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Drastic growth effect may explain sympatric cannibalistic polymorphism

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Abstract

Cannibalistic polyphenism is observed in many fishes and amphibians. In the case of amphibian larvae, cannibal morph and typical morph coexist. Benefits and costs of the cannibal morph have been studied empirically but the mechanism of the maintenance of polymorphism is not well known. Here, we construct a game model of typical and cannibal morph strategies to obtain the condition of stable coexistence. Generally, once an individual succeeds in cannibalism, it grows very quickly, which facilitates the next cannibalism. In a model without this 'drastic growth effect', stable coexistence cannot occur. To represent drastic growth effect, it is assumed that cannibal/typical morph stage is followed by giant/normal stage. A cannibal morph that performs cannibalism in the first stage can become a 'giant' in the next stage. This model allows stable coexistence of cannibal and typical morphs. The condition for coexistence is that payoff of a giant is two times larger than normal individuals. As long as direct consumption of victim's body is considered as reward for successful cannibalism, coexistence cannot be explained. When the reward is considered as social standing of being outstanding size in a population, sympatric cannibalistic polymorphism is possible, without regard to the initial size variation or resource shortage.
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1. Introduction

Intra-specific predation, or cannibalism, is a commonly observed ecological interaction in many animal taxa (for review, Polis, 1981). Cannibalistic polyphenism is known in many fishes and amphibians (Polis, 1981; Crump, 1992). Cannibalistic polyphenism consists of two cases. First, all members of the population are potentially cannibal, although small differences in success of cannibalism ultimately result in an explicit polymorphism, for example, in body size. Second, cannibalistic and typical individuals coexist as alternative strategies or tactics with different morphology. There are few experimental studies which clearly distinguish the two cases. If only size variation is observed, it might be the result of cannibalism, i.e. the former case. On the other hand, cannibal morph, which

is characterized by a greater head width (and thus larger mouth) relative to body length, is known in *Ambystoma* salamanders (Rose and Armentrout, 1976), *Hynobius* salamanders (Wakahara, 1995) and *Scaphiopus* toads (Pfennig, 1990). As cannibalism is gape-limited, cannibal morph has an advantage in performing and avoiding cannibalism. The cannibal morph appears in *Hynobius* salamanders in very early developmental stage when they do not perform cannibalism (Nishihara-Takahashi, 1999). In addition, cannibal morph usually has specialized oral structures (Crump, 1992). These facts suggest that cannibalistic polymorphism in amphibian is of the second kind. Such kind of cannibalistic polymorphism may exist in other species in which individual with the disproportionately large organ related to cannibalism is observed.

It is known that cannibal morphology is a plastic phenotypic response to environmental conditions (Nishihara, 1996; Hoffman and Pfennig, 1999; Nishihara-Takahashi, 1999; Kohmatsu et al., 2001). These studies might imply that tactics (cannibal or typical) are different phenotypes of a single genotype. On the other

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hand, there is a study demonstrating differences in allozyme frequency between cannibal and non-cannibal morphs (Pierce et al., 1981). The study implies that each morph has a corresponding genotype (or genotypes). These empirical studies suggest two opposite hypotheses and the reality probably lies in between.

In the present study, we study the case in which each tactic results from each strategy and the condition for the stable coexistence of two pure strategies is mathematically analysed. Evolution of cannibalistic polymorphism is discussed later. The model might be applied to the different situation where a single mixed strategy dominates the population. This point will also be discussed later.

In this paper, we study the simple case with only two strategies, typical and cannibal morphs. For example, *Ambystoma* salamanders meet the condition (Pfennig, 1989). Generalized "cannibal morph" is defined as a strategy which specializes in cannibalism and enjoys larger probability of cannibalism and smaller probability of being cannibalized but suffers larger natural mortality.

Even when population density is very high, many individuals retain the typical morph features, resulting in a polymorphic population (Pfennig and Collins, 1993; Wakahara, 1995). To understand the phenomenon, the previous studies focused on the cost of cannibalism (Pfennig et al., 1998; Pfennig, 2000; Kohmatsu et al., 2001). Eating relatives (Pfennig and Collins, 1993; Wakahara, 1995) and pathogen infection (Pfennig et al., 1991, 1998) are considered as such cost. These studies have answered the question why all individuals do not always develop cannibal morph. As cost and benefit of cannibal morph depend on the environment, cannibal morph is not always adaptive. The next question is how two morphs can coexist under the same environmental conditions. In order to establish stable coexistence, frequency dependence of the payoff must satisfy certain criteria such as in a Hawk–Dove game (Maynard-Smith, 1982). Some studies (Pfennig, 1992; Maret and Collins, 1997) explained cannibalistic polymorphism based on the experiments, suggesting that the resources for each morph are limited and independent, i.e. cannibal morphs are escapee from intense competition among typical morphs. However, cannibalism has very strong and complex impact on population and thus cannibalistic polymorphism might be explained without regard to resource shortage. The present study explores such possibility.

Most previous theoretical studies on cannibalism have focused upon sized-population dynamics (Van den Bosch et al., 1988; Henson, 1997; Cushing, 1992; Fagan and Odell, 1996; Claessen et al., 2000; Wakano et al., 2002). In these studies, the occurrence of cannibalism is not caused by the difference of strategies but size dependent. There are few theoretical studies where

alternative strategies regarding cannibalism are defined and the condition for the polymorphism is obtained (but see, Dercole and Rinaldi, 2002).

Here, we propose a simple game model to explain the mechanism of the maintenance of sympatric cannibalistic polymorphism. First, the simplest game model of typical and cannibal morph strategies is analysed. The model appears unable to account for coexistence. The reason why coexistence is not reproduced can be explained in a general way (independent of the function form). "Drastic growth effect of cannibalism" is introduced as a possible mechanism of coexistence. The extended model is proposed and the mathematical analysis shows that it can reproduce stable coexistence. Further analysis and numerical calculation confirms that the result remains qualitatively the same when assumptions of analysis are relaxed.

2. Models and results

2.1. The simplest model

The strategies in the game are cannibal morph and typical morph, which are fixed from birth. For simplicity, all individuals start growing at the same time with the same size. The initial population is defined as one without loss of generality. Let p and $1 - p$ be the initial frequency of cannibal morph and typical morph, respectively. For simplicity, we assume that there is only one opportunity for cannibalism, which occurs at the end of the growth period and that at every encounter cannibal morph preys on typical morph. The frequency of encounters between cannibal and typical morphs is

$$\Gamma = \min \left[\gamma p(1 - p), 1 - p \right]$$
$$= \begin{cases} \gamma p(1 - p) & (\gamma p < 1), \\ 1 - p & (\gamma p \geqslant 1), \end{cases} \tag{1}$$

where γ represents population density. Minimum function is required to represent the situation in which all typical morphs are cannibalized. Γ typical morphs out of $1 - p$ become victims of cannibalism. Energy gain of typical morph consists of only regular food consumption, denoted by A. As described above, in order to exclude the effect of resource shortage, regular food consumption is assumed to be constant. Energy gain of cannibal morph is

$$kA \frac{\Gamma}{p} + B. \tag{2}$$

The first term is energy gain from cannibalism. kA corresponds to energy transfer per victim, which is proportional to the energy gain of typical morph. $0 < k < 1$ is a conversion factor. $\frac{\Gamma}{p}$ represents the average frequency of victims per cannibal morph. The second

term B comes from regular food consumption. Payoff of each strategy is defined as the product of the energy gain during growth and the survival rate:

$$F_T = A\frac{1-p-\Gamma}{1-p}$$
$$= \begin{cases} A - A\gamma p & (\gamma p < 1), \\ 0 & (\gamma p \geqslant 1), \end{cases} \quad (3a)$$

$$F_C = \left(kA\frac{\Gamma}{p} + B\right)m$$
$$= \begin{cases} mkA\gamma + mB - mkA\gamma p & (\gamma p < 1), \\ mB + mkA\dfrac{1-p}{p} & (\gamma p \geqslant 1). \end{cases} \quad (3b)$$

The model is summarized in Table 1. Survival rate of typical morph in the absence of cannibalism is assumed to be one without loss of generality. Survival rate of cannibal morph is denoted by $m < 1$, representing cost of cannibal morph strategy.

Hereafter, we consider the payoff as the fitness of each strategy. For simplicity, we assume no generation overlap. Then, the frequency of cannibal morph strategy in the next generation, p', is written as

$$p' = \frac{pF_C}{pF_C + (1-p)F_T} \quad (4)$$

and the evolutionary dynamics of two strategies can be analysed. Both F_T and F_C are monotone decreasing linear functions of the frequency p when $\gamma p < 1$. If the inclination of F_C is steeper, $F_T - F_C$ is decreasing function of p, which means stable coexistence. However, as $0 < m < 1$ and $0 < k < 1$, $A\gamma > mkA\gamma$ always holds and thus the relationship will be as illustrated in Fig. 1. For arbitrary parameter values A, B, γ, m, k, there are only three possibilities: (1) typical morph is always successful ($m < (A - A\gamma)/B$), (2) cannibal morph is always successful ($m > A/(kA\gamma + B)$) and (3) bistable (otherwise). In other words, if rare cannibal morphs are more successful than resident typical morphs, cannibal morphs are always successful regardless of frequency. Thus, the stable coexistence of two pure strategies is not expected. This model cannot explain cannibalistic polymorphism as a stable equilibrium of the game.

Table 1
Energy income and survival rate of each strategy when $\gamma p < 1$

	Energy income	Survival rate
Cannibal morph	$kA\dfrac{\Gamma}{p} + B$	m
Typical morph	A	$\dfrac{1-p-\Gamma}{1-p}$

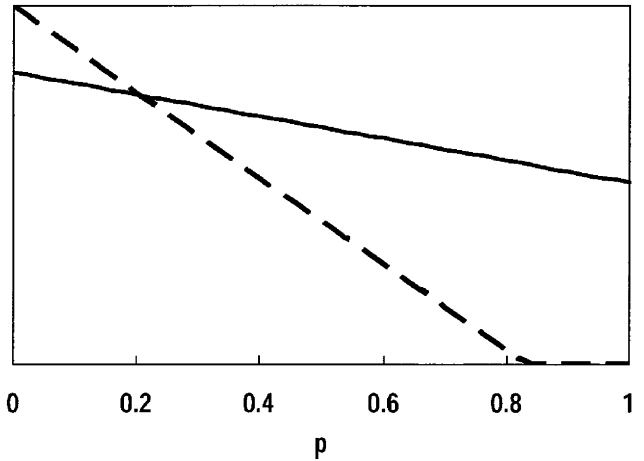Payoff is measured by a product of them.

Fig. 1. Payoff of cannibal morph (solid line) and typical morph (dashed line) drawn against cannibal morph frequency. A bistable case is shown. The position or existence of the intersection may vary, but the latter is always steeper.

2.2. Where does the difficulty come from?

The difficulty comes from the difference in sensitivity to frequency, i.e. the coefficient of p in the payoff function. Regardless of the details of the model, both payoffs are decreasing function of p. For F_T, increase in cannibal morph means increase in frequency of being cannibalized, resulting in decrease in survival rate of typical morph. For F_C, the frequency of potential victims per cannibal morph is proportional to $1 - p$, i.e. decreasing function of p. The other factors, such as regular food consumption, energy transfer rate, additional mortality of cannibal morph, etc., are independent of frequency of cannibal morph.

In this simplest model, the sensitivity to frequency is always larger for the typical morph. The reason is as follows. Frequency-dependent term in the payoff function is determined by the frequency of cannibalistic interactions. At each cannibalistic interaction, a typical morph is killed; however, not all energy lost by typical morph population is transferred to cannibal morph population. This is due to conversion factor $k < 1$ and additional mortality $1 - m > 0$. Therefore, payoff of cannibal morph is always less sensitive to cannibalistic interaction. In conclusion, as long as the payoff of each strategy is measured by total energy income, stable coexistence cannot occur. Although the model is very simple, it grasps the essence. Generally, as long as only energy balance is considered, at each cannibalism, the amount of energy lost by typical morph population is always larger than that transferred to cannibal morph population. It is because energy conversion factor can never exceed one, regardless of formulation. Therefore, in order to explain the coexistence, the biologically reasonable mechanism should be studied in which the sensitivity of cannibal morph strategy becomes larger.

2.3. Drastic growth effect of cannibalism

Most cannibalistic amphibian populations consist of many normal-sized individuals and a few very large-sized individuals, or giants (Pfennig and Collins, 1993; Wakahara, 1995). Giants are also observed in fish (LeCren, 1992; Claessen et al., 2000). Giants are those that succeeded in cannibalism in the early stage of the growth period. Supposing that all individuals have similar size at the beginning of growth and that a cannibal makes use of most of the victim's body, a giant will be almost two times as large as normal. Head width difference between giants and normals is much greater than difference between typical morphs and cannibal morphs of a similar size (usually less than 20%). Once an individual becomes a giant, the next cannibalism becomes much easier. Subsequent cannibalism most likely occurs between a giant and a normal. As a result, once a giant appears in population, advantage of a cannibal morph strategy becomes negligible compared with overwhelming size of a giant. Thus, the aim of taking cannibal morph strategy is thought to be increasing the probability of becoming a giant by developing a slightly larger head width. In this paper, the advantage gained by becoming a giant is called the 'drastic growth effect'.

Does considering drastic growth effect change the form of frequency dependence? If a cannibal morph individual succeeds in cannibalism to become a giant, it receives great reward, while it pays only cost if it cannot become a giant. When the frequency of cannibal morph is larger, the probability of becoming giant is presumably smaller. Therefore, considering drastic growth effect, the sensitivity of cannibal morph's payoff to the frequency might be increased. In the next section, the possibility of stable coexistence is studied in a model with drastic growth effect.

2.4. Extended model with drastic growth effect of cannibalism

Here, we consider an extended model of population with giants (Fig. 2). Growth period is split into two phases: no giant phase and giant normal phase. In the first phase, the population consists of typical morphs and cannibal morphs both of which have similar body size. The existence of giants is neglected. Individuals who performed cannibalism become giants in the second phase. Individuals who did not perform cannibalism but survive the first phase become normals in the second phase. As cannibalism is monopolized by giants, the type of morph of a normal individual in the first phase does not change the final payoff. The initial population size is taken as one without loss of generality. As a framework, we consider the general case in which both morphs potentially perform cannibalism in the first
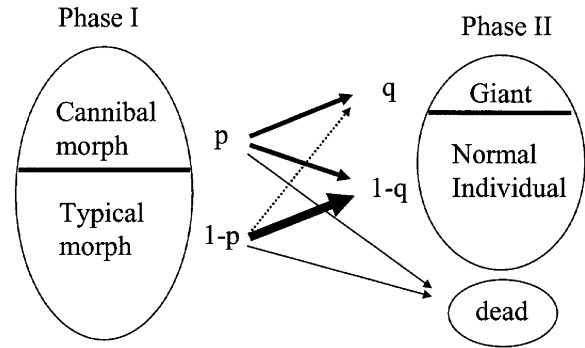

Fig. 2. Schematic illustration of the model with drastic growth effect.

phase. It is natural to assume that the likelihood of cannibalism is determined by head width difference. So, it is assumed that the probability of cannibalism among the same morphs is the same. Let c as probability of cannibalism among the same morph and c' as probability of cannibal morph eating typical morph. Note that the initial difference in head width precludes the possibility of typical morph eating cannibal morph. Let C_{XY} be the frequency of cannibalism where a morph X cannibalizes a morph Y. In order to calculate C_{XY}, an encounter rate must be defined, which is assumed to be included in c and c'. The frequencies of cannibalism are denoted by

$$C_{CC} = cp^2, \tag{5a}$$

$$C_{CT} = 2c'p(1-p), \tag{5b}$$

$$C_{TC} = 0, \tag{5c}$$

$$C_{TT} = c(1-p)^2, \tag{5d}$$

respectively. Here, we assume that cannibalism in the first phase does not occur very often and can neglect the possibility of extinction of typical morph. In the first phase, no individual cannibalizes more than twice. Thus, C_{XY} represents the frequency of cannibals and victims. The frequency of cannibal morphs which succeed in cannibalism, i.e. become giants is

$$G_C = C_{CC} + C_{CT}. \tag{6}$$

The frequency of typical morphs which become giants is

$$G_T = C_{TT}. \tag{7}$$

The frequency of cannibal morphs which are cannibalized is

$$D_C = C_{CC}. \tag{8}$$

The frequency of typical morphs which are cannibalized is

$$D_T = C_{CT} + C_{TT}. \tag{9}$$

Payoff of a normal individual is taken as one without loss of generality. Payoff of a giant is $g > 1$. As in the

previous model, natural survival rates of typical and cannibal morphs in the first phase are assumed to be 1 and m, respectively. Finally, payoff functions are calculated as follows:

$$F_C = \frac{1}{p}[G_C g + (p - G_C - D_C)]m$$
$$= m[(cg - 2c'g - 2c + 2c')p + 2c'(g-1) + 1], \quad (10a)$$

$$F_T = \frac{1}{1-p}[G_T g + (1 - p - G_T - D_T)]$$
$$= (-cg + 2c - 2c')p + cg + 1 - 2c. \quad (10b)$$

2.5. Analysis of a simple case

First, we deal with the special case of $c = 0$, i.e. cannibalism in the first phase occurs only between cannibal morph and typical morph. We also assume fitness of a giant g is constant. Then, payoff functions are

$$F_C = -2mc'(g-1)p + m\{2c'(g-1) + 1\}, \quad (11a)$$

$$F_T = -2c'p + 1, \quad (11b)$$

which are linear functions of p with the coefficients now depending on g. Difference in payoffs is

$$F_C - F_T = -2c'\{m(g-1) - 1\}p$$
$$+ m\{2c'(g-1) + 1\} - 1. \quad (12)$$

Thus, equilibrium p^* is

$$p^* = \frac{m\{2c'(g-1) + 1\} - 1}{2c'\{m(g-1) - 1\}}. \quad (13)$$

For any $0 < p^* < 1$, p^* is stable if and only if

$$m > \frac{1}{g-1}. \quad (14)$$

When this stability condition holds, $p^* > 0$ holds if and only if

$$m > \frac{1}{2c'(g-1) + 1}. \quad (15)$$

Similarly, when the stability condition holds, $p^* < 1$ holds if and only if

$$m < 1 - 2c'. \quad (16)$$

These three conditions (Eqs. (14)–(18)) and corresponding p^* value are illustrated in Fig. 3. All three curves intersect at $(g, m) = ((2 - 2c')/(1 - 2c'), 1 - 2c')$. The $p^* = 0$ curve is monotonically decreasing for $g > 1$. Therefore, the necessary condition for a stable coexistence solution to exist is

$$g > \frac{2 - 2c'}{1 - 2c'}. \quad (17)$$
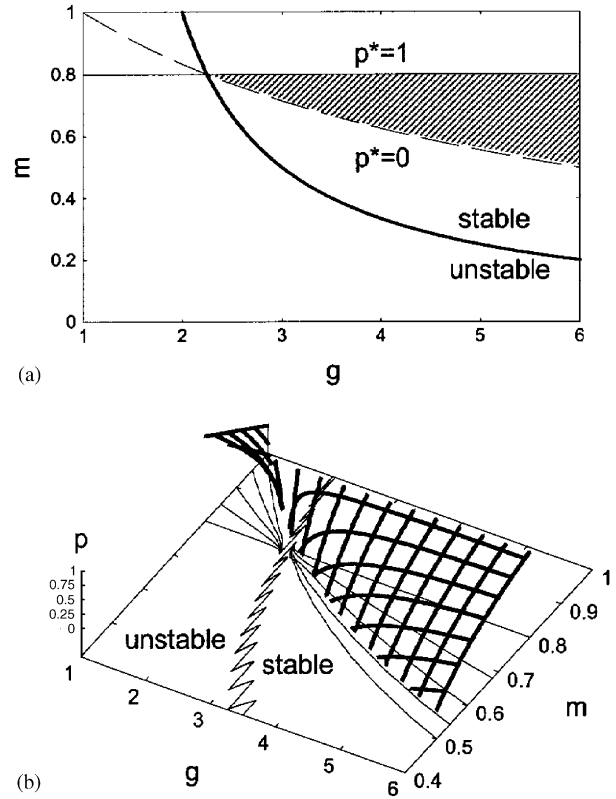

(a)

(b)

Fig. 3. Analytic result of the case $c = 0$ and $c' = 0.1$. (a) Conditions for stability (bold line), $p^* = 1$ (solid line) and $p^* = 0$ (dashed line) are shown in (g, m) space. Parameter region where a stable equilibrium $0 < p^* < 1$ is realized is shown by shaded area. (b) Corresponding p^* is shown in three-dimensional graph. Only $0 < p^* < 1$ surface is drawn. Five contour lines drawn in the bottom of the graph correspond to $p = 0, 0.25, 0.5, 0.75$ and 1.0, respectively. Notched line corresponds to a stability condition where $p^* \to \pm \infty$. Beyond the stability condition, p^* becomes unstable equilibrium, which means bistability.

2.6. Relaxing the assumptions

In this section, we relax the two assumptions. (A) constant fitness for giants and (B) $c = 0$. In order to keep the model tractable, we deal with the special case of $c, c' \ll 1$ and apply approximation. In other words, only few cannibalisms occur in the first phase. Let $g(q)$ and $n(q)$ be payoffs of a giant and a normal, where

$$q = \frac{mG_C + G_T}{m(p - D_C) + (1 - p - D_T)}$$
$$= \frac{mcp^2 + 2mc'p(1-p) + c(1-p)^2}{m(p - cp^2) + \{1 - p - 2c'p(1-p) - c(1-p)^2\}} \quad (18)$$

is frequency of a giant in the second phase. The denominator represents the initial population of the second phase while the numerator represents the frequency of giants. Due to $c, c' \ll 1$ assumption, $q \ll 1$ holds. Applying the arguments leading to Eq. (3), the

actual forms of $\hat{g}(q)$ and $\hat{n}(q)$ becomes

$$\hat{g}(q) = kA\gamma + B - kA\gamma q, \quad (19a)$$

$$\hat{n}(q) = A - A\gamma q, \quad (19b)$$

where we have used $\gamma q < 1$. Additional mortality of a giant is assumed to be zero. The relative fitness of a giant to a normal is

$$g = \frac{kA\gamma + B - kA\gamma q}{A - A\gamma q}$$

$$\approx k\gamma + \frac{B}{A} - k\gamma q + \left(k\gamma + \frac{B}{A}\right)\gamma q. \quad (20)$$

Notice that $g(q)$ can be written as a linear function of the infinitesimal variable q. Putting these results into Eq. (4.6) we get

$$F_C = m[(cg - 2c'g - 2c + 2c')p + 2c'(g - 1) + 1], \quad (21a)$$

$$F_T = (-cg + 2c - 2c')p + cg + 1 - 2c. \quad (21b)$$

In these equations, g always appears in a product with c or c', which are small by assumption. Therefore, to the first order we can neglect the dependence of g on q. Putting

$$g \approx k\gamma + \frac{B}{A} \quad (22)$$

into Eq. (21) yields

$$F_C - F_T = [m\{cg - 2c'g - 2c + 2c'\} - \{-cg + 2c - 2c'\}]p + m\{2c'(g - 1) + 1\} - (1 + cg - 2c).$$

Thus, equilibrium p^* is

$$p^* = \frac{m\{2c'(g - 1) + 1\} - (1 + cg - 2c)}{-m\{cg - 2c'g - 2c + 2c'\} + \{-cg + 2c - 2c'\}}. \quad (23)$$

For any $0 < p^* < 1$, p^* is stable if and only if

$$m > \frac{(2a - 1) + (g - 1)}{(2a - 1)(g - 1) + 1}, \quad (24)$$

where $a \equiv c'/c > 1$. When this stability condition holds, $p^* > 0$ holds if and only if

$$m > \frac{1 + (g - 2)c}{2ac(g - 1) + 1} \approx 1 + (g + 2a - 2 - 2ag)c. \quad (25)$$

Similarly when the stability condition holds, $p^* < 1$ holds if and only if

$$m < \frac{1 - 2c'}{1 + c(g - 2)} \approx 1 - (g + 2a - 2)c \quad (26)$$

when $1 + c(g - 2) > 0$. When $1 + c(g - 2) < 0$, the sign of the inequality is reversed. These three conditions (Eqs. (24)–(26)) are illustrated in Fig. 4. $p^* = 0$ line and $p^* = 1$ line intersect at $(c, m) = (0, 1)$. The difference in the inclination of the two lines in (c, m) space is

$$-(g + 2a - 2) - (g + 2a - 2 - 2ag)$$
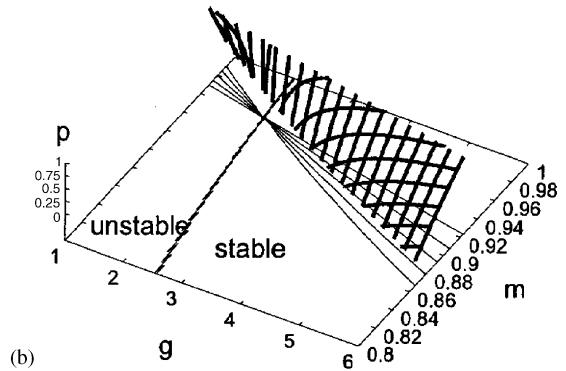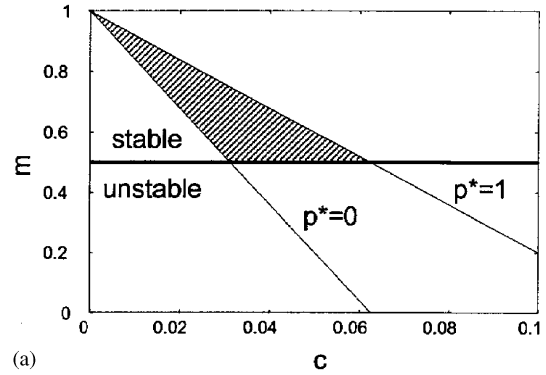$$= 2(a - 1)(g - 2)$$

(a)

(b)

Fig. 4. Analytic result of the case $c, c' \ll 1$. (a) Conditions for stability (bold line), $p^* = 1$ (solid line) and $p^* = 0$ (dashed line) are shown in (c, m) space. Parameter region where a stable equilibrium $0 < p^* < 1$ is realized is shown by shaded area. $g = 6$, $a = 2$. (b) Analytic result of the case $c = 0.01$ and $c' = 0.02$. Equilibrium p^*, contour lines and a stability condition are shown as in Fig. 3b.

and thus, when following conditions

$$2(a - 1)(g - 2) > 0 \quad \text{and} \quad 1 + c(g - 2) > 0$$

hold, there is region in the (c, m) parameter space where $0 < p^* < 1$. The area of this region increases with a or g. If $g > 2$, these conditions are always met as $a > 1$. Moreover, as the right hand of Eq. (24) is a decreasing function of g, there always exists $0 < m < 1$ which meets the stability condition if $g > 2$. Therefore, the condition for a stable coexistence is

$$g > 2. \quad (27)$$

Note that Eq. (17) converges to Eq. (27) when the first-order approximation for c' is applied.

2.7. Numerical calculation

Without applying any approximation, Eqs. (18)–(21) are directly numerically calculated by computer. When $c, c' \ll 1$ condition is relaxed, payoff function becomes a complicated nonlinear function of p. A stable equilibrium is searched numerically (Fig. 5). The search was done for an appropriate region in (g, m) space and the stable coexistence region is achieved (Fig. 6). Validity of

analysis in the previous sections is confirmed. All coexistence solutions are found at $g > 2$. Moreover, the general tendency remains the same that coexistence more likely occurs when c'/c or g is larger.

3. Discussion

The stable coexistence of cannibal and typical morphs can be explained by introducing drastic growth effect of
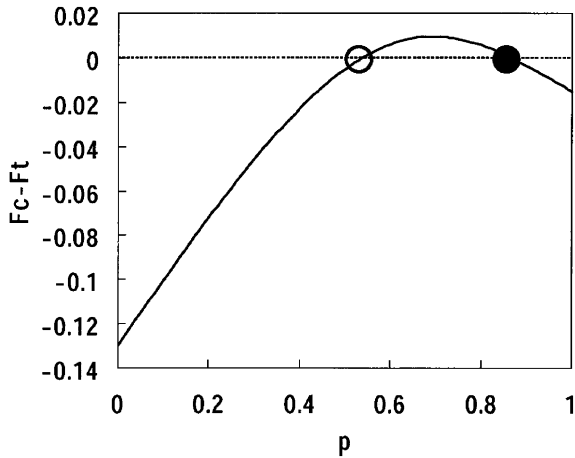

Fig. 5. Difference in payoff of cannibal and typical morphs, $F_C - F_T$, is shown against frequency of cannibal morph, p. In this case ($c = 0.1$, $c' = 0.2$, $k = 0.5$, $\gamma = 4$, $A = B = 1$, $m = 0.45$), both unstable (open circle) and stable (filled circle) equilibriums exist. The p^* value of stable equilibrium is numerically obtained.

cannibalism. The intuitive reason for coexistence is as follows. To grasp the mechanism easily, assume that the typical morph does not perform cannibalism, g (payoff of a giant) is a constant and the frequency of cannibalism is very small in the first stage. In addition, assume that payoff is linear function of p (frequency of cannibal morph). Survival rate and hence payoff of typical morph decreases as p increases with the coefficient X, which corresponds to loss of life. Payoff of a cannibal morph is also decreasing function of p, whose coefficient is Y. Y represents benefit received by a cannibal after cannibalism. The important point is that Y is not the amount of energy (or meat or nutrition, etc.) but the social standing of being a giant. As long as Y is considered as energy, the conversion rate cannot exceed one and thus $X > Y$ always holds. Coexistence cannot occur when $X > Y$ as we have argued above. Cannibalism in the early stage gives very large social profit to a cannibal, which is exactly what Y means. Then, Y can be larger than X. So, in a sense, the drastic growth effect model is a $k > 1$ version of the simplest model. Drastic growth effect explains how k can exceed one. This is the essential mechanism of coexistence of cannibal and typical morph strategies in our model.

At polymorphic equilibrium, cost and benefit of cannibal morph should be balanced, which has been discussed a lot. For example, population density (encounter rate γ) or the ability to cannibalize (c' or a) increases equilibrium frequency of cannibal morph. The present study focuses upon stability of polymorphism
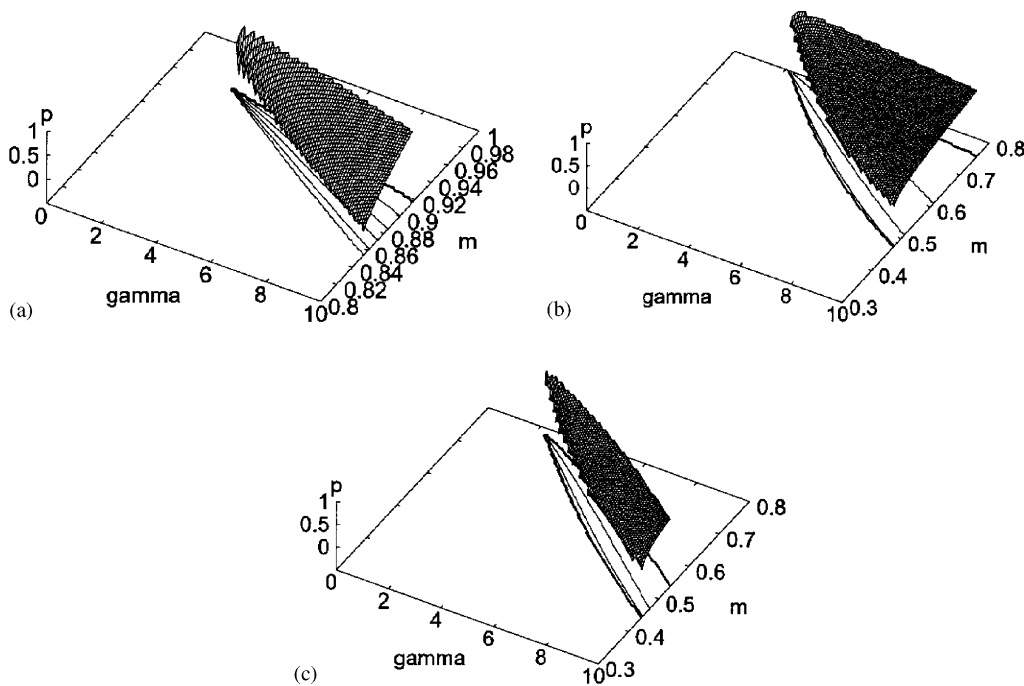

Fig. 6. Numerically derived stable coexistence solution is shown as in Fig. 3b. Energy transfer coefficient is fixed at $k = 0.5$. Energy gain from regular food consumption $A = B = 1$. γ is varied to change payoff of a giant. The shown interval $\gamma \in [0, 10]$ roughly corresponds to $g \in [1, 6]$. (a) $c = 0.01$, $c' = 0.02$ (corresponding to Fig. 4a), (b) $c = 0.01$, $c' = 0.1$ and (c) $c = 0.05$, $c' = 0.1$.

and we conclude that cannibalistic polymorphism occurs when fitness of a giant is larger than two. If energy conversion rate is 0.5, performing two cannibalisms doubles a cannibal's size. In real salamander larvae population, there are only a few cannibals. In *Ambystoma tigrinum*, no more than one cannibal appeared per aquarium containing 16 larvae (Pfennig and Collins, 1993). In *Hynobius retardatus*, there were 102 typical morphs and 17 cannibal morphs (Wakahara, 1995). From such fact, one can guess that a few (around 10%) cannibals monopolize cannibalism and one can easily imagine that fitness of these despots is much larger than the others.

Cost of cannibal morph in our study is assumed to be additional mortality only. It is important to distinguish the cost of performing cannibalism from the cost of having cannibal morph. Cannibal morph is less likely to be attacked by conspecifics and thus the strategy in which an individual develops as a cannibal morph but does not perform cannibalism, is adaptive when the cost of performing cannibalism is greater than the benefits. Therefore, the induction of typical morph cannot be explained without regard to the cost of having cannibal morph (Wakano et al., 2002). Eating relatives or pathogen infection are the cost of performing cannibalism and should not be considered as the cost of cannibal morph in our model. It is reported that the imbalanced body shape of cannibal morph causes a change in behavior or decline in swimming speed, which results in increased risk of predation by natural enemies (Kohmatsu et al., in preparation). It is also known that cannibal morph is slow to metamorphose under drying condition (Rose and Armentrout, 1976; Kohmatsu et al., in preparation). On the other hand, cannibal morph fed with only regular food grows as quick as typical morph (Kohmatsu et al., 2001). Thus, in our model, additional mortality is considered as the cost of cannibal morph.

In the model, growth period is assumed to consist of two phases. In the first phase, cannibalisms mostly occur between cannibal morphs and typical morphs and the existence of giants are neglected. Therefore, we assumed that cannibalism in the first phase does not occur very often. In the second phase, most cannibalisms are performed by giants and cannibalism among normal individuals are neglected. The last assumption can be justified by the following argument. For normal individuals, potential victims of cannibalism are as large as cannibals, which means long handling time and thus the vulnerability to predators. Under the existence of a giant, such vulnerability is too costly and cannibalisms among normals might be suppressed. It is also assumed that growth period consists of two discrete phases and that there is only one opportunity of cannibalism at the end of growth period. These are introduced just for mathematical simplicity and do not seem very realistic because cannibalisms in reality are performed by many individuals in continuous time space. However, dealing continuous time directly makes the model very complicated, so we decided to keep the model as simple as possible to achieve the result analytically. As a candidate of the full model, we could assume a 'normal' population and a 'giant' population and define the probability of the transition in continuous time space. At each cannibalism, a victim is removed from a 'normal' population and a cannibal is moved from 'normal' into a 'giant' population. However, the probability of cannibalism is dependent on the frequencies of cannibal morph, typical morph and a giant. Thus, this process is not Markov chain, which makes analysis of the system very difficult. Computer simulation might be able to be performed, which is left for future works.

Conditions for coexistence of two morphs is independent of regular food abundance. The result is achieved under the assumption of constant regular food consumption rate. Relaxing this assumption may cause the escape effect from intense competition for regular food and may increase the possibility of the coexistence (Pfennig, 1992; Maret and Collins, 1997).

We studied the game model of two pure strategies and the condition for the stable coexistence is shown. In order to explain the observed cannibalistic polymorphism by evolutionary scenario, two points should be discussed. The first point is the relationship between the payoff and fitness. It is natural to assume that the body size at the end of larval period has positive correlation with the adult survival rate and the number of offspring. Cannibalism on adult stages is generally rare in amphibians (Crump, 1992), suggesting that it is the adult size rather than the type of morph in the larval period that affects fitness directly. To the author's knowledge, there is no evidence of the dependence of reproductive success on the morph itself in fish. The second point is the relationship between tactics and strategies. In evolutionary biology, strategy must have genetic basis. Phenotypic trait without genetic basis is called tactic in general. However, as is discussed in the introduction, genetic basis of the morph determination is unclear. The study showing difference in allozyme frequency does not necessarily indicate an allelic dimorphism on a locus (or loci) concerning the morph development. For example, different migration rate among morphs or assortative mating can also result in the difference in allozyme frequency. On the other hand, the observed phenotypic plasticity of morph determination does not necessarily deny the existence of genetic basis of morph determination. Further experimental study would be necessary for the point.

Under the assumptions of the model, the present study implies that the coexistence of two strategies can be established as an evolutionarily stable state. As genetic background of cannibalism is unclear, we

assumed two pure strategies. However, evolution of single mixed strategy can also be analysed with few alterations to the present model and the result will not change. Moreover, all analytic result not only shows that coexistence is evolutionarily stable but also shows that the convergence to the stable state is guaranteed because the payoff is a linear function of frequency. Considering drastic growth effect, sympatric cannibalistic polymorphism can be explained as an evolutionary consequence.

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