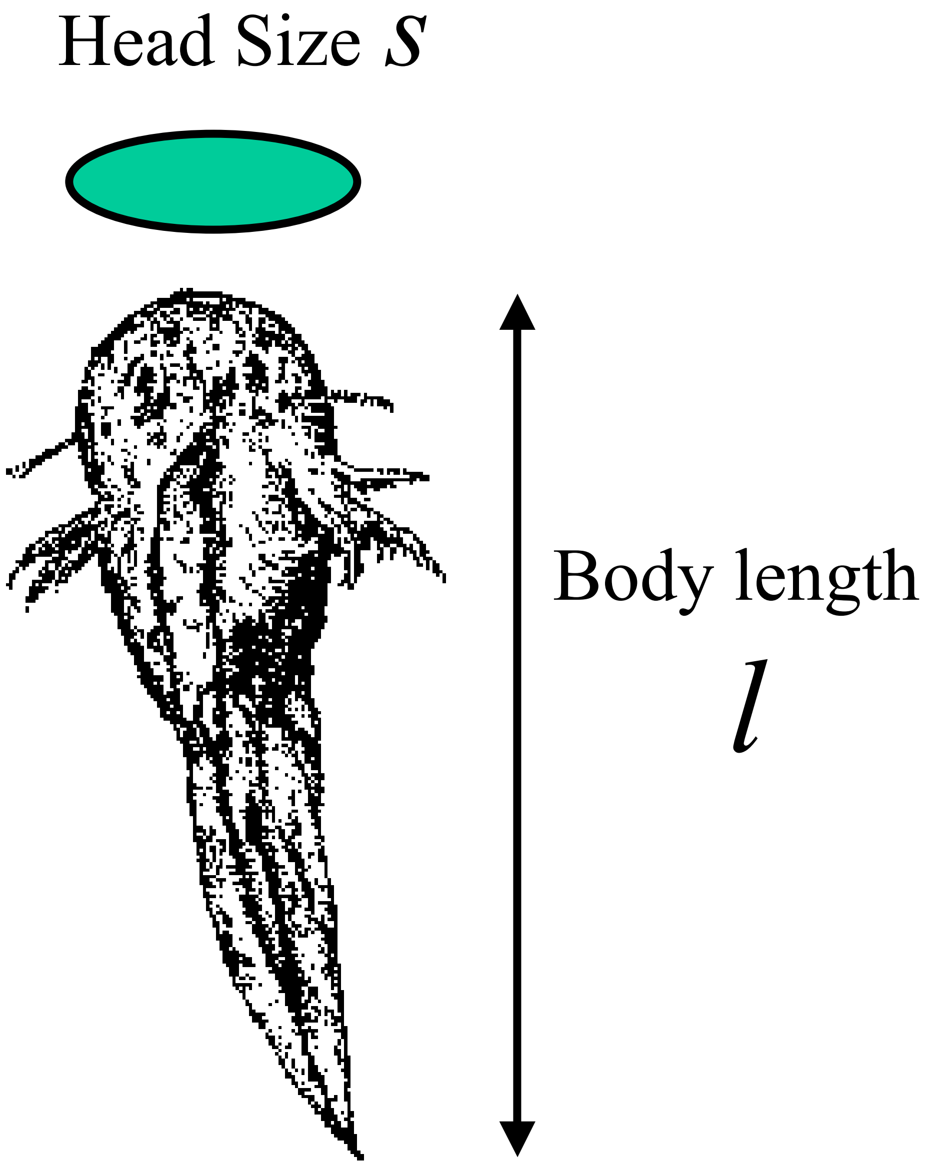
- suffers from high predation pressure.

absolute body shape

↓

Evolutionary game model of optimal growth schedule

Model



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

Model

$$\frac{d}{dt}\left(sl\right)=E$$

total incoming energy

$$\begin{cases} l\dfrac{ds}{dt}=uE \\ s\dfrac{dl}{dt}=(1-u)E \end{cases}$$

investment to head size

investment to body length

Model

For simplicity, we substitute loss of energy intake for being predated by cannibal or natural enemy.

$$E = asl + C(s, p(s)) - B(\frac{s}{l^2})$$

regular food

interaction term
due to cannibalism

predation by
natural enemy

Model

- Unbalanced body shape brings higher intensity of predation.

$$B(\frac{s}{l^2}) \geq 0 \quad (\textit{equation holds when } s = kl^2)$$

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

- **Fitness** is measured by volume at time T.

$$F = \left(s(T)l(T)\right)^2$$

BOUNDARY CONDITIONS

- 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.

- $0 \leq u \leq 1$

Analytic Result

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 $B(x) = b(x-k)^2$,

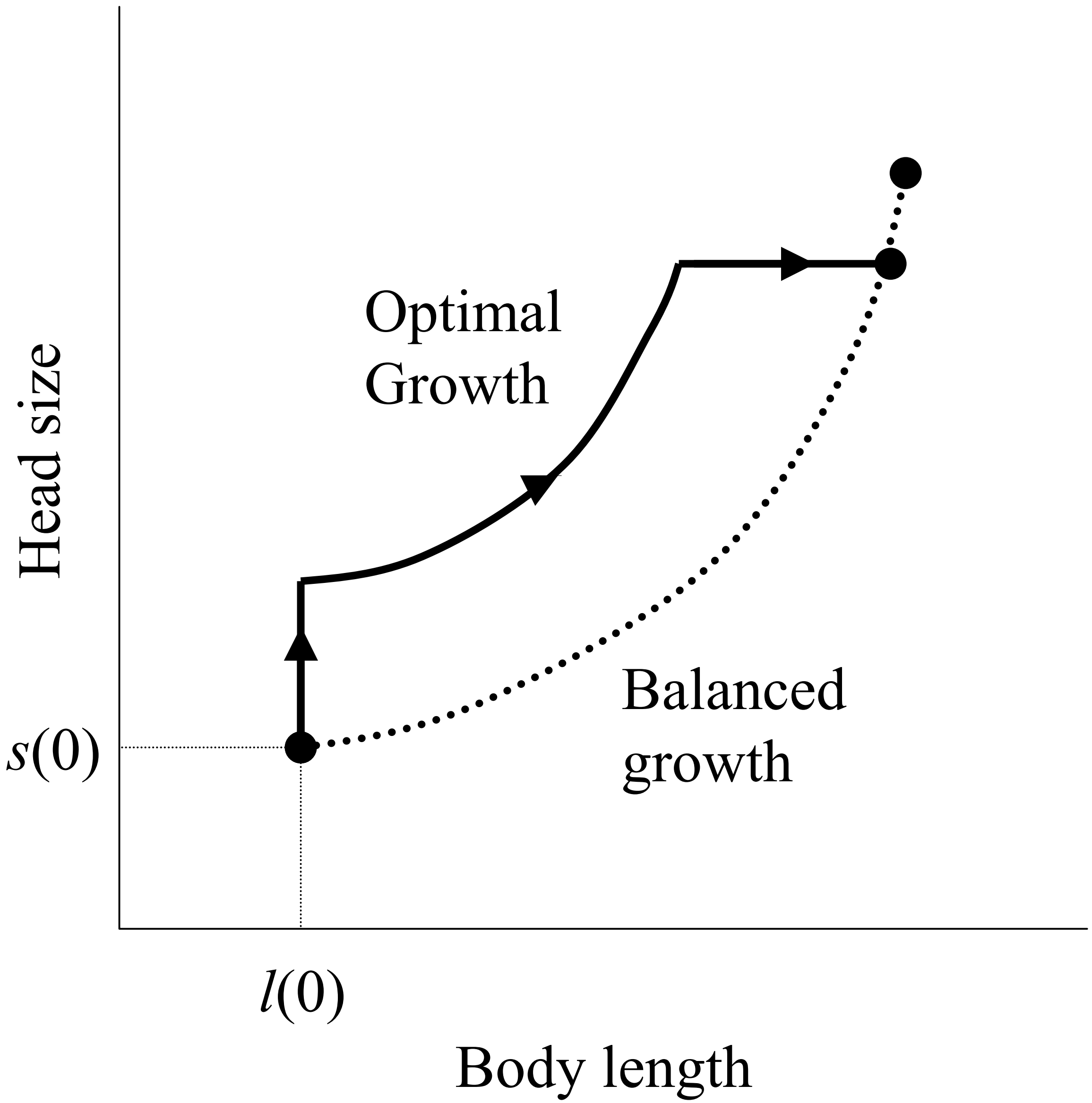
$$s = kl^2 + \frac{c}{6b} l^4$$

$$\left\{\begin{array}{l}\text{High predation pressure}\\ \text{Low cannibalistic interaction}\end{array}\right.$$

↓

Balanced growth

Analytic Result



Computer simulation 1

Derived analytic solutions are only **candidates of ESS**.

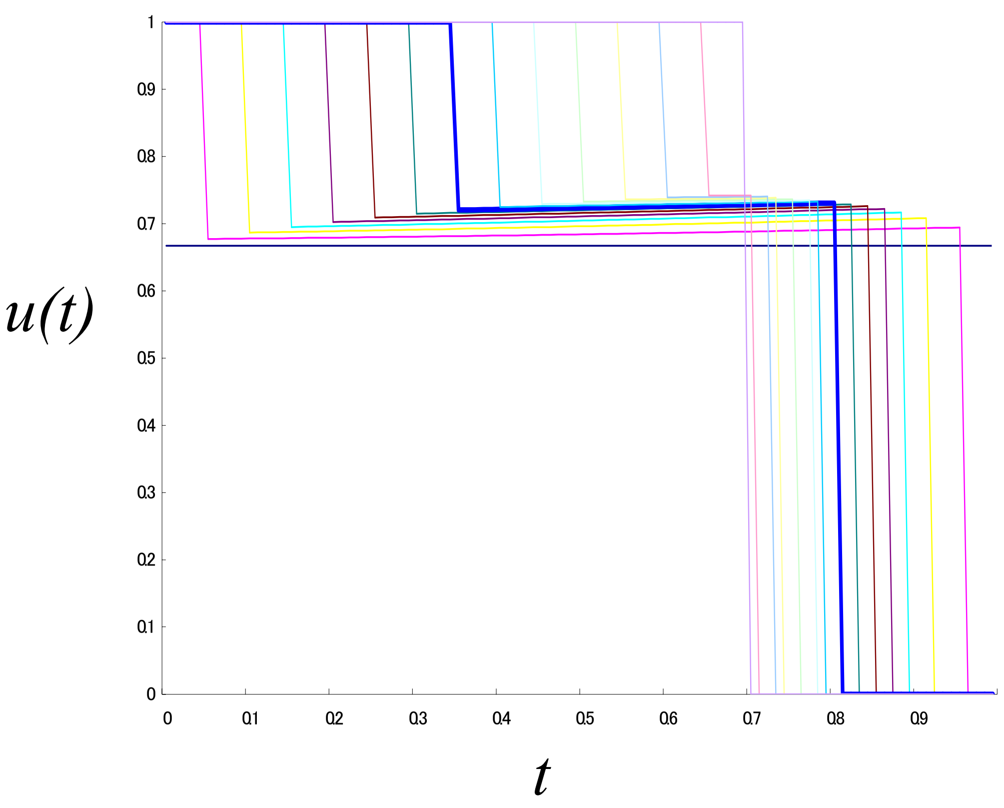
We perfom computer simulation including **growth dynamics** and **evolutionary dynamics**.

$$\begin{cases} E_i = as_i l_i + \underline{C} - b(\frac{s_i}{l_i^{\,2}} - k)^2 \\ \frac{\dot{s}_i}{s_i} = u_i \frac{E}{l_i s_i} \\ \frac{\dot{l}_i}{l_i} = (1-u_i)\frac{E}{l_i s_i} \end{cases}$$

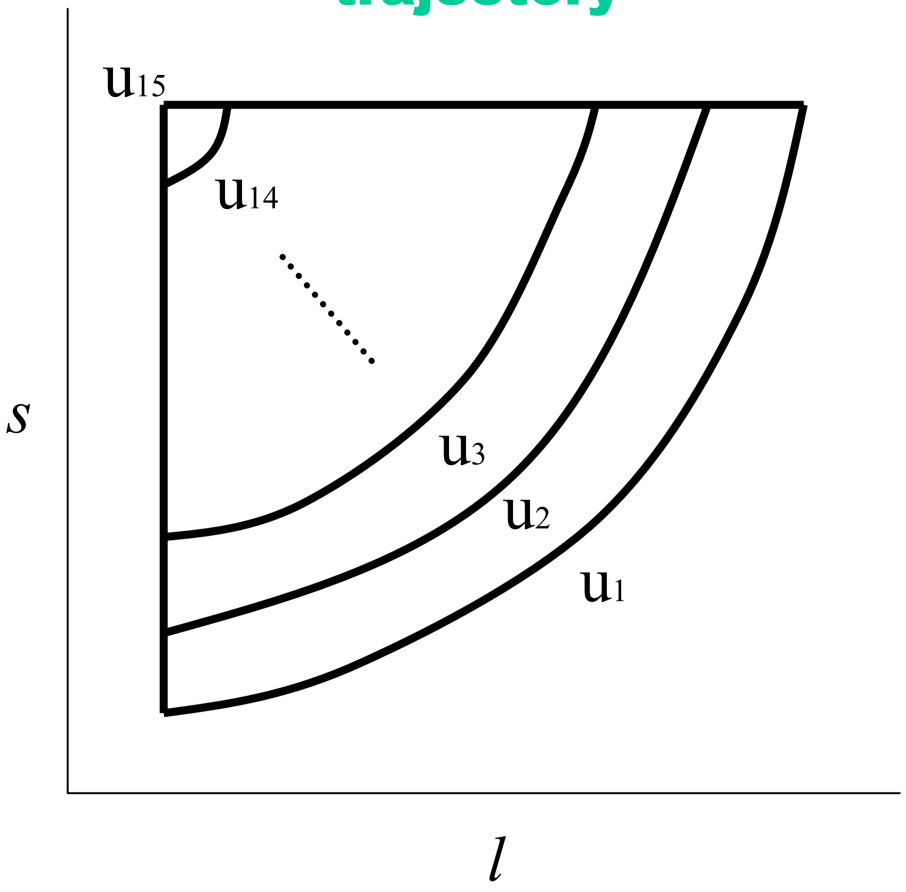
i :genotype

Computer simulation 1

Genetically fixed 15 strategies



strategy



trajectory

Computer simulation 1

Interaction term C has an explicit form as

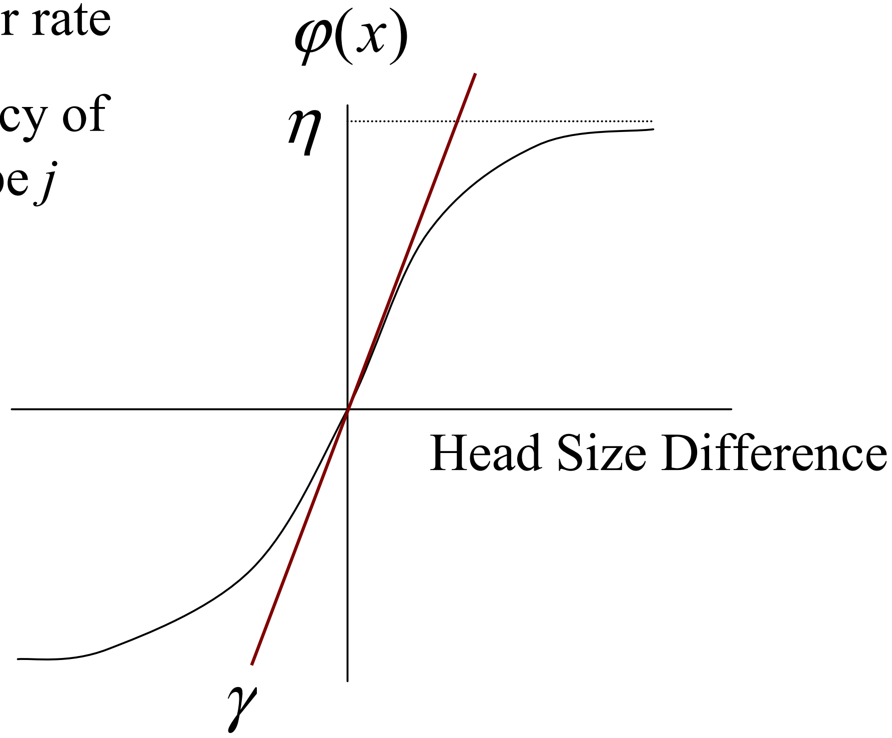
$$C = \delta \sum_{j=1}^{15} p_j \varphi(s_i - s_j)$$

δ : encouter rate

p_j: frequency of genotype j

$$\varphi(x) \equiv \eta \left(\frac{2}{1 + \exp(\frac{-2\gamma x}{\eta})} - 1 \right)$$

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



$\Gamma \equiv \gamma\delta$ corresponds to C'(0) in analytic model.

Computer simulation 1

growth dynamics

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.

evolutionary dynamics

Computer simulation 1

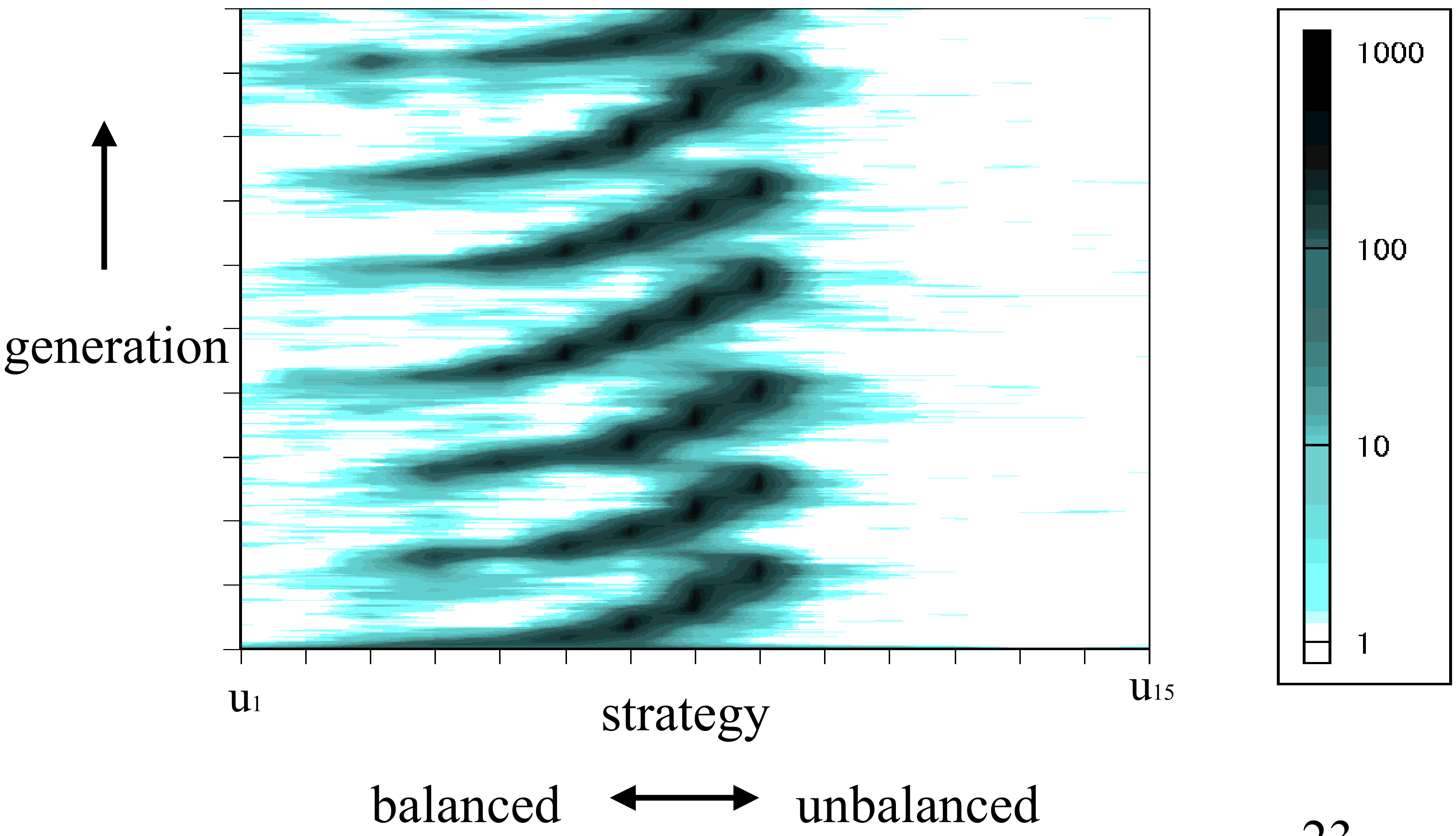
Result ($\Omega \equiv \delta\eta \quad \Gamma \equiv \gamma\delta$)

									corresponding strategy						
Ω									Γ						
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
	0	0.6	1.3	2	2.8	3.5	4.2	5	5.6	6.2	6.8	7.3	7.7	8	8.3
0.2	1+	2+	3+	4+	4,5	4,5	3,4,5	3,4,5	3,4,5	3,4,5	3,4,5	3,4,5	3,4,5	3,4,5	3,4,5
0.4	1+	2+	3+	4+	5+	6+	6,7	6,7	5,6,7	5,6,7	4,5,6,7	4,5,6,7	4,5,6,7	4,5,6,7	5,6,7
0.6	1+	2+	3+	4+	5+	6+	7+	8	8	8,9	6,7,8,9	6,7,8,9	6,7,8,9	6,7,8,9	6,7,8,9
0.8	1+	2+	3+	4+	5+	6+	7+	8+	9+	10+	10,11	10,11	10,11	9,10,11,12	10,11,1
1.0	1+	2+	3+	4+	5+	6+	7+	8+	9+	10+	11+	12,13	13	13,15	15

Genotypes with more than 10% time average frequency are shown.
i+ means correspoding genotype has >90% time average frequency.

Some ESS candidates are **not always** realized.

Computer simulation 1



Computer simulation 1

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.

↓

Endless replacement of the dominating strategies.

similar to Taxon cycle

Computer simulation 2

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)

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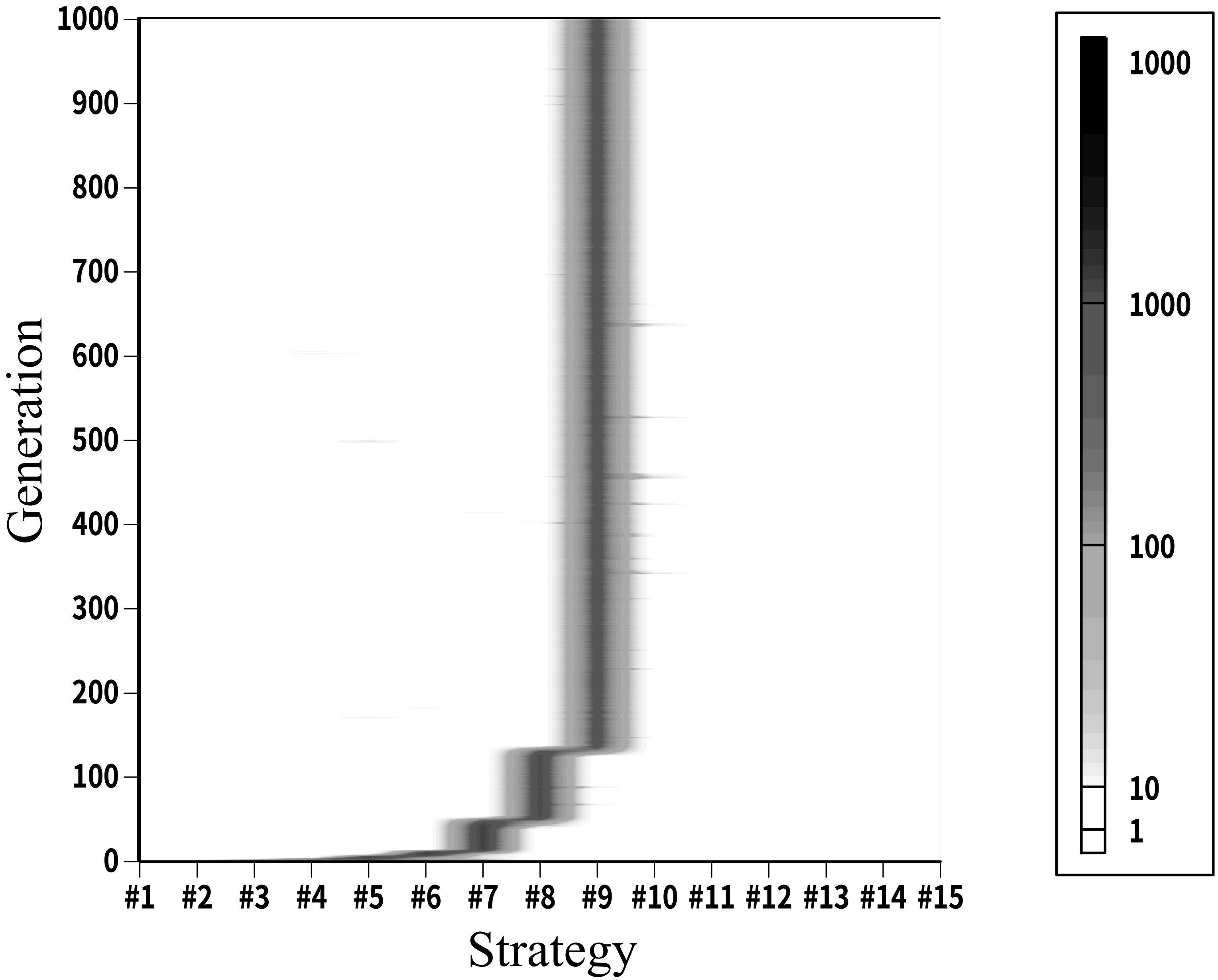
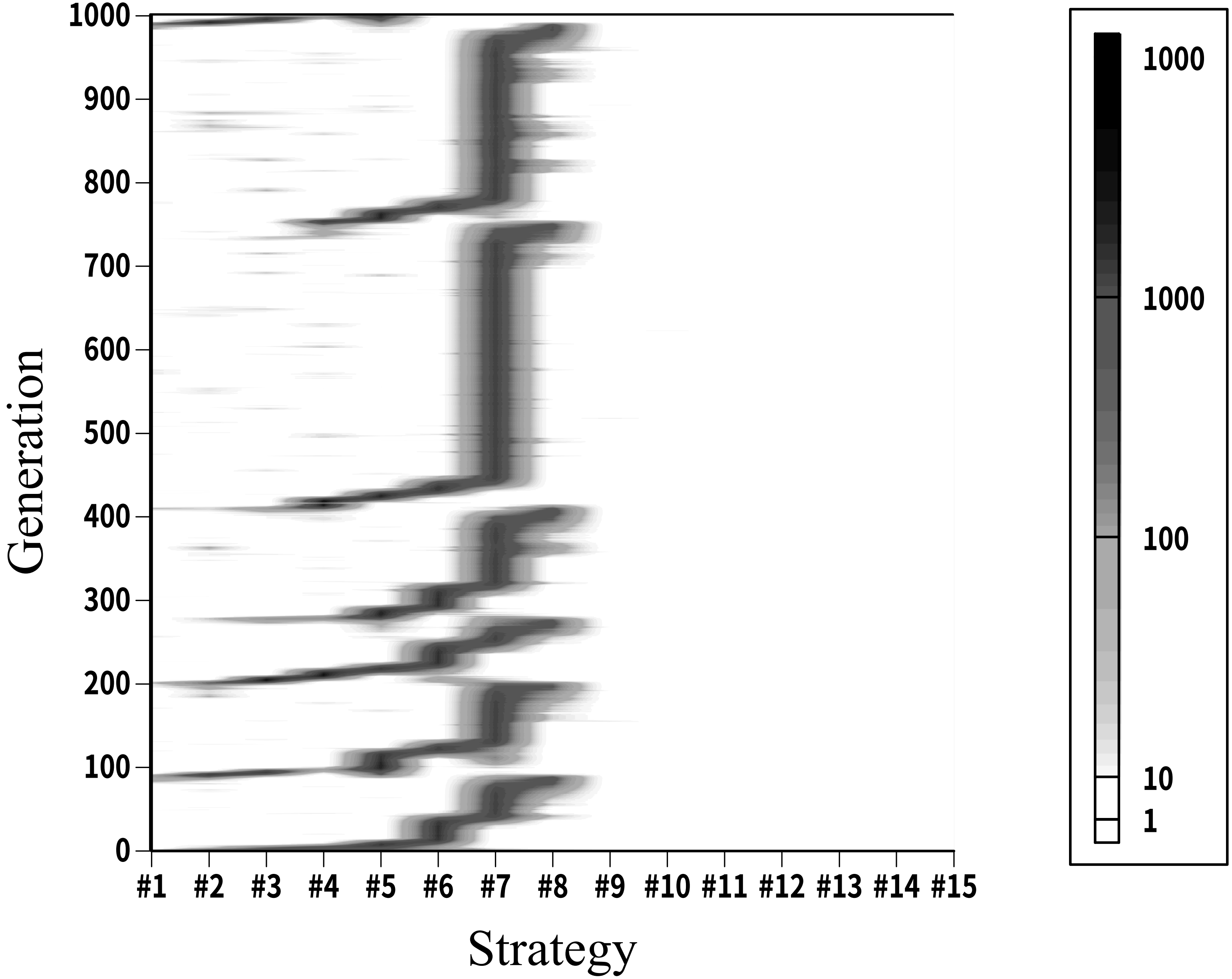
Qualitative results remain the same.

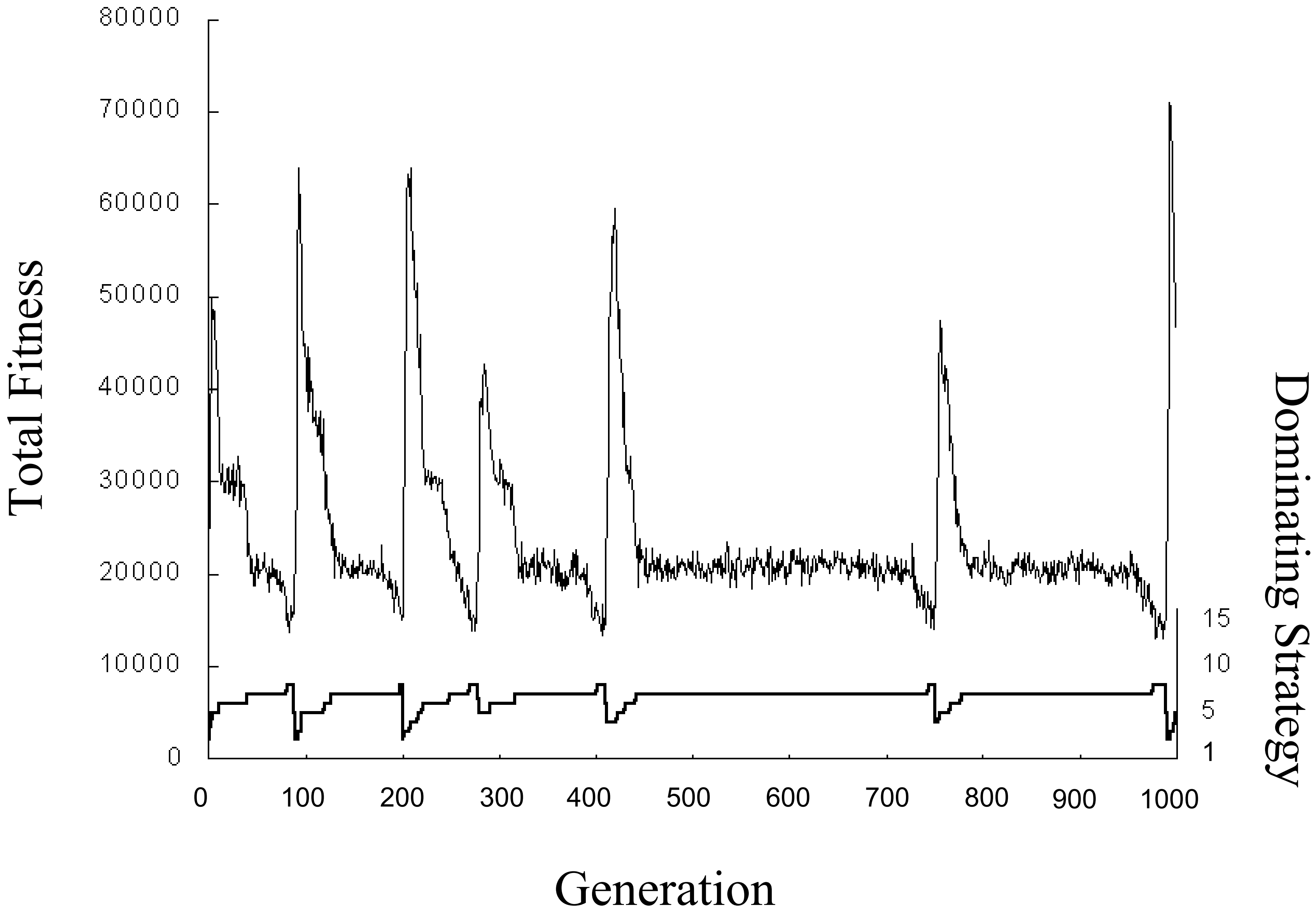
Computer simulation 2



Computer simulation 2



Computer simulation 2



Conclusion

Evolution of growth strategy might be either

$$\left\{\begin{array}{l}\textbf{convergence to the single strategy}\\ \qquad\text{or}\\ \textbf{the cyclic evolution}\end{array}\right.$$

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).