

Evolution of cannibalism: referring to costs of cannibalism

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Abstract

A rational explanation for cannibalism is that it would be favored under conditions of crowding of conspecific individuals and/or low availability of alternative prey with the fear of starvation, so as to maximize individual fitness. Cannibalism has, however, not evolved and is not maintained by a simple individual optimization, while it has evolved and is maintained as a game among population members. We analysed the attainable state of an evolutionary cannibalism game within a framework that reflects the minimum essence of cause-effect in the cannibalism phenomenon. Cannibalism is predator-prey interaction among conspecifics. Immediate direct payoffs (survival in the interaction among conspecifics) and indirect payoffs (growth results in potential productivity and survival against the threat of starvation) would be included. No morphological specialization and no size priority of cannibalism individuals are assumed as conservative situations in which we analyse the possibility of cannibalism. Cannibalism would be possible under the conservative condition, if initially the wild population's cannibalism rate is not sufficiently lower than a threshold value. Crowding and/or low availability of alternative prey with the fear of starvation facilitates cannibalism evolution. Energy gain from conspecific prey would be attenuated by costs of counterattacks by conspecific victims and by challenge cost of its own. Discounting net intake energy required in the arms race for cannibalism challenge result in a relative disadvantage of having a high cannibalism rate and makes an evolutionary equilibrium of low cannibalism rate, even when potential profitability of conspecific prey is high.

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1. Introduction

Intraspecific predation or cannibalism is common in the wide taxonomic groups (Elgar and Crespi, 1992; Fox, 1975). Observation of cannibalism in an organism leads us to take a variety of attitudes. Crowding and stress promote cannibalism, and because of this, cannibalism was considered merely a laboratory artifact (Britz and Pienaar, 1992; Tartabini, 1991). Even if it is accepted as natural behavior, the possible interpretation of the behavior is sometimes a secondary outcome of other contexts (Arnqvist and Henriksson, 1997; Caldwell and Araujo, 1998; Fitzgerald, 1992; Johnson, 2001). A variety of ecological and social contexts, however, gives various biological interpretations of the cannibal-

ism phenomena (Elgar and Crespi, 1992; Fox, 1975; Polis, 1981).

Life history position and physiological condition of an individual and the ecological and social conditions modify the likelihood of cannibalism. Sexual cannibalism where females partially or entirely eat the body of encountered males before, during or immediately after copulation is widely known among arthropods (Arnqvist and Henriksson, 1997; Elgar and Crespi, 1992; Johns and Maxwell, 1997; Johnson, 2001; Johnson et al., 1999). Parental care that includes territory defense and offspring guard shows frequent filial cannibalism (Belles and Fitzgerald, 1993; Hoelzer, 1992; Lindstrom, 2000). Male and female parents have a few different or inconsistent reasons for filial cannibalism (Candolin, 2000; Dickinson, 1992; Hoelzer, 1992; Karrk, 1996; Marconato and Rasotto, 1988). Some cannibals possess the ability of kin recognition to avoid eating their relatives and offspring (Dickinson, 1992; Pfennig, 1997; Pfennig et al., 1993, 1994, 1999; Schausberger and Croft, 2001).

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Consideration of benefits to the cannibalizing individual sheds light on a functional explanation of cannibalism phenomena. In view of these circumstances, the common reasoning is that cannibalism is a decision in trade-off situations, for example value as a meal versus value as a mate, or current offspring versus future reproductive success (Belles and Fitzgerald, 1993; Lindstrom, 1998; Sargent, 1992; Sargent et al., 1995). Mathematical modeling and theoretical analyses were conducted in view of the decision-making of an individual so as to maximize the currency of the individual's fitness (Karrk, 1996; Lindstrom, 2000; Newman and Elgar, 1991; Rohwer, 1978). Energetic advantage is believed to be the most cogent function (Belles and Fitzgerald, 1993; Ebensperger et al., 2000; Hoelzer, 1992; Lindstrom, 1998; Polis, 1981; Sowig, 1997), and therefore, it is argued that cannibalism is an optimal foraging process (Dong and Polis, 1992). Cannibalism is promoted in environments where food is often limited (Hopper et al., 1996; Samu et al., 1999) and it has an adaptive function (Giray et al., 2001) with genetic basis (Baur, 1994; Wagner et al., 1999).

Even though cannibalism has complex functions that work at any level from individual fitness to community structure pattern, we consider it here as a phenomenon related to the fitness of an individual, as mentioned in previous studies (Newman and Elgar, 1991; Tuomi et al., 1997). Resources that are owned or produced by an individual or a group are sometimes shared, scrounged or usurped by other group members (Giraldeau and Caraco, 2000; Maynard Smith, 1982). Cannibalism should be considered as a resource reallocation process with conflict between individuals of a population. In such a case, acquisition depends not only on an individual's own strategy (Stephens and Krebs, 1986) but also on the strategies of other members of the population (Giraldeau and Caraco, 2000; Mesterton, 1994). Regardless of the energy benefit acquired through cannibalism, individuals that fail to adopt cannibalism will always suffer a disproportionate threat because non-cannibalistic individuals always risk of death when they encounter cannibals. This illustrates how the fitness of an individual depends not only on its own trait but also those of other individuals. Such dependence requires that the optimal strategy use be established based on a game analysis.

Recently, theoretical studies of cannibalism evolution based on the evolutionary game theory were presented. Dercole and Rinaldi (2002) analysed size dependent cannibalism game under assumptions of mortality factors, that is, cannibalism and intraspecific competition. They demonstrated the possibility of evolutionary branching that arise a dimorphism population from a monomorphism population of a cannibalism character. Wakano et al. (2002) analysed the evolutionary dynamics of cannibalism morphology under assumption

of trade-off between cannibalism specialization and vulnerability to predation.

Here, we take the position that cannibalism is a survival-foraging game in which individuals of a population participate. In the game, the purpose of each player is to maximize its profit with survival. According to this generalization, cannibalism should be interpreted as an extreme form of usurpation of another individual's resources, those that make up its whole body. We made no assumptions of morphological specialization, of size priority of cannibalistic individuals, and of consideration of vulnerability of cannibal to heterospecific predator.

Under the simplifying situation, we consider the antagonistic effects to spread cannibalism propensity in the population; the act of cannibalism of its own and/or the act of cannibalism of other population members clamp energy costs on the focal individual. The key costs and benefits in the game of cannibalism are "challenge" and "counterattack" costs, and "growth" and "survival", respectively. Consideration of these costs under the simplifying situation leads us the most parsimonious analysis of evolutionary conditions for spreading and inhibition of cannibalism in a population. The goal of this paper is to predict conditions under which cannibalism is expected to evolve/not evolve and when an intermediate cannibalism rate is likely in the minimum simple situation.

2. The model

2.1. A cannibalism game

We consider cannibalism among individuals of an identical generation, and trace growth and survival from birth to a certain terminal time in a cannibalism game by incorporating a simple life history scenario that reflects the essence of the cannibalism game.

Potential profitability of the conspecifics as prey item and profitability and availability of heterospecific prey affect whether a cannibalistic propensity is favored in the view of energy acquisition (Stephens and Krebs, 1986). Individual that is apt to cannibalistic tends to survive struggle with the conspecifics in the cannibalism population. In the aspects of fear of starvation, however, cannibalism is not necessarily favored, if cannibalism results in low energy acquisition rate and thus, small body size. Thus, the cannibalism game has two components, i.e. the foraging game and the survival game which are interrelated.

We consider two types of potential prey; one is conspecific and the other is heterospecific. Utilization of heterospecific prey is obligatory. Facultative utilization of conspecifics (i.e. cannibalism) increases or decreases the energy intake rate depending on the relative profit-

ability of conspecifics and availability of the alternative prey (Stephens and Krebs, 1986). We considered the probability to act cannibalism, $U = \{u \in R : 0 \leq u \leq 1\}$, upon encounter with an opponent as an individual's evolutionary character. $u = 1$ and $u = 0$ are special cases in which the individual obligatorily commits cannibalism and completely does not commit cannibalism, respectively. In the following, we introduce the detailed mechanisms of the foraging game and the survival game.

2.2. Behavioral process involved in cannibalism

Imagine that an individual of type- u' encounters an individual of type- u . The encounter ends with either of three situations, individual of type- u' eats the opponent, is eaten by the opponent, or both are alive. The possibility of the occurrence of any of these events depends on the strategy of both individuals. Suppose that, among all possibilities in an encounter, proportion $\zeta(u', u)$ represents the type- u' individual eating the opponent of type- u , and proportion $\xi(u', u)$ represents the type- u' individual being eaten by the type- u opponent. We can assume that $\zeta(u', u)$ is an increasing function and a decreasing function of u' and u , respectively, and $\xi(u', u)$ is a decreasing function and an increasing function of u' and u , respectively, under condition $0 \leq \zeta(u', u) + \xi(u', u) \leq 1$.

To simplify the evolutionary scenario, we considered situations in which the population consists of resident individuals of identical trait value and only a few mutants emerge at arbitrary points of the evolutionary process. Let u_w be the cannibalism rate of the resident type and u_m be the rate of the rare mutant ($u_w, u_m \in U$).

2.3. Foraging and growth

We designate B_j as the size of a type- u_j individual ($j = w, m$) in the type- u_w population at time t . We assume that growth trajectories are described by the following differential equations given that the number of mutant is sufficiently small

$$\frac{dB_j}{dt} \approx g \left(\frac{\eta(u_j, u_w, t)e_1 + \lambda e_2}{1 + \eta(u_j, u_w, t)h_1 + \lambda h_2} \right)^\theta. \quad (1)$$

$\eta(u_j, u_w, t) = aN l(u_w, t)\zeta(u_j, u_w)$ is the instantaneous encounter rate of conspecific prey, where N is the total population number at birth, $l(u_w, t)$ is the survival probability of a type- u_w individual at t , and a is the encounter coefficient of conspecific individuals. The fractions in the parentheses of Eq. (1) indicate the net energy gain per unit time, where e_1 and e_2 are energy intake, h_1 and h_2 are handling times for conspecific victims and heterospecific prey, respectively, λ is the constant of instantaneous encounter rate of the heterospecific prey, and g and θ are positive constants.

2.3.1. Intake energy and handling time of conspecifics

We assume that e_1 and h_1 are basically proportional to the size of the cannibalized victim. However, the net energy gain should be discounted due to the two types of energetic cost under the assumptions of no morphological specialization and no size advantage in cannibalism. Firstly, adopting high cannibalism rate incurs high challenge energy cost in the cannibalism struggle. Secondly, relating to an opponent with high cannibalism rate incurs high counterattack energy cost also in the cannibalism struggle.

Suppose that the focal individual is of type- u' and is against an opponent of type- u . We assume a general discounting function ϕ . $\phi(u', u)$ is a non-increasing function of u' (i.e. increasing u' incurs a challenge cost) and u (i.e. increasing u incurs a counterattack cost), and $\phi(0, 0) = 1$. In cases where there exist both or either of the energy costs, ϕ is a monotonically decreasing function of u' and/or u . Net intake energy and handling time for a type- u' cannibal dealing with a type- u prey are $e_1 = \phi(u', u)B(u, t)$ and $h_1 = \beta B(u, t)$, respectively, where β is a handling time parameter.

2.4. Survival

Survival probability l_j of a type- u_j individual at time t is described by the following differential equations

$$\frac{dl_j}{dt} \approx - \left[\frac{1}{B_j} \left(\frac{b}{\lambda + \eta(u_j, u_w, t)} \right) + \gamma(u_j, u_w, t) \right] l_j, \quad (2)$$

where $\gamma(u_j, u_w, t) = aN l(u_w, t)\xi(u_j, u_w)$ is the instantaneous encounter rate of conspecific predators. The term in the brackets indicates the instantaneous death rate, which has two components. The first term in the brackets indicates the hazard of starvation that comes under the influences of the intervals of inter prey encounters and state of the individual (i.e. body size). Assuming that the encounters occur by Poisson processes, the expected waiting time of successive events is reciprocally proportional to the sum of the instantaneous rates (i.e. the fraction term in the parentheses). The last terms in the brackets indicate the hazard of intraspecific predation (cannibalism).

2.5. Analysis of the foraging game

The cannibalism game consists of two fitness components, growth and survival. The two components are related each other by the nonlinear dynamical relationships (i.e. Eqs. (1) and (2)). Analysis of each component of the system is insufficient, but analysis of the total system leads hardness to understand the underlying processes. Therefore, we first analyse the aspects of the foraging process, and in the next, analyse the aspects of the survival process, separately, to clarify the underlying processes of the cannibalism game. We focus here on the

energy intake rate that corresponds to the term in the parentheses of Eq. (1).

In the classical foraging theory, as far as focusing on maximization of the long-term energy intake rate, conspecific victims and heterospecific prey are ranked according to their relative profitability. The relative values of profitability and abundance of the higher ranked prey determine the optimal decision as to whether or not the protagonist should include lower ranked prey encountered (Stephens and Krebs, 1986). Utilization of heterospecific prey is obligatory, thus, the cannibalism rate is the decision parameter for the forager. We argue here which cannibalism rate is favored in view of the foraging game.

Ratios of intake energy to handling time of both types of prey, conspecifics and heterospecifics, are $e_1/h_1 \propto \phi/\beta$ and e_2/h_2 , respectively. Suppose a focal individual of type- u' cannibalizes a type- u conspecific individual, and $\phi(u', u)/\beta < e_2/h_2$ holds. The profitability of conspecific prey is lower than that of heterospecific prey. In this case, if the encounter rate with heterospecifics is low and condition $\phi(u', u)/\beta > \lambda e_2/(1 + \lambda h_2)$ is satisfied, cannibals have a higher long-term energy intake rate than non-cannibals (Stephens and Krebs, 1986).

The above argument is based on the conventional diet model without considering the game situation among members of the population. Game theoretical analysis should be applied to our scenario. Let $f(u_m, u_w)$ be the energy intake rate of the mutant in the population at a certain time, t , of the life history

$$f(u_m, u_w) = \frac{aNl_w \zeta(u_m, u_w) \phi(u_m, u_w) B_w + \lambda e_2}{1 + aNl_w \zeta(u_m, u_w) \beta B_w + \lambda h_2}, \quad (3)$$

where $l_w = l(u_w, t)$ and B_w is the body size of a common wild individual at the time, t . Eq. (3) is the term in the parentheses of Eq. (1) at a certain time of the life history.

The gradient of f with respect to u_m at (u_w, u_w) , i.e. $\partial f(u_m, u_w)/\partial u_m|_{u_m=u_w}$ (hereafter, denoted as f'), indicates the change of reward rate due to a positive infinitesimal change in the cannibalism rate of the focal individual from that of the residents, compared to the reward rate of residents:

$$f' = f'_1 + f'_2 = C_1 \phi' + C_2 \zeta', \quad (4)$$

where

$$\phi' = \left. \frac{\partial \phi(u_m, u_w)}{\partial u_m} \right|_{u_m=u_w}, \quad \zeta' = \left. \frac{\partial \zeta(u_m, u_w)}{\partial u_m} \right|_{u_m=u_w},$$

$$C_1 = \frac{aNl_w \zeta B_w}{1 + \lambda h_2 + aNl_w \zeta \beta B_w}, \quad C_2 = \frac{aNl_w B_w (\phi - f \beta)}{1 + \lambda h_2 + aNl_w \zeta \beta B_w},$$

$$\phi = \phi(u_w, u_w), \quad \zeta = \zeta(u_w, u_w), \text{ and } l_w = l(u_w, l_t).$$

Note that ϕ' and ζ' represent the change in the discounting rate of acquiring energy from conspecifics prey and the change in the probability of eating the

encountered conspecifics prey with respect to infinitesimal positive change in u_m from u_w . ϕ' and ζ' are designated the marginal discounting rate and the marginal encounter rate of conspecific prey, respectively. Therefore, Eq. (4) represents the additive effect of the component of the marginal discounting rate (f'_1) and the component of the marginal encounter rate (f'_2). If $f' = 0$ holds at $u_w = u^*$, u^* is an equilibrium population cannibalism rate in the foraging game.

2.5.1. Invasion analysis

The values of f' are considered to evaluate invasion intensity of mutants for resident populations of $0 \leq u_w \leq 1$. We consider a simple encounter scenario of a type- u_m mutant individual with a type- u_w resident. Both individuals try to eat their opponent with probability $u_m u_w$ at the encounter. Then, the type- u_m individual cannibalizes the opponent with probability $\frac{1}{2} u_m u_w$. The type- u_m tries to eat the type- u_w and the type- u_w does not try to cannibalize the type- u_m with probability $u_m(1 - u_w)$, and thus the type- u_m cannibalizes the type- u_w individual. Summing up all cases of the events, we obtain $\zeta(u_m, u_w) = \frac{1}{2} u_m u_w + u_m(1 - u_w)$. We further assume an arbitrary descriptive function, $\phi = 1/(1 + c_1 u_m)(1 + c_2 u_w)$, that satisfies the properties of ϕ . The challenge cost and counterattack cost are realized with positive values of c_1 and c_2 , respectively.

We apply these functions, ζ and ϕ , to Eq. (4), and evaluate f' with respect to the handling time parameter, β , as an example of analysis that shows the property of mutant's invasion conditions (Fig. 1). In the case that there exist neither a counterattack cost nor a challenge cost, the attainable equilibrium state is $u^* = 0$ or $u^* = 1$ depending solely on the optimal diet criterion of the classical foraging theory. When the profitability of conspecific victims is higher than an optimal diet criterion, a mutant with a higher cannibalism rate than the residents enjoys a high long-term reward rate, and vice versa (Fig. 1(a)).

If there is a counterattack cost, the equilibrium cannibalism rate is also determined by the optimal diet criterion. However, counterattack decreases the profitability of the victim in population of higher cannibalism rate, and this changes the equilibrium population cannibalism rate. Around the range of β in which the optimal diet policy provides a marginal condition, the discounting effect of intake energy causes a decrease in the equilibrium rate from $u^* = 1$ to certain interior values (Fig. 1(b)). If there is a challenge cost, increasing the cannibalism rate incurs cost and this effect decreases the equilibrium rate (Fig. 1(c)). Because $f' < 0$ for $u^* < u_w$ and $0 < f'$ for $u_w < u^*$, the interior equilibrium is attainable and stable. In summary, in the foraging game, either cost of counterattack or challenge realizes interior equilibrium cannibalism rate, $0 < u^* < 1$.

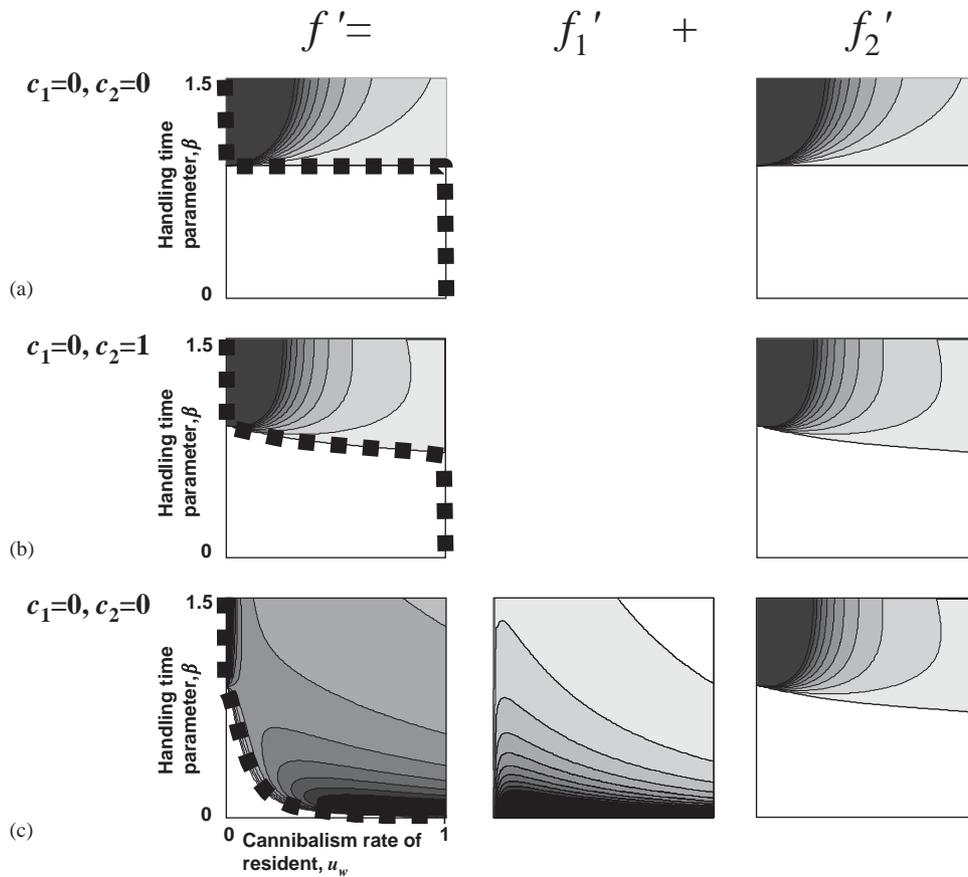


Fig. 1. Total gradient, f' , and its additive components, f_1' and f_2' . The bold dashed lines in f' 's indicate the attainable equilibrium cannibalism rate in the foraging game. f_1' is negative for the entire range of parameters. f_2' is negative in gray and black areas, and positive in white areas. Gray–black gradient shows absolute magnitude of the values. In f_2' , the contours were omitted in the areas of positive values. Black shows a large absolute value and gray shows a small absolute value. Parameters are $e_2 = 1.5$, $h_2 = 1$, $\lambda = 3$, $aNl_w B_w = 1000$. (a) No cannibalism cost. (b) Counterattack cost. (c) Challenge cost.

In case of existence of challenge cost, the component of the marginal discounting rate is seriously negative when conspecific prey is potentially highly profitable (i.e. small β) (see f_1' of Fig. 1(c)), and the component of the marginal encounter rate is seriously negative when conspecific prey is not profitable and population cannibalism rate is low (see f_2' of Fig. 1(c)).

2.6. Analysis of the survival game

Survival is another aspect of the cannibalism game. Individual that is apt to cannibalistic tends to survive struggle with the conspecifics in the cannibalism population. In the aspects of fear of starvation, however, cannibalism is not necessarily favored, if cannibalism results in low energy acquisition rate and thus, small body size. Therefore, the survival game involves the mechanism of foraging game, and this leads a complication analysis.

Let $k = k(u_m, u_w)$ be the instantaneous death rate of a focal mutant individual at a certain time, t , of the life

history (i.e. the term in the brackets of Eq. (2)),

$$k = k_1 + k_2 = b \frac{1}{B_m} \left(\frac{1}{\lambda + \eta(u_m, u_w)} \right) + \gamma(u_m, u_w), \tag{5}$$

where $\eta(u_m, u_w) = aNl_w \zeta(u_m, u_w)$, $\gamma(u_m, u_w) = aNl_w \xi(u_m, u_w)$ and $l_w = l(u_w, t)$, respectively, and B_m is the body size of the focal individual at a certain time, t . The first term of Eq. (5) includes the causes of starvation, i.e. the susceptibility to starvation (body size) and expected time intervals spending with no prey utilization. The second term implies the cause of death due to cannibalism. Gradient, $k' = \partial k / \partial u_m |_{u_m = u_w}$, represents the change in the death rate due to a positive infinitesimal change in the cannibalism rate of the focal individual from that of the residents. In $k' = k_1' + k_2'$

$$k_1' = -C_3 \zeta' - C_4 B_m' \tag{6.1}$$

$$k_2' = C_5 \xi', \tag{6.2}$$

where

$$B'_m = \left. \frac{\partial B_m}{\partial u_m} \right|_{u_m=u_w}, \quad \zeta' = \left. \frac{\partial \zeta}{\partial u_m} \right|_{u_m=u_w},$$

$$C_3 = \frac{abNl_w}{(\lambda + aNl_w\zeta)^2 B_w} > 0,$$

$$C_4 = \frac{abNl_w}{(\lambda + aNl_w\zeta) B_w^2} > 0, \text{ and } C_5 = aNl_w > 0.$$

The terms in Eq. (6.1) represents the additive effect of the marginal encounter rate of conspecific prey ζ' and the marginal body size B'_m , respectively. Eq. (6.2) represents the effect of the marginal encounter rate of conspecific predators ζ' . Applying the logic to make function $\zeta(u_m, u_w)$, we assume the encounter rate of conspecific predators as $\zeta(u_m, u_w) = \frac{1}{2}u_mu_w + u_w(1 - u_m)$.

Since $\zeta' = 1 - u_w/2 > 0$ and $\zeta' = -u_w/2 < 0$ for any u_w , we can find that the direct effects of cannibalistic interaction work to keep k' negative, and favor increasing cannibalism rate in the population. On the contrary, B'_m has a positive or negative value according to the consequences of the foraging game. Therefore, if the consequences of the cannibalism game shows no monotonic patterns to the change of parameters characterized the environmental condition, these patterns are emerged by the consequences of the foraging game.

2.7. Fitness in the cannibalism game and evolutionary dynamics

We analysed the cannibalism game consists of the two components, foraging and survival sub-games. Let the fitness of a mutant be $W_m(u_m, u_w) \propto l_m(u_m, u_w, T) B_m(u_m, u_w, T)$, where T is an arbitrary terminal time of fitness evaluation. We conduct a global invasibility analysis, under the assumption that rare mutants randomly emerge and their cannibalism rate is sufficiently close to the value of the residents (e.g. Geritz et al., 1998). If $W'_m = \partial W_m(u_m, u_w) / \partial u_m |_{u_m=u_w} = 0$ at $u_w = u^*$, u^* is the equilibrium cannibalism rate. Furthermore, invasibility map graphically tells us whether the equilibrium is attainable from a given initial population cannibalism rate, u_w , other than u^* (e.g. Ebenman et al., 1996).

Again, we list here the common inferences of stability/instability of cannibalism: (1) Cannibalism does not tend to be favored if profitability of conspecific victims is low and density of the alternative prey is high, and (2) cannibalism is favored if scarcity of alternative prey leads to death by starvation. Other inferences are (3) crowding of conspecifics would promote cannibalism, and (4) energy costs of cannibalism may suppress cannibalism evolution.

According to the analyses of the foraging game, the counterattack cost has little influence on the invasion

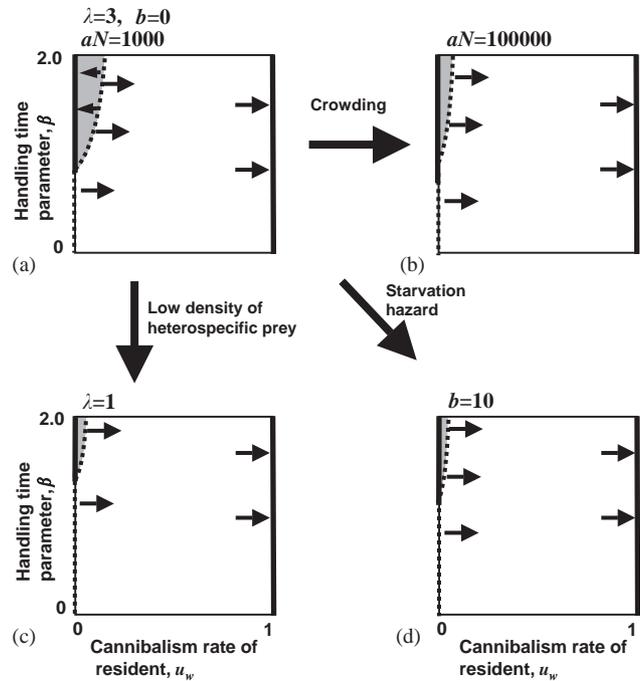


Fig. 2. Invasibility maps in the case of no energy cost. In gray areas, a lower cannibalism rate than that of the residents is favored. In white areas, a higher cannibalism rate than that of the residents is favored. The bold dotted lines indicate unstable equilibrium states and the bold solid lines indicate stable equilibrium states. Non-zero value of b means existence of starvation hazard, large value of aN means crowding of conspecific individuals, and large value of λ means high availability of alternative prey. Parameters are $e_2 = 1.5$ and $h_2 = 1$. The initial conditions are $g = 5$, $\theta = 2.5$, $B_{0m} = B_{0w} = 1$ and $l_{0m} = l_{0w} = 1$, and the terminal time is $T = 1$.

condition of a mutant. Even though we conducted invasion analysis for three cases (no energy cost, only counterattack cost, and only challenge cost), we refer only to the cases of no energy cost and challenge cost. We plotted maps of W'_m for the initial population's cannibalism rate u_w , and the handling time parameter β with a variety of scenarios involving cannibalism evolution (Figs. 2 and 3).

2.7.1. No energy cost

In case of no challenge cost, the cannibalism rate evolves to either the boundary maximum ($u = 1$) or the boundary minimum ($u = 0$) depending on the initial population's cannibalism rate u_w , and the potential profitability of conspecific victims characterized by the handling parameter β (Fig. 2).

When profitability of conspecific prey is low (large value of β), the change in the cannibalism rate toward a larger value than that of the residents would incur a disadvantage in the foraging game (see Fig. 1(a)). Under the condition of low profitability of conspecific prey, the direct advantage via survival in the cannibalism struggle in the survival game for a mutant that changes the cannibalism rate toward a larger value does not offset

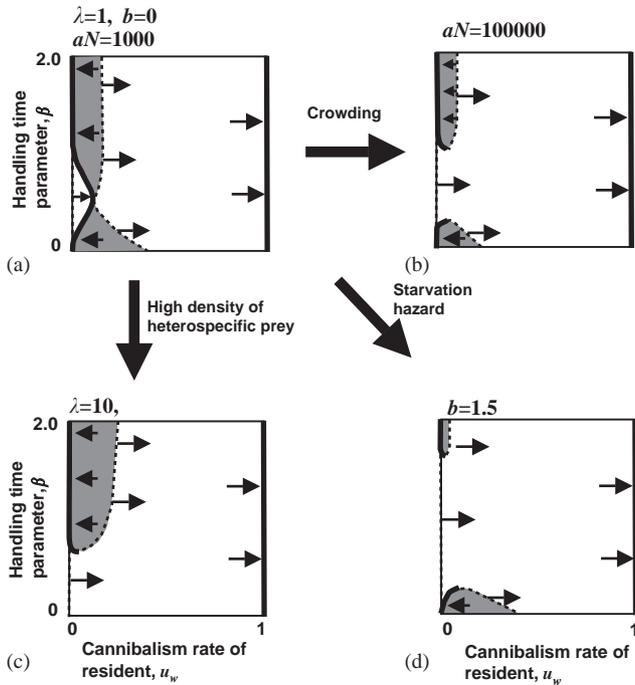


Fig. 3. Invasibility maps in the case of challenge cost. In gray areas, a lower cannibalism rate than that of the residents is favored. In white areas, a higher cannibalism rates than that of the residents is favored. The bold dotted lines indicate unstable equilibrium states and the bold solid lines indicate stable equilibrium states. Non-zero value of b means existence of starvation hazard, large value of aN means crowding of conspecific individuals, and large value of λ means high availability of alternative prey. Parameter values, initial conditions and terminal time are the same as in Fig. 2.

the disadvantage in energy acquisition in the foraging game, when a population consists of individuals of a low cannibalism rate. Even under the condition of low profitability of conspecific prey, when a population consists of individuals of higher cannibalism rate, however, the advantage via direct cannibalism interaction in the survival game offsets the disadvantage of the foraging game.

When the profitability of conspecifics is high, the facilitation of the cannibalism rate is favored and the population cannibalism rate necessarily reaches $u = 1$ for all initial population conditions, because that the all aspects of the foraging game and the survival game favor higher cannibalism rate of mutant than the population cannibalism rate.

Crowding conditions (large value of aN) promote cannibalism, even if the conspecific prey has a low profitability. This is because the effect of reduction in the encounter rate with conspecific “predators” by adopting a higher cannibalism rate than the others would predominate under crowding conditions (compare (a) vs. (b) in Fig. 2). As is intuitively appealing, a low density of heterospecific prey (low value of λ) makes narrow the possible range of the initial population that leads to evolution of non-cannibalism (compare (a) vs.

(c) in Fig. 2). In the case that there exists fear of starvation, reduction in intervals of consecutive prey encounters by expansion of the prey menu to conspecifics may reduce death by starvation (compare (a) vs. (d) in Fig. 2).

2.7.2. Challenge cost

As is same of the case of no energy cost, crowding of conspecifics and/or existence of starvation risk promote cannibalism evolution, and high density of heterospecific prey inhibits cannibalism evolution, when the profitability of conspecifics is not high. However, an increase in the cannibalism rate of a focal individual decreases the net energetic intake from conspecific victim due to increment of the challenge cost, and this process promote evolution of non-cannibalism not only for low profitability but also for high profitability of conspecific prey (Fig. 3). This qualitative consequence arises from the underlying mechanism of the foraging game.

A decrease in the profitability per se (implied in ϕ) is, however, not the direct cause of favoring a low cannibalism rate. Even if all the other factors support evolution of a higher cannibalism rate, the relative discounting rate of the net energetic intake from conspecific victims compared with other members of a lower cannibalism rate (implied in a negative value of the marginal discounting rate ϕ') results in disadvantage of the mutant that adopts a higher cannibalism rate. The relative disadvantage of energy acquisition of a mutant that changes toward a higher cannibalism rate than the residents predominate, when profitability of conspecific prey is high (see contour of f'_1 in Fig. 1). This effect predominates when the population cannibalism rate is low. This effect causes a decrease in the equilibrium cannibalism rate, even though the conspecifics are highly profitable (see Fig. 3(a)). In this case, the evolutionary attainable stable cannibalism rate is $u^* = 0$ for high or low profitability of conspecific prey, and $0 < u^* < 1$ for intermediate profitability of conspecific prey with a condition of low initial population cannibalism rate.

We can recognize the qualitative effects of the consequences by evaluating the foraging game (Eq. (4) and Fig. 1). In the second term of Eq. (4), $\phi - f\beta$ has a larger absolute value, when discrepancy between the long term reward rate, f , and the profitability of conspecific prey at the population cannibalism rate, ϕ/β , is large. This would occur, when the difference of the profitabilities between conspecific and heterospecific prey is large (i.e. β is sufficiently large or small), population cannibalism rate is low (i.e. u_w is small), and encounter rate of heterospecific prey is high (i.e. λ is large). When these conditions meet, the second term of Eq. (4) (see also f'_2 in Fig. 1) predominates and reflects it to the consequence of the foraging game (see Fig. 3(c)).

When there exists the risk of starvation, mutant with higher cannibalism rate than the resident gets high survival with decreasing the intervals of between prey encounters, particularly in low food available condition (i.e. low profitability of conspecific prey and low density of alternative prey). This mechanism makes vanish the region which leads non-cannibalism equilibrium in large value of β (Fig. 3(d)).

3. Conclusion

We analysed the evolutionary dynamics of cannibalism in a framework of interspecific interaction. Cannibalism portrays a predator–prey interaction among conspecific individuals. We evaluated immediate direct payoffs (survival in the interaction among conspecifics) and indirect payoffs (growth results in potential productivity and survival in a harsh environment) as consequences of cannibalistic phenomena. Cannibalism is a Nash equilibrium state in the sense of survival among intraspecific encounters. An increase in the cannibalism rate among all members in a population always decreases the expected survival of all members. The expected survival of a cannibal, however, remains higher than that of a non-cannibal, even when cannibals are common in the population. Thus, cannibalism is a unique evolutionary endpoint in terms of survival among the intraspecific interaction.

In the extant cannibalism phenomenon, we often observe that cannibalistic organisms have specialized morphology for cannibalism, and it would be considered that conspecifics provide a superior diet for growth than heterospecifics, because that the composition of the prey is similar to that of the cannibal, (Crump, 1992; Folkvord and Otterå, 1993; Meffe and Grump, 1987). If we consider that these conditions have been satisfied throughout the history of extant cannibalistic organisms, the major disadvantageous aspects in either the survival or growth game vanish (but see, Wakano et al., 2002). However, even in the extant cannibalism phenomenon, the utilization of conspecific results in lower growth than the utilization of heterospecific prey (Michimae and Wakahara, 2002). Our model is based on the assumption with neither morphological specialization nor unconditional energetic advantage of cannibalism.

Our results show that cannibalism is an attainable and evolutionarily stable state in an evolutionary scenario even under a conservative assumption that conspecific victims are less profitable prey than the available alternatives. The general predictions that cannibalism would be an evolutionary consequence under circumstances of low availability of alternative prey, crowding of conspecifics, and fear of starvation, are qualitatively supported under the conservative condition. This con-

sequence is not merely determined by simple optimization of individuals' decisions. Relative harm and profit of subcomponents of the fitness of mutants versus that of other members in the game situation control the direction of cannibalism evolution.

The essential effects of an increased cannibalism rate in the game situation are the relative increase in the frequency of encountering conspecific prey (denoted by ζ' in our model) and the relative decrease in the frequency of encountering conspecific predators (denoted by ξ' in our model), compared with the others. Fights that reduce the risk of predation by the encountered opponent would make the members of the population fall into a survival war of attrition. This aspect would consistently hold in the cannibalism game.

However, not all conditions that support cannibalism were present at the onset of cannibalism. When conspecific victims have low potential profitability, there exists a relative harmful effect for mutants with a higher cannibalism rate in the foraging game, and this is reflected in growth and starvation risk, particularly, in case that population members' cannibalism rate is low.

Under the condition of energy attrition for cannibalism challenge, the relative disadvantage of more positive challenger compared to the others is serious when the potential profitability of conspecific prey is high (implied in f'_1 of Eq. (4)). This produces a dilemma: High profitability of conspecifics is attractive to utilize for increasing the energy acquisition without considering game situation. An increase in the cannibalism rate compared with that of the other members leads to high utilization of the profitable conspecific prey. However, the cost of the increase in the cannibalism rate decreases the energy acquired from the victim relative to that of the other members that eat the same victim, and consequently, a cannibalism rate higher than that of the others is not favored in the foraging game.

Therefore, in the case of challenge cost, non-cannibalism is favored for both low and high profitable conspecific prey for different reasons, and an intermediate cannibalism rate becomes a possible evolutionary consequence in the case of a mid-range profitability of conspecifics. These predictions in our study are qualitatively supported for other functions of $\zeta(u', u)$ (probability that a type- u' individual eating the opponent of type- u upon encounter), $\xi(u', u)$ (probability that a type- u' individual is eaten by the opponent of type- u upon encounter), $\phi(u', u)$ (intake energy discounting for a type- u' forager with type- u prey), dB/dt , and dI/dt that satisfy the qualitative conditions of our model.

We surveyed the evolutionarily attainability equilibrium cannibalism rate. Further analysis of the second derivative $\partial^2 W_m(u_m, u^*)/\partial u_m^2|_{u_m=u^*}$ gives the possibility of instability of the attainable equilibrium (ESS-instable) and trait branching at the equilibrium (Geritz et al., 1998). Even though we did not demonstrate the

analysis, the attainable equilibrium is ESS-stable in the model. However, we should pay attention to the possibility of evolutionary branching in cannibalism evolutionary game (Dercole and Rinaldi, 2002; Nishimura and Isoda, in review).

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