# Evolutionary dynamics of frequency-dependent growth strategy in cannibalistic amphibians

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## ABSTRACT

Cannibalistic amphibian larval morphs, which have greater head widths than typical morphs and therefore have larger mouths, provide the basis for the construction of a simple model of cannibalism that describes the growth dynamics of body shape. As the relative head sizes of interacting individuals determine the occurrence of cannibalism, the situation is frequency-dependent. Because natural enemies prey more often upon individuals with a more unbalanced body shape, an optimal growth schedule should exist. The necessary conditions for an evolutionarily stable strategy (ESS) are derived analytically; these conditions are checked by evolutionary simulation. When the probability of cannibalism is low, an ESS exists. In such cases, the body shape is more balanced (less adaptive to cannibalism) when predation pressure is higher and population density is lower. When the probability of cannibalism is high, there is no ESS. For such cases, a computer simulation of the evolutionary dynamics revealed that the dominant growth strategy changes cyclically. The development of a more detailed model of individual-based population dynamics showed that the qualitative results of the simple model held for the individual-based model. Accompanied by cyclic evolution, the number of surviving individuals at metamorphosis oscillated. The frequency-dependent models suggested that the evolutionary dynamics of cannibalism change dramatically depending upon environmental conditions.

*Keywords*: cannibalism, cannibalistic morph, evolutionary cycling, evolutionary dynamics, frequency dependence, polymorphism.

## INTRODUCTION

Animals adapt not only to abiotic environments, but also to social interactions. Intraspecific predation, or cannibalism, is one of the most important factors among a variety of social interactions, being commonly observed in many animal taxa (for a review, see Polis, 1981). It may be a strong factor in natural selection, because being cannibalized means instant death of the individual.

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In amphibians, cannibalism is common during the period from hatching until meta-morphosis. An unbalanced growth strategy (cannibalistic morph), which is characterized by a greater head width (and thus larger mouth) relative to body length, has been recorded in *Ambystoma* salamanders (Rose and Armentrout, 1976), *Hynobius* salamanders (Wakahara, 1995) and *Scaphiopus* toads (Pfennig, 1990). As an individual can eat conspecifics with a smaller head width (Kusano *et al.*, 1985; Ohdachi, 1994), the cannibalistic morph is con-sidered to be an adaptive growth strategy (Fig. 1). However, if all individuals become cannibalistic morphs, they cannot cannibalize other individuals. Thus, the situation is game-theoretical or frequency-dependent.

Several experiments have shown that the magnitude of imbalance in body shape of the cannibalistic morph was greater when the population density was higher (Nishihara, 1996; Hoffman and Pfennig, 1999). Even when the density was very high, some individuals retained the typical morph features, resulting in a polymorphic population (Pfennig and Collins, 1993; Wakahara, 1995). Generally, the frequency of cannibalism increases as food resources decrease (Polis, 1981), as has been clearly demonstrated in amphibian larvae (Crump, 1992; Wakahara, 1995). However, the induction of the cannibalistic morph is not related to food availability (Collins and Cheek, 1983; Lannoo and Bachmann, 1984).

The benefit of an unbalanced growth strategy is clear, while individuals do not develop cannibalistic morphs without stimulus from other individuals (Hoffman and Pfennig, 1999). Factors such as pathogen infections (Pfennig *et al.*, 1991, 1998; Kiesecker and Blaustein, 1999) and the eating of relatives (Pfennig and Collins, 1993) are considered to be costs of executing cannibalism. However, cannibalistic morph individuals are less likely to be cannibalized by conspecifics and the strategy in which an individual develops as a cannibalistic morph but does not perform cannibalism is adaptive when the cost of executing cannibalism is greater than the benefits that are accrued. Therefore, the induction of typical morphs cannot be explained without regard to the cost of having a cannibalistic morph. As an example of such cost, a recent study has shown that an imbalance of body shape (greater head width) causes a change in behaviour or a decline in swimming speed, which results in increased risk of predation by natural enemies such as dragonfly larvae (Y. Kohmatsu *et al.*, in prep.). The existence of benefits and costs implies that the optimal growth strategy depends upon environmental factors such as population density or predation pressure.

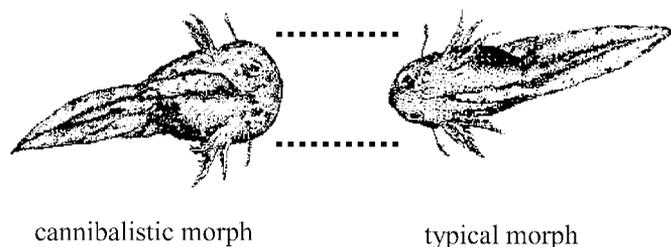Previous theoretical studies on cannibalism have focused mainly upon population



cannibalistic morph                    typical morph

**Fig. 1.** Schematic representation of amphibian larvae. Larger headed individual (cannibalistic morph) cannibalizes smaller headed individual (typical morph). Cannibalism occurs even when their body sizes are almost the same.

dynamics and the dynamics of size distribution (e.g. Cushing, 1992; Fagan and Odell, 1996; Henson, 1997). Recently, Claessen *et al.* (2000) ran an integrated simulation of population dynamics, to which size-dependent resource competition was introduced together with size-dependent cannibalism, resulting in the dynamics showing complex behaviour. However, the evolutionary dynamics of cannibalistic characters remains unexplored.

In this study, we develop theoretical models to analyse the evolution of cannibalistic morphs. Two distinct phenotypes, typical morph and cannibalistic morph, have been noted in the study of morphological characteristics in some amphibian species (Pfennig, 1989; for a review, see Crump, 1992). However, relative head width does not always show a bimodal distribution (Nishihara, 1996), which suggests that intermediate morphs exist between the typical and cannibalistic morphs. For this reason, a continuous set of strategies for body shape is adopted in the model. The model has an explicit representation of body shape growth dynamics because growth strategy (allocation of incoming energy to head width and body length at each stage of growth) plays an important role in cannibalism among amphibian larvae. We assume the growth strategy to be genetically determined and unchanging during growth (see the Discussion for empirical evidence supporting this assumption). Head width dependent cannibalism and body shape (ratio of body length and head width) dependent mortality from natural enemies are introduced to population dynamics.

The evolutionary dynamics of the growth strategy are analysed to determine whether polymorphism could be attained and whether the appearance of the cannibalistic morph depends on food availability. First, a dynamic model of the growth process including body shape is developed and the optimal growth strategy is sought. Candidates for an evolutionarily stable strategy (ESS) are derived analytically and whether they are actual ESSs is tested by computer simulation. The evolutionary dynamics in the absence of an ESS is also examined. Thereafter, an individual-based model is developed, a computer simulation demonstrating the evolutionary dynamics of the growth strategies, together with the population dynamics.

The distinct feature of this study is that two-dimensional traits are considered. When only a one-dimensional trait (size, in most studies) is considered, there is only one social relationship, larger or smaller. In the case of two-dimensional traits, two independent relationships exist, which is exactly the case with amphibian larvae – that is, wider or narrower head width (trait regarding cannibalism) and balanced or unbalanced body shape (trait regarding predation). Growth of a trait benefits growth of the other trait by increasing energy income. Thus, maximization of fitness is the problem of optimal growth trajectory in two-dimensional trait space.

## MODEL AND RESULTS

### Optimal growth model

Two types of predation, cannibalism and predation by natural enemies, are considered. Although individuals are killed if cannibalized or caught by a natural enemy in reality, an integrated model of individual and population growth is too complicated to be dealt with analytically and in the first step we assume that a decrease in mean growth rate is substituted for death. Later, an individual-based model, including the death process, is developed (see Table 1 for primary assumptions of models in this paper).

**Table 1.** Primary assumptions of three models

|  | Analytic model | Evolutionary simulation | Individual-based model |
|---|---|---|---|
| Strategy set | Continuous | $u_1, u_2, \ldots, u_{15}$ | $u_1, u_2, \ldots, u_{15}$ |
| Individual death | Replaced by reduction of growth | Replaced by reduction of growth | Directly included |
| Stochastic effect on growth | None | None | Included |
| Energy transfer from victim to cannibal | Indirect | Indirect | Direct (50%) |

For simplicity of analysis, the body shape of amphibian larvae is taken as a column defined as $\{(x, y, z) \in R^3 : x^2 + y^2 \leq r^2, 0 \leq z \leq l\}$. The cross-sectional area $s$ is regarded as head size and the length $l$ as body length. Body shape is considered to be balanced when $s = kl^2$, where $k$ is a constant, because the shape remains unchanged with growth under this relationship. The rate of growth of the volume $sl$ is determined by energy intake per unit time $E$ (we omit conversion factors for the sake of clarity):

$$\frac{\mathrm{d}}{\mathrm{d}t}(sl) = E \tag{1}$$

where $E$ is composed of three terms:

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

The first term is energy intake resulting from consumption of regular food, being proportional to the volume. The coefficient $a$ is a constant, representing food availability. The second term, $C(s, p(\hat{s}))$, is energy intake or loss following cannibalism. Each individual can eat other individuals with smaller heads but may be eaten by individuals with larger heads. Thus $C(s, p(\hat{s}))$ is a function of head size distribution in the population, $p(\hat{s})$, as well as its own head size, $s$. The third term, $B(s/l^2)$, is the cost of imbalance, representing risk of predation from natural enemies. At balanced growth, there is no cost – that is, $B(k) = 0$. Because cost increases as the magnitude of imbalance increases, we set $B(s/l^2) = (b\,(s/l^2) - k)^2$, where $b$ represents intensity of predation pressure. This term could be interpreted as cost of imbalance in terms of lowered foraging efficiency.

The growth of volume $sl$ is written as

$$\frac{\mathrm{d}}{\mathrm{d}t}(sl) = l\frac{\mathrm{d}s}{\mathrm{d}t} + s\frac{\mathrm{d}l}{\mathrm{d}t} \tag{3}$$

where the first and second terms indicate increase in head size and body length, respectively. The distribution function of the total energy to increase in head size at a given time is a growth strategy, $u(t)$:

$$l\frac{\mathrm{d}s}{\mathrm{d}t} = uE \tag{4}$$

and

$$s\frac{\mathrm{d}l}{\mathrm{d}t} = (1 - u)E \tag{5}$$

We assume that both adult survival rate and adult fecundity are proportional to body size $sl$ and that both constants of proportionality are one. Fitness $F$ is defined as their product at metamorphosis time $T$:

$$F = (s(T)l(T))^2 \tag{6}$$

Because a balanced body shape is required for metamorphosis (Y. Kohmatsu, in prep.), the terminal condition is $s(T) = kl(T)^2$. Initial values, $s(0)$ and $l(0)$, are given such that they are also balanced: $s(0) = kl(0)^2$.

## Necessary conditions for an evolutionarily stable strategy

The strategy $u^*(t)$ is defined as an ESS when any rare mutant sub-population has lower fitness in a monomorphic $u^*(t)$ population. Thus, if the growth function $u^*(t)$ is an ESS, the fitness of a mutant strategy with growth function $u(t)$ must be at a maximum at $u(t) = u^*(t)$. An optimal growth schedule $u_0(t)$ against a wild-type schedule $u^*(t)$ can be derived using Pontryagin's theory (see Appendix 1). The necessary condition for an ESS is $u_0(t) = u^*(t)$. In other words, we can analytically derive a candidate of ESSs. When we consider only two strategies, the cannibalistic interaction term of a mutant, $C(s, p(s))$, can be written as $C(s - s^*)$, a function of difference in head sizes between wild-type and mutant, which is used in ESS analysis. If an ESS exists, the growth trajectory of the ESS must satisfy

$$s = kl^2 + \frac{c}{6b}l^4 \tag{7}$$

as long as $0 < u(t) < 1$, where $c = C'(0)$, which represents the intensity of gain resulting from cannibalism when an individual interacts with other individuals of similar size. Note that the result (7) is independent of the actual form of function $C(s - s^*)$. As $s = kl^2$ represents a balanced shape, the second term represents the extra investment in a greater head size. Since the initial and terminal conditions are $s = kl^2$, evolutionarily stable growth should be as shown in Fig. 2: only $s$ increases first, then both $s$ and $l$ increase according to (7), and finally only $l$ increases (see Appendix 1 for proof). The second term says that the organism can put energy into growth of both head size and length only if its shape is already sufficiently biased towards head size. The magnitude of the bias is determined only by intensity of cannibalism, $c$, and intensity of predation pressure, $b$. As expected in (7), high $c$ leads to unbalanced growth and high $b$ leads to balanced growth. This is independent of food availability, $a$, or the balanced body shape, $k$.

## Existence of ESS and results of evolutionary simulation

Generally, an ESS or the best single strategy does not always exist. In the previous section, we showed that if a monomorphic population cannot be invaded by a rare mutant, then it must have the form of Fig. 2. But we have not shown the converse, that a Fig. 2 strategy can
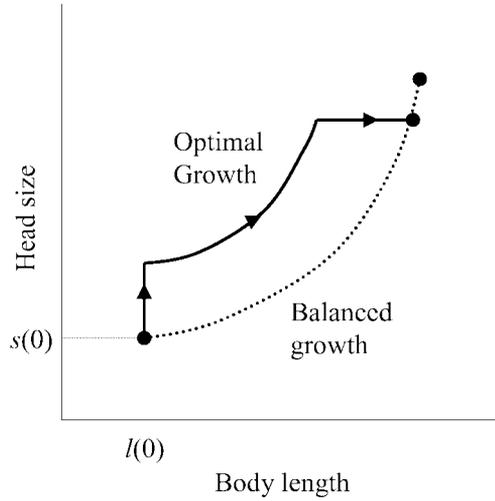
**Fig. 2.** An example of analytically derived optimal growth (solid line) and balanced growth (dotted line).

be a monomorphic ESS. Namely, we have not derived sufficient conditions for the existence of an ESS. In this section, evolutionary simulation is performed to explore the question.

In the simulation, each growth strategy is assumed to be genetically fixed. Fifteen strategies $\{u_1(t), u_2(t), \ldots, u_{15}(t)\}$ are chosen from candidates of ESSs, corresponding to different values of $C'(0)$ (see Fig. 3), and introduced into the simulation. Thus, energy intake and growth of an individual with genotype $i$ are given as:

$$\begin{cases} E_i = as_il_i + C - b\left(\dfrac{s_i}{l_i^2} - k\right)^2 \\[2mm] \dfrac{\dot{s}_i}{s_i} = u_i\dfrac{E}{l_is_i} \\[2mm] \dfrac{\dot{l}_i}{l_i} = (1 - u_i)\dfrac{E}{l_is_i} \end{cases} \tag{8}$$

where the interaction term, $C$, is given as

$$C = \delta\sum_{j=1}^{15} p_j\,\theta(s_i - s_j) \tag{9}$$

with

$$\theta(x) \equiv \eta\left(\frac{2}{1 + \exp\left(\dfrac{-2\gamma x}{\eta}\right)} - 1\right) \tag{10}$$

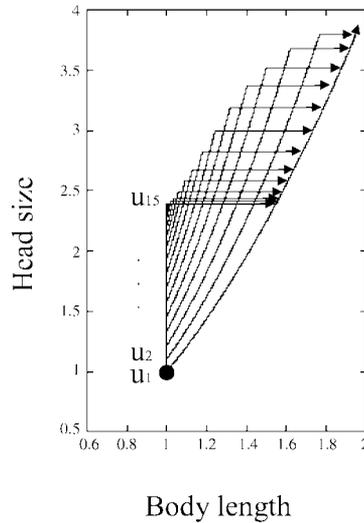$$(-\eta < \theta(x) < \eta,\ \theta(0) = 0,\ \theta'(0) = \gamma)$$

**Fig. 3.** Candidates for evolutionarily stable strategies. The growth trajectory of an individual with strategy $u_i(t)$ when the population is monomorphic is shown. Note that actual realization of the trajectory is varied due to interactions among strategies. $u_1(t)$ corresponds to balanced growth and $u_{15}(t)$ to the most extreme case of unbalanced growth. $u_i(t)$ is an analytically derived candidate of an evolutionarily stable strategy when $\Gamma = 0.0, 0.6, 1.3, 2.0, 2.8, 3.5, 4.2, 5.0, 5.6, 6.2, 6.8, 7.3, 7.7, 8.0, 8.3$, respectively.

where $p_i$ is the frequency of genotype $i$. For positive $x$, $\theta(x)$ represents the benefit per encounter in which the opponent's head size is smaller by $x$. For negative $x$, $\theta(x)$ is negative, which represents cost per encounter in which the opponent's head size is larger by $|x|$. The parameter $\delta$ represents the encounter rate, $\eta$ is the maximum benefit/cost per interaction and $\gamma$ represents benefit/cost per encounter when the head size difference is very small. Here $\gamma\delta$ corresponds to $C'(0)$, as shown in Appendix 1, and thus $\gamma\delta$ is an important parameter. By defining $\Omega \equiv \delta\eta$ and $\Gamma \equiv \gamma\delta$, the equation for $C$ is rewritten as

$$C(s_i) = \Omega \sum_{j=1}^{15} p_j \left[ \frac{2}{1 + \exp\left\{ -2\frac{\Gamma}{\Omega}(s_i - s_j) \right\}} \right] \tag{11}$$

The initial genotype distribution is taken to be uniform. The dynamics of genotype frequency is determined by the following rule (roulette selection). Genotype $i$ is chosen with probability

$$\frac{p_i f_i}{\sum_j p_j f_j}$$

where $f_i$ is fitness of genotype $i$:

$$f_i = (s_i(T)l_i(T))^2$$

Selection is continued until the population of the next generation reaches $N$, so that the population size is always $N$. Smaller $N$ represents greater genetic drift. For the computer simulation, $N$ is set at 1000 and random mutations are introduced. At the beginning of each generation, each individual's genotype mutates into a genotype randomly chosen from $\{u_1(t), u_2(t), \ldots, u_{15}(t)\}$ at probability $\varepsilon$ per individual per generation; $\varepsilon$ is set to $10^{-5}$ in the simulation.

The results are summarized in Table 2, each strategy of average frequency greater than 10% being indicated. As a result of the simulation, when one strategy dominates, it is an analytically derived ESS candidate (equation 7) in most cases (Table 2). One example of the evolutionary dynamics for this case is shown in Fig. 4a. However, the simulation revealed that an analytically derived ESS candidate does not always dominate. In such cases, the strategy frequency distribution averaged over generations exhibited polymorphism. In particular, in most cases, the dynamics of strategy frequency is not stable, changing cyclically (Fig. 4b). This strategy distribution is unimodal at each instant in time. Such cyclic evolution is observed when $\Gamma$ is large and $\Omega$ is small (upper right in Table 2). In such cases, the magnitude of imbalance is determined mainly by $\Omega$. As $\Omega$ becomes larger, selected strategies become more unbalanced.

Why is cyclic evolution found in such a parameter space? A balanced growth strategy benefits from a low risk of predation but suffers from cannibalization. Conversely, an unbalanced growth strategy benefits from cannibalization but suffers from a high risk of predation. An ESS candidate (equation 7) is at equilibrium where an increase in benefit from cannibalization matches an increase in cost from predation. However, the most balanced strategy (strategy 1) might invade the ESS candidate if the benefit from a low risk of predation overcomes the cost of being cannibalized by the latter. The magnitude of imbalance of an ESS candidate is determined by $\Gamma$. When $\Gamma$ is larger, an ESS candidate is more unbalanced and suffers from a higher risk of predation. The maximum of benefit/cost from cannibalization is represented by $\Omega$. When $\Omega$ is smaller, strategy 1 suffers less from cannibalization. Therefore, when $\Gamma$ is large and $\Omega$ is small, an ESS candidate is not the actual ESS because it is invaded by strategy 1. When strategy 1 invades and becomes dominant, strategy 2 has greater fitness as it can cannibalize strategy 1 without much difference in intensity of predation. Following the invasion of strategy 2, which becomes dominant, strategy 3 does likewise, and so on. The displacement of the dominating strategy continues until strategy 1 invades again.

## INDIVIDUAL-BASED MODEL

In the previous model, death is replaced by a decrease in mean growth rate, which is an artificial assumption. An individual-based model that deals directly with mortality due to cannibalism and predation is developed. When cannibalism occurs, a victim is killed and its fitness becomes zero. Consequently, the cannibal grows very quickly. The more the latter succeeds in cannibalism, the easier the next act of cannibalism becomes. It has been observed that individuals that have cannibalized are much larger among larvae that are collected from the same population and hatched at the same time (Wakahara, 1995; Kohmatsu *et al.*, 2001). Such a phenomenon cannot be represented without developing an individual-based model. The evolutionary simulation of an individual-based model is performed (for details, see Appendix 2).

Both a monomorphic solution and a cyclic solution are found (Fig. 5). The cyclic solution

**Table 2.** Results of evolutionary simulation under some parameter sets $(\Gamma, \Omega)$

| | Corresponding strategy $\Gamma$ | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 10 |
| $\Omega$ | **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** | **10** |
| **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 | 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 | 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 | 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 | 9,10,11,12 | 8,9,10,11,12,13 |
| **1.0** | 1+ | 2+ | 3+ | 4+ | 5+ | 6+ | 7+ | 8+ | 9+ | 10+ | 11+ | 12,13 | 13 | 13,15 | 15 | 15+ |

Note that $\Omega = \delta\eta$ and $\Gamma = \delta\gamma$, where $\delta$ represents population density or encounter rate, $\eta$ is maximum benefit/cost per encounter when head size difference is very small. Each ESS candidate is determined only by the value of $\Gamma$. Corresponding strategy types $(1, 2, 3, \ldots, 15)$ are shown above each $\Gamma$ value. Average frequencies of strategies between 1000th and 10,000th generation are calculated for each parameter set $(\Gamma, \Omega)$. All strategies of average frequency greater than 10% are indicated; $i+$ indicates average frequency of strategy $i$ greater than 90%.
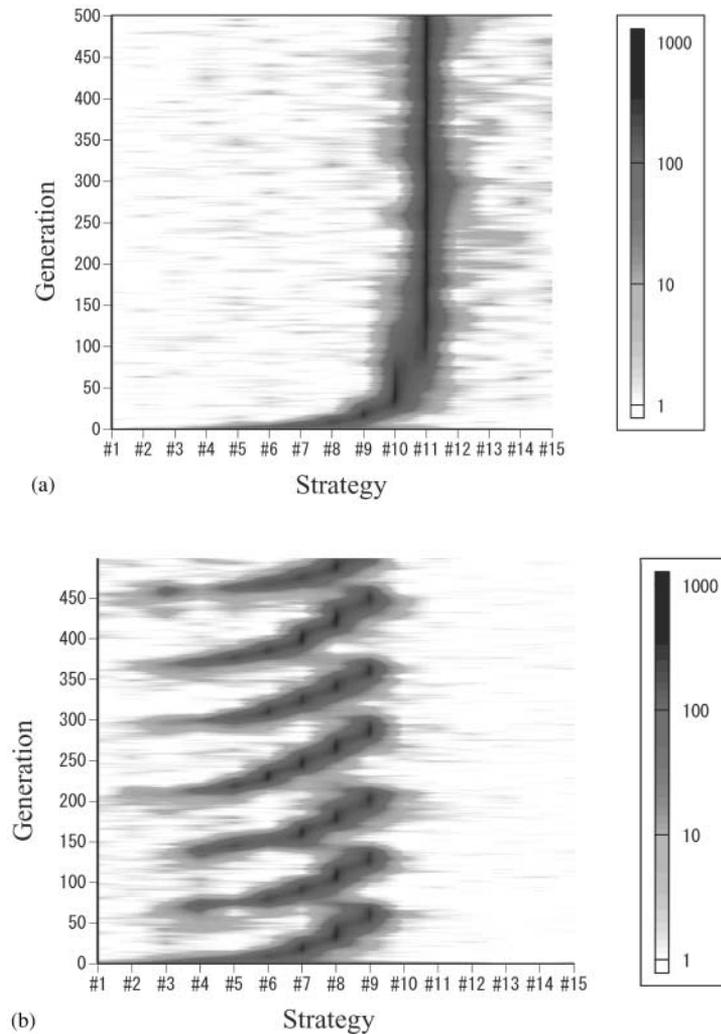
**Fig. 4.** Examples of the results of evolutionary simulation. The higher strategy frequency is represented by the darker grey. Although the original data contain time-series of frequencies of only 15 strategies, continual visualization over the strategy axis is applied to make it easier to grasp the dynamics. $\Gamma = 6.8$, which corresponds to strategy 11 ($u_{11}$). (a) When $\Omega = 1.0$, strategy 11 dominates. (b) When $\Omega = 0.6$, the dominating strategy gradually changes from strategy 4 to strategy 9, then suddenly reverts to strategy 4. The time period for the cycle is constant.

is qualitatively similar to the one in the previous model, but the period of the evolutionary cycle is not constant. The other types of dynamics (such as chaos, etc.) are not found. The result implies that the behaviour of an individual-based model is essentially the same as that of the previous model. The total fitness of the population at the cessation of larval growth (time *T*), determined by the number of surviving individuals and average body size at metamorphosis, are also surveyed (Fig. 6). The total fitness varies depending on the
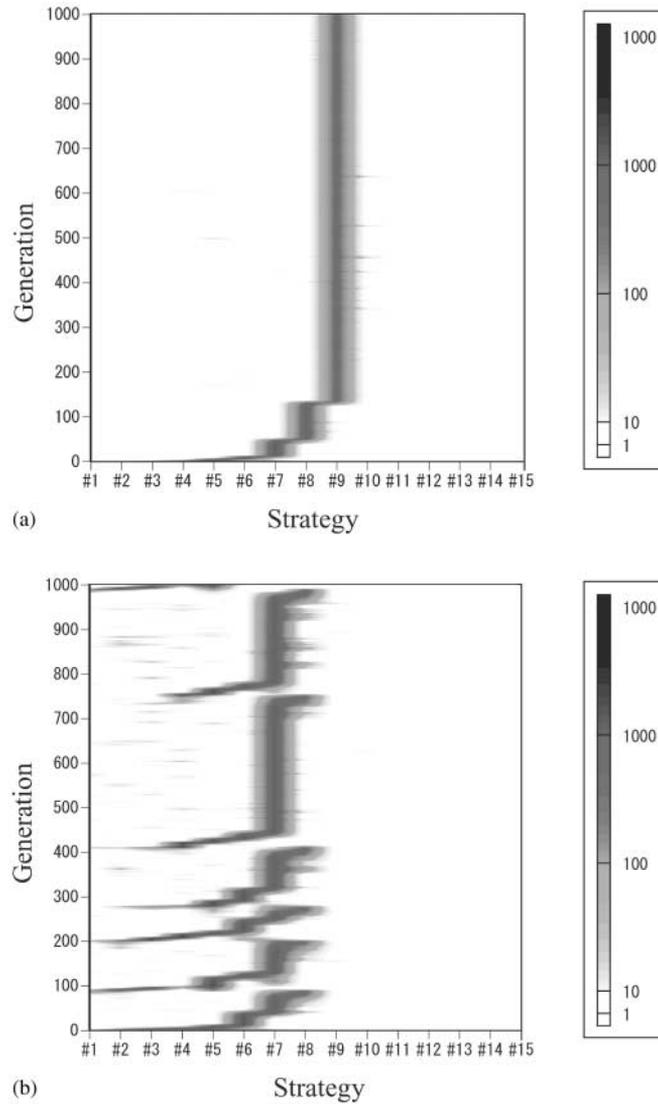
**Fig. 5.** Examples of the results of individual-based simulations, with $\gamma = 1000$ and $\rho = 1$. (a) $\delta = 5000$, strategy 9 dominant. (b) $\delta = 200$, irregular cycle of dominating strategy. The amplitude and time period for the cycle are not constant.

position, or phase, of the evolutionary cycle. In the phase where more balanced growth strategies dominate, the total fitness is high.

## DISCUSSION

As represented by equation (7), analytically derived optimal growth is more unbalanced when the intensity of cannibalism ($c$) is high or the intensity of predation pressure ($b$) is low,
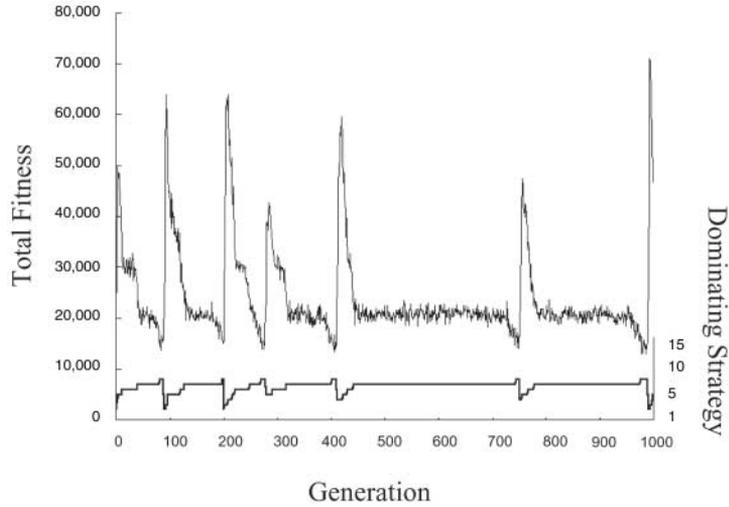
**Fig. 6.** Dynamics of total fitness at metamorphosis (thin line) and dominating strategy (thick line), with $\delta = 200$, $\gamma = 1000$, $\rho = 1$. Total fitness is greater when the number of the dominating strategy is smaller (more balanced).

while it is independent of food availability. When food availability is low, the relative importance of cannibalism is greater. The frequency of cannibalism actually increases in such circumstances (Crump, 1992; Wakahara, 1995). However, some empirical studies have shown that the appearance of cannibalistic morphs is independent of food availability (Collins and Cheek, 1983; Lannoo and Bachmann, 1984), which is consistent with the present results that optimal growth is independent of food availability.

As a result of simulation, unbalanced strategies dominate when $\Gamma$ or $\Omega$ is increased (see Table 2). Note that $\Omega \equiv \delta\eta$ (product of population density and maximum benefit/cost per interaction) and $\Gamma \equiv \delta\gamma$ (product of population density and benefit/cost per interaction with very small head size difference). The value of $\gamma$ could be measured by the reciprocal of the minimum difference in head size for cannibalism to occur. Thus, the prediction can be made that amphibian larvae acquire an unbalanced shape when maximum benefit/cost per interaction is large, population density is high or the difference in head size necessary for cannibalism is small. The relationship between induction of a cannibalistic morph and population density has been reported in several studies (Pfennig and Collins, 1993; Wakahara, 1995; Nishihara, 1996; Hoffman and Pfennig, 1999), while the effect of the other two factors should be studied in the future.

Convergence to an ESS candidate occurs with small $\Gamma$ and large $\Omega$, although we performed no analysis for convergence stability (Christiansen, 1991). The result suggests that an ESS candidate has convergence stability as well as evolutionary stability in corresponding parameter regions. Moreover, in the case of cyclic evolution, we cannot exclude the possibility that an ESS candidate is actually an ESS but not convergently stable. Due to limitation of numerical calculation, we cannot rule out the possibility of a stable polymorphism with just the right mix of strategies.

Cyclic evolution occurs with large $\Gamma$ and small $\Omega$. Whether evolutionary dynamics is cyclic or convergent is determined for the most part by $\Gamma/\Omega$, as seen from Table 2. Since $\Gamma/\Omega$

is equivalent to $\gamma/\eta$, the reciprocal of the ratio of head size difference necessary for cannibalism to maximum benefit/cost per interaction plays a very important role in the evolutionary time-scale dynamics of the system.

This cyclic evolution could be considered as one realization of Van Valen's (1973) Red Queen hypothesis. As we dealt with the actual biological phenomenon, the model is rather complicated and mathematically sophisticated analysis of interesting characters such as a period of cycle is almost impossible. However, using a more abstract model to derive analytical results (e.g. Dieckmann *et al.*, 1995) is another powerful tool. Evolution of traits related to cannibalism has received little attention and thus we expect various interesting behaviours of this system to be discovered in the future.

Differences in the frequencies of cannibalistic morphs among populations have been widely observed (Pfennig, 1990; Nishihara, 1996), the possible main cause being differences in environmental factors such as population density or predator density. In the present model, when population density is higher, the optimal growth becomes more unbalanced, which has been observed previously (Nishihara, 1996; Hoffman and Pfennig, 1999). The model predicts that a decrease in predator density also unbalances the optimal growth. This remains to be confirmed by field and experimental studies. Cannibalistic polymorphism among populations might also be explained by phase differences during cyclic evolution. Cyclic evolution predicts that completely different strategies may be observed between populations under similar environmental conditions. The time period for an evolutionary cycle is dozens of generations, even though a high mutation rate is set in computer simulations. Consequently, direct verification of this hypothesis for amphibian larvae is extremely difficult. If a large difference in the frequency of cannibalistic morphs among populations under similar environmental conditions is observed, it may be indirect evidence in support of the hypothesis.

The cost of having a cannibalistic morph is also introduced to the model. The cost of executing cannibalism is not the same as the cost of having a cannibalistic morph. For example, when all individuals in a population have cannibalistic morphs, cannibalism does not occur. In such a case, the cost of having a cannibalistic morph is applicable, whereas the cost of executing cannibalism is not. However, when polymorphism occurs, the cannibalistic morph has a greater probability of eating conspecifics. Thus, the cost of executing cannibalism might affect the former more strongly. An apparent cost of executing cannibalism is vulnerability to predators during handling time of eating conspecifics. When a cannibal has a victim that has a similar body size to itself, it might be easily caught by a natural enemy. Eating relatives is another cost of executing cannibalism, although some kin-recognition ability has been reported in amphibian larvae (Pfennig and Collins, 1993). An increase in mortality due to pathogen infection has also been suggested as a cost of executing cannibalism (Pfennig *et al.*, 1991, 1998; Sadler and Elgar, 1994; Kiesecker and Blaustein, 1999). The introduction of such costs into the present model appears to be a necessary next step.

Some studies have shown that growth patterns are environmentally controlled, which is known as phenotypic plasticity (Collins and Cheek, 1983; Pfennig and Collins, 1993), although another study has demonstrated differences in allozyme frequency between cannibalistic and non-cannibalistic morphs (Pierce *et al.*, 1981). The factors responsible for the induction of a cannibalistic morph are not clear (Crump, 1992). The assumption that growth strategies are genetically fixed in evolutionary simulation does not necessarily hold, since plasticity is known in amphibian larvae. Although an analysis based on plasticity was

not undertaken here, a likely result might be as follows. If an ESS exists, all individuals with plasticity will choose it. If an ESS does not exist (cyclic evolution), their strategy choice will be polymorphic, for the following reason. Assume all individuals take the same strategy *X*. As strategy *X* is not an ESS, there exists strategy *Y*, which increases fitness. Accordingly, some individuals will choose strategy *Y*. This leads to polymorphism. The present study suggests that polymorphism can be expected, even if the growth strategy choice is affected by plasticity.

## ACKNOWLEDGEMENTS

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## APPENDIX 1

If a growth function $u^*(t)$ is an ESS, the fitness of a mutant strategy with growth function $u(t)$ must be at a maximum at $u(t) = u^*(t)$, when the wild-type grows as $(s^*, l^*)$ with growth function $u^*(t)$. As a mutant is very rare, it interacts with only wild-type individuals. The interaction term for a mutant $C(s)$ is a function of $s$ and $s^*$, and we assume $C(s)$ is a function of $s - s^*$. Defining new variables $G \equiv E/ls$, $x \equiv \ln s$ and $y \equiv \ln l$, equations (2), (4) and (5) in the text are rewritten as

$$G = a + \frac{1}{sl}\left\{ C(s - s^*) - B\left(\frac{s}{l^2}\right)\right\} \tag{A1}$$

$$\dot{x} = uG \tag{A2}$$

$$\dot{y} = (1 - u)G \tag{A3}$$

and the terminal condition $s = kl^2$ as

$$x = \ln k \cdot 2y \tag{A4}$$

Maximization of $(sl)^2$ is equivalent to maximization of $x + y$. Hamiltonian and adjoint variables in this system are written as

$$H = \lambda_x uG + \lambda_y (1 - u)G \tag{A5}$$

$$\begin{cases} -\lambda_x = \partial_x H = s\partial_s H \\ -\lambda_y = \partial_y H = l\partial_l H \end{cases} \tag{A6}$$

We rewrite adjoint equations as

$$\begin{cases} -\lambda_x = \{\lambda_x u + \lambda_y(1-u)\} s \partial_s G \\ -\lambda_y = \{\lambda_x u + \lambda_y(1-u)\} l \partial_l G \end{cases} \tag{A7}$$

or

$$\begin{cases} \dot{\lambda}_x = -\{\lambda_x u + \lambda_y(1-u)\} s\left[-\dfrac{1}{ls^2}(C-B) + \dfrac{1}{ls}\left\{C'(s-s^*) - \dfrac{1}{l^2}B'\left(\dfrac{s}{l^2}\right)\right\}\right] \\[4mm] \dot{\lambda}_y = -\{\lambda_x u + \lambda_y(1-u)\} l\left[-\dfrac{1}{sl^2}(C-B) + \dfrac{1}{ls}\left\{\dfrac{2}{l^3}sB'\left(\dfrac{s}{l^2}\right)\right\}\right] \end{cases} \tag{A8}$$

An optimal control variable $u$ is chosen so that Hamiltonian $H$ is maximized. If optimal $u$ is neither 0 nor 1 for a given time period, $\lambda_x = \lambda_y$ must hold and thus $\dot{\lambda}_x = \dot{\lambda}_y$ holds:

$$\frac{1}{l}\left\{C'(s-s^*) - \frac{1}{l^2}B'\left(\frac{s}{l^2}\right)\right\} = \frac{2}{l^3}B'\left(\frac{s}{l^2}\right) \tag{A9}$$

or

$$l^2 C'(s-s^*) - 3B'\left(\frac{s}{l^2}\right) \tag{A10}$$

The above equation represents the optimal growth trajectory for a mutant when a wild type grows as $(s^*, l^*)$. If $u^*$ is an evolutionarily stable strategy, $u = u^*$, $s = s^*$ and $l = l^*$ must hold. Therefore,

$$l^2 C'(0) = 3B'\left(\frac{s}{l^2}\right) \tag{A11}$$

Note that this is a necessary condition. Also note that this equation depends on only $C'(0)$, the actual form of $C(x)$ being independent of this condition. Defining $B(x) = b(x-k)^2$ and $c = C'(0)$ results in the trajectory of optimal growth being

$$s = kl^2 + \frac{c}{6b}l^4 \tag{A12}$$

Applying (A12) to equations (4) and (5) in the text, $u(t)$ is given as a function of $l(t)$

$$u = \frac{2k + 4\beta l^2}{2k + 1 + 5\beta l^2} \tag{A13}$$

where

$$\beta \equiv \frac{c}{6b} \tag{A14}$$

The interaction term $C(s)$ is zero when all individuals in the population take the same strategy. Therefore,

$$\frac{E}{s} = al - \frac{1}{s}b\left(\frac{s}{l^2} - k\right)^2 \tag{A15}$$

Inserting $s = kl^2 + \beta l^4$ into (A15) and equation (5) in the text, we finally obtain (after some calculation)

$$\frac{dl}{dt} = \frac{1 + \beta l^3}{2k + 1 + 5\beta l^2}\left(a - \frac{b\beta^2 l}{k + \beta l^2}\right)l \tag{A16}$$

It is difficult to solve this equation and explicit solutions of $s(t)$, $l(t)$ and $u(t)$ cannot be derived. Accordingly, in computer simulations, numerically calculated values of $u(t)$ are used.

A growth trajectory of an ESS is derived where $0 < u(t) < 1$. The optimal trajectory consists of the curve derived above, line segments where $u(t) = 0$ and line segments where $u(t) = 1$. We here prove that optimal growth is as shown in Fig. 2. The case $c \equiv C'(0) > 0$ is considered owing to greater head sizes benefiting more from cannibalism. Two variables are defined:

$$\phi \equiv \lambda_x - \lambda_y$$

$$\varphi \equiv \frac{d\phi}{dt}$$

$$= 6b\left(\frac{s}{l^2} - k\right) - l^2 c$$

Note that $\varphi$ is a function only of $s$ and $l$. Optimal control $u$ is chosen so that $u(t) = 0$ where $\phi(t) < 0$ and $u(t) = 1$ where $\phi(t) > 0$. The body shape space $(l, s)$ is divided according to the sign of $\varphi$; the positive $\varphi$ space, zero $\varphi$ curve and negative $\varphi$ space (Fig. A1). Both the starting and finishing points are in the negative $\varphi$ space. As $\lambda_x$ and $\lambda_y$ are continuous functions, $\phi = 0$ must hold where the value of $u$ changes. If $u$ changes from 0 to 1, $\phi$ changes from negative to positive and then $d\phi/dt = \varphi > 0$. Therefore, $u$ does not change from 0 to 1 in negative $\varphi$ space. By the same consideration, $u$ does not
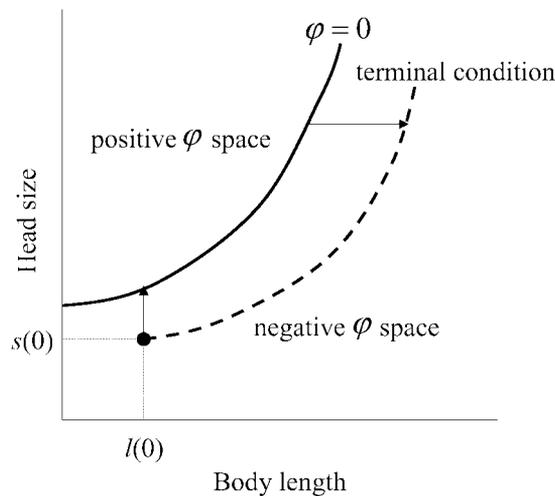


**Fig. A1.** Body shape space is divided into three parts; positive $\varphi$ space, zero $\varphi$ curve and negative $\varphi$ space. Optimal growth is proven as in Fig. 2b using this figure and Appendix 1.

change from 1 to 0 in positive φ space. The trajectory, which meets the above conditions, is restricted to that shown in Fig. 2, where only *s* increases at first ($u = 0$), then both *s* and *l* increase ($0 < u < 1$) and, finally, only *l* increases ($u = 0$).

## APPENDIX 2

Details of the individual-based model are as follows. At the beginning of growth and population dynamics, *N* individuals are alive. Each individual has its own strategy *u*, head size *s*, body length *l* and alive/dead flag *f*. Energy intake of each individual consists of the regular food consumption term only, which is proportional to the volume. The effect of cannibalism and predation by a natural enemy is dealt with in the following way. Two randomly chosen individuals encounter one another at a constant probability per unit time δ. When one of the chosen individuals is dead, the model proceeds to the next encounter – that is, the actual encounter rate is dependent upon population density (the number of alive individuals). At each encounter, the probability that the larger headed individual eats the smaller headed individual is

$$c(x) = \frac{2}{1 + \exp(-2\gamma x)} - 1$$
$$(0 \leq x, 0 \leq c(x) < 1)$$
$$x = |s_1 - s_2|$$

With large γ, only a slight difference in head size is sufficient for cannibalism to occur. When cannibalism occurs, the victim is marked as 'dead' and 50% of the volume of the victim is immediately added to the cannibal's energy intake. The probability that predation by a natural enemy occurs per unit time per each individual is

$$p = \left(\frac{s}{l^2} - 1\right)^2 \cdot \rho$$

where ρ is a constant representing predator density. This probability corresponds to *B* in the previous model. The individual that becomes the prey is also marked as 'dead'; the population, therefore, decreases monotonously with time. At the end of growth and population dynamics, the fitness of each individual is calculated (volume squared). Averaging fitness of individuals adopting the same strategy produces the fitness of each strategy.

The strategy set consists of 15 strategies ($u_1, u_2, \ldots, u_{15}$). Initial genotype distribution is taken as uniform. The dynamics of genotype frequency is determined by the roulette selection rule with population size $N = 1000$ in the same way as the previous simulation. The random mutation rate ε is set at $10^{-5}$. See text for details of the roulette selection and the mutation.