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The optimal strategy for brood-parasitism: how many eggs should be laid in the host's nest?

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Abstract

We consider the optimal strategy for intra-specific brood-parasitism, especially with respect to the number of eggs laid by the parasitic individual in the nest of non-parasitic individual, in particular, a host that does not reject the parasite's eggs. With a fundamental mathematical model, assuming that the survival probability of the parasite's offspring in the nest of the host is significantly smaller than that in parasite's own nest, we determine the optimal number of eggs laid in the nest of host that maximizes the expected reproductive fitness of the parasite. We show that the invasion success of brood-parasitism could significantly depend on the total number of eggs laid by the parasite in a breeding season, and that the successfully invading brood-parasitism could realize maximum fitness with a specific number of parasite's eggs laid in the nest of the host. © 1999 Elsevier Science Inc. All rights reserved.

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1. Introduction

For a number of species of birds, brood-parasitism by laying eggs in the nest of the other individuals has been reported [1,2]. There are two categories of such nest parasitism. One is inter-specific brood-parasitism, in which eggs are laid in the nests of different species, and the other is intra-specific brood-parasitism in which eggs are laid in the nests of other individuals of the same species.

Many researchers have studied intra- and inter-specific brood parasitisms from various points of view. Hamilton and Orians [3] and Payne [4] argued that intra-specific brood-parasitism is an intermediate stage in the evolution of inter-specific brood-parasitism. Yamauchi [5,6] discussed their opinion from a theoretical point of view, making use of a kind of quantitative genetic model. Takasu et al. [7] analyzed a mathematical model of population dynamics between parasite and host according to inter-specific brood parasitism, and discussed the evolution of host behaviour in which the host rejects the eggs laid by the parasite.

Intra-specific brood-parasitism has been reported in many articles, and the reports have been increasing during this decade. Rohwer and Freeman [2] reported the intra-specific brood-parasitism of 64 species of waterfowl and 77 species of other birds in their paper: the White-fronted Bee-eater *Meropus bullockoides*, the swallow *Hirundo rustica*, the cliff swallow *Hirundo pyrrhonota*, the eastern kingbird *Tyrannus tyrannus*, the moorhen *Gallinula chloropus*, and so on.

The moorhen inhabits all parts of the world except for Australia. Its breeding season is generally from April to August or September. Almost all females lay a maximum of one egg per day, and the expected number of eggs per female per breeding season is generally from five to eight. But the number of eggs in some nests is sometimes significantly larger than this. We might therefore infer that other female birds which are not the owner of the nest lay eggs in it. Three pieces of evidence would indicate that more than one female has laid eggs in a nest [1]: (i) More than one egg was laid in a single nest in a day; (ii) Eggs were laid in the nest after the owner female had finished laying her eggs; (iii) Eggs with characteristics different from those of the owner female were laid in the nest. Eggs from different females are in general different in size, weight, shape, background colour and spot patterns [1,8,9].

Field work by Gibbons [9] was conducted in 1982–1984 at the Wildfowl Trust's Peakirk Waterfowl Gardens in Cambridgeshire. In this investigation, Gibbons [9] found that the number of nests in which more than two birds laid eggs was 31 of the 128 investigated nests.

There could be two types of phenomena in which more than one bird lays eggs in the same nest. First is cooperative nesting. The moorhen is generally monogynous and its pairs cooperate in defending the breeding territory.

Gibbons [9] reported that 10% of pairs consist of a group of one male and more than one female. In each group, two or three females laid eggs in a common nest, and they incubated eggs and brought up fledglings cooperatively. In five cases out of 11 polygynous territories among a total of 97 breeding territories, females consisted of mothers and daughters.

Second is brood-parasitism. In the investigation by Gibbons [9], 20% of females laid their eggs in the nests of others. The average number of such eggs laid in the nests of others was four. After such parasitic females had laid eggs in the nests of others during the early part of breeding season, they then laid eggs in their own nests. The host did not remove eggs laid by parasites, and brought them up as well as her own fledglings. However, the expected survival rate of parasitic eggs could be regarded as low. The reasons are as follows: Parasitic females dumped their eggs some time after the host had initiated her own clutch. Therefore, those dumped eggs in general hatched later than do the eggs of host, so that the fledglings from the parasitism were subordinate in physical strength compared with the host's own fledglings. So the survival probability of dumped eggs was low relative to that of the host's own offspring. Also, many of the eggs dumped in the latter half of host's hatching period were deserted because the host did not hatch eggs after the host's own fledglings left the nest. From this argument, we can consider that the dumped eggs are at a disadvantage with respect to survival.

Lyon [10] theoretically discussed the optimal clutch size under intra-specific brood-parasitism. He gave a possible theoretical explanation for the possibility that, under intra-specific brood-parasitism in which every individual is assumed to be parasitic and might become host for the other, the clutch size could be smaller than the 'Lack clutch size' [11] predicted by the limitation of food amount parents could provide for their offsprings. Further, he also reported data from a field study of American coots *Fulica americana*, which supports his theoretical arguments.

Maruyama and Seno [12] considered an aspect of the intra-specific brood-parasitism using mathematical modelling. As in the case of the moorhen, *Gallinula chloropus*, in the case dealt with in their paper it was assumed that just a part of the whole population has parasitic behaviour against the individuals belonging to another subpopulation that does not have parasitic behaviour. Analyzing the expected fitness gain from the brood-parasitism, they considered the condition that parasitic individuals coexist with non-parasitic ones within a population. From their mathematical modelling analysis, it was shown that a stable equilibrium frequency of parasite individuals within a population, if it exists, depends on the difference among individuals in terms of the individual quality reflected in the survival probability of offspring being raised. As discussed by a mathematical population dynamics in May et al. [13], the evolutionary process could cause the parasitism disappear from the population, or keep it failing to invade the population. However, Maruyama and Seno [12]

showed the possibility of the stable coexistence of parasitic and non-parasitic individuals within a population.

In this paper, for the case of intra-specific brood-parasitism in which the parasitic individuals and the non-parasitic individuals (i.e. possible hosts) could stationarily coexist with each other, we consider the optimal strategy for intra-specific brood-parasitism, especially focusing on the number of eggs laid by the parasite in the nest of a host that does not reject the parasite's eggs. With a mathematical model, assuming that the survival probability of parasite's offspring in the nest of a host is significantly smaller than in the parasite's own nest, we determine the optimal number of eggs laid in the nest of the host to maximize the expected fitness for the parasite. Moreover, the dependence of the optimal strategy for the brood-parasitism on the total number of eggs laid by the parasitic individual is also discussed.

2. Assumptions and modelling

From the data on the moorhen, *Gallinula chloropus*, reported by Gibbons [9], more than 60% of observed parasitized nests had eggs from just two different female individuals, and around 70% of observed parasitic females laid their eggs in their own nests and just one other nest. In addition, the observation of behaviour of parasitic females indicates that the parasite tends to perform her parasitic behaviour before making her own nest and stops her parasitic behaviour after making it. As a general tendency, brood-parasitism can be observed mainly in the early half of breeding season, and becomes rare in the latter half. These observed facts can be regarded as characterizing the specific natures of intra-specific brood-parasitism of the moorhen, in contrast, for instance, with that of American coots *Fulica americana* reported by Lyon [10], in which every individual is assumed to be parasitic and might become host for the other.

From the above-mentioned observed facts, in this paper, we consider the mathematical modelling with the following assumptions: The whole population consists of separate parasite and host subpopulations; the parasite does not parasitize the nest of any other parasite; the host population is large enough that exploitative competition among parasites over hosts can be neglected; for each host, parasitism by more than one parasite does not occur in the breeding season under consideration; and each parasite parasitizes a specific host, and does not utilize more than one host; that is, each parasite individual is related to a host nest that is different from the host nest of any other parasite.

In our assumptions, the existence of two subpopulations of parasite and host in the considered population does not necessarily mean the existence of two strains in terms of parasitic behaviour. We just assume that, from the viewpoint of optimal behaviour to maximize fitness, there exist two types of

reproductive behaviours: one is parasitic and another is without any parasitic behaviour. So we might consider such a case that, in the earlier part of breeding season, one part of population could get the appropriate nest sites, while another part could not. In such a case, the latter part would take the parasitic behaviour, while the former part would not. In the observation of moorhen by Gibbons [9], the younger females tended to have the parasitic behaviour. This may mean that the younger females could not get nest sites appropriate for high reproductive fitness, for instance, because they lost the competition for nest sites due to their relatively small body size. In this case, each individual could have both non-parasitic and parasitic behaviours during its lifetime, depending on their age or body size.

Let k_s and k_b be, respectively, the number of eggs laid by the parasite in the own nest of parasite and in the nest of host, and let k_t denote the total number of eggs the parasitic individual lays per breeding season. Then, the relation among k_s , k_b and k_t is

$$k_s + k_b = k_t. \tag{1}$$

The following assumptions are made for the mean or expected survival probability P_s of the fledgling with its own parents' care and P_b with the host parents' care:

$$P_s = P_s(k_s), \text{ a monotonically non-increasing function of } k_s; \tag{2}$$

$$P_b = P_b(k_b), \text{ a monotonically non-increasing function of } k_b; \tag{3}$$

$$0 \leq P_b(k) \leq P_s(k) \quad (0 \leq \forall k \leq k_t). \tag{4}$$

Assumptions (2) and (3) mean that the survival probability of the nestling decreases as the number of eggs in the same nest gets larger. This is because the larger the number of eggs in the same nest, the smaller the amount of food there is per nestling. Condition (4) means that the survival probability with its own parents' care is not less than that with the host parents' care. The reason that we assume condition (4) is that parasite's eggs dumped in the host's nest in general hatch later than the host's own eggs do, and the parasite's fledglings are subordinate in physical strength compared with the host's own fledglings, so the survival probability of parasite's eggs dumped in the host's nest can be considered rather low.

We define the fitness F for the parasite individual as the following reproductive success:

$$F = k_s P_s + k_b P_b. \tag{5}$$

From relation (1), the fitness F can be rewritten as follows:

$$F(k_b) = (k_t - k_b) P_s(k_t - k_b) + k_b P_b(k_b). \tag{6}$$

In this paper, as a convention of mathematical modelling, we consider the following functions for P_s and P_b :

$$P_s = P_s(k_s) = \begin{cases} -\frac{b_1}{c_1}k_s + b_1 & (0 \leq k_s < c_1), \\ 0 & (k_s \geq c_1), \end{cases} \tag{7}$$

$$P_b = P_b(k_b) = \begin{cases} -\frac{b_2}{c_2}k_b + b_2 & (0 \leq k_b < c_2), \\ 0 & (k_b \geq c_2), \end{cases} \tag{8}$$

where $0 < b_2 \leq b_1 \leq 1$ and $0 < c_2 \leq c_1$ from the assumption (4) (see Fig. 1). These functions mean that, if the number of parasite’s eggs in a nest is above a critical value, the expected survival probability is zero. This is a simplification in our mathematical modelling. Instead of (7) and (8), we could assume some monotonically decreasing function that asymptotically approaches zero, such as an exponential function. However, such assumed functions could frequently increase some of the difficulties in the mathematical analyses which are not essential for our arguments. In our discussion about the results from this modelling, the effect of zero survival probability will be translated as that of extremely low survival probability.

The parasite is expected to select its strategy so as to maximize the fitness $F(k_b)$. The strategy is now represented by the choice of k_b . We analyse the model and determine what value of k_b , say k_b^* , leads to maximal fitness $F(k_b^*)$, depending on the total number of eggs k_t and the other parameters.

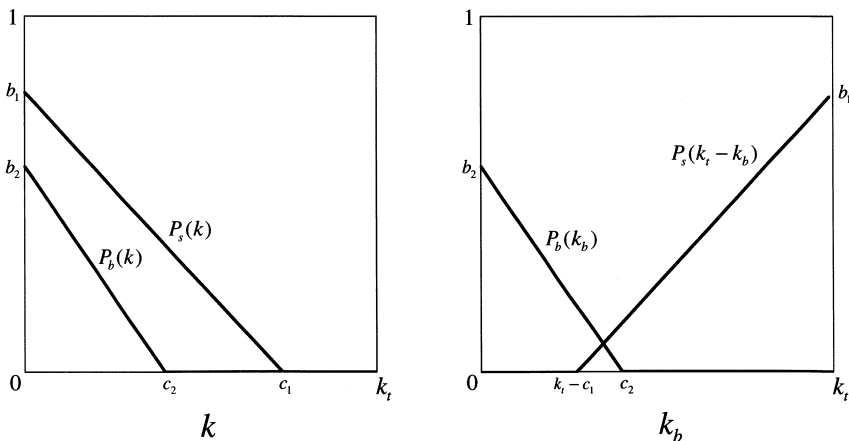


Fig. 1. The survival probabilities P_s and P_b given by (7) and (8) with the condition (4).

3. Analysis

3.1. Optimal number of parasitized eggs

3.1.1. Parameter translation

Now, for mathematical convenience, we define the following:

$$K_b \equiv \frac{k_b}{c_1},$$

$$K_t \equiv \frac{k_t}{c_1},$$

$$B \equiv \frac{b_2}{b_1},$$

$$C \equiv \frac{c_2}{c_1}.$$

From assumption (4), $0 < C \leq 1$ and $0 < B \leq 1$.

We note that the fitness F given by (6) with (7) and (8) is always a parabolic function of k_b , which can be rewritten with K_b , K_t , B and C as follows:

$$F(K_b) = b_1 c_1 \left\{ (K_t - K_b)(1 - K_t + K_b)\theta_s + BK_b \left(1 - \frac{K_b}{C} \right) \theta_b \right\}, \tag{9}$$

where

$$\theta_s = \begin{cases} 1 & \text{for } K_t - 1 < K_b \leq K_t, \\ 0 & \text{for } K_b \leq K_t - 1, \end{cases} \tag{10}$$

$$\theta_b = \begin{cases} 1 & \text{for } 0 \leq K_b < C, \\ 0 & \text{for } C \leq K_b \leq K_t. \end{cases} \tag{11}$$

To consider the maxima of $F(K_b)$ given by (9), we analyze the following function φ of K_b :

$$\varphi(K_b) = \frac{F(K_b)}{b_1 c_1} = (K_t - K_b)(1 - K_t + K_b)\theta_s + BK_b \left(1 - \frac{K_b}{C} \right) \theta_b. \tag{12}$$

We find that $\varphi(K_b)$, that is, $F(K_b)$, can have a variety of shapes, depending on the parameters B and C , as shown in Fig. 2.

In one case, $F(K_b)$ has no maximal extremum for $0 \leq K_b \leq K_t$, and takes its maximal value when $k_b = 0$ (the case of I_0 in Fig. 2). In the other cases, it has one or more than one (three at most) maximal extrema: The possible maxima are $K_b = C/2$, \hat{K}_b , $K_t - 1/2$, where

$$\hat{K}_b = \frac{C}{B + C} \left(K_t - \frac{1 - B}{2} \right). \tag{13}$$

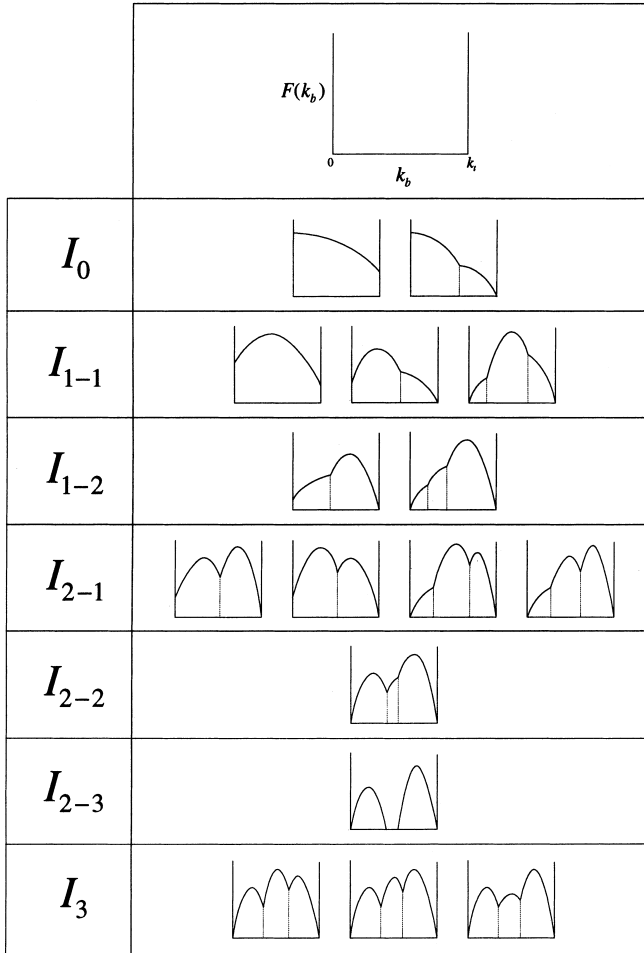


Fig. 2. Graphs of $F(k_b)$. The shape of graph significantly depends on the parameters. Each of seven categories of I_i corresponds to a parameter region. The shape of graph is categorized by the number of extremal maxima, and the composition of values of k_b for those extremal maxima. For a detailed explanation, see the main text.

3.1.2. Cases with unique maximum

In the case of I_{1-1} in Fig. 2, the unique maximal extremum of φ is at $K_b = \hat{K}_b$, and

$$\varphi(\hat{K}_b) = \frac{1 + BC}{4} - \frac{B}{B + C} \left(K_t - \frac{1 + C}{2} \right)^2.$$

In case of I_{1-2} in Fig. 2, the unique maximal extremum of φ is at $K_b = K_t - 1/2$, and the maximal value of φ is $1/4$.

3.1.3. Cases with two or three maxima

In the case of I_{2-1} in Fig. 2, there are two distinct maximal extrema of φ , which are at $K_b = \widehat{K}_b$ and $K_b = K_t - 1/2$. We can easily prove that it is always true that $\widehat{K}_b \leq K_t - 1/2$. In contrast, in the case of I_{2-2} , two distinct maximal extrema are at $K_b = C/2$ and $K_b = K_t - 1/2$. We can easily prove that it is always true that $C/2 < K_t - 1/2$ whenever these two maxima appear. Since the value of φ at $K_b = C/2$ is $BC/4$, and since $B \leq 1$ and $C \leq 1$ from our modelling assumption (4), the extremal value at $K_b = C/2$ is always less than or equal to $K_b = K_t - 1/2$.

The case of I_{2-3} is a specific one, when two distinct maximal extrema at $K_b = C/2$ and $K_b = K_t - 1/2$ appear with a finite range of K_b with which the fitness F is zero.

There is another case when three maximal extrema exist, as shown by I_3 in Fig. 2. The extremal maxima are at $K_b = C/2$, \widehat{K}_b , $K_t - 1/2$, and the value of F at $K_b = C/2$ is always less than or equal to $K_b = K_t - 1/2$, while the relative value of F at $K_b = \widehat{K}_b$ significantly depends on the parameters B and C .

From the results indicated by Fig. 2, we can immediately conjecture that our model shows the possible existence of polymorphism in the strategy of brood-parasitism, since some cases in Fig. 2 show the existence of more than one local maximum: The strategically selected number of parasitized eggs per individual could be different depending on which population is considered. In other words, different parasitism behaviours could be observed in different populations even within the same species. However, in the subsequent sections, we will show that the possible evolution of the total number of eggs laid by the parasite in order to make its fitness increase would make those local maxima disappear and eliminate the possibility of the occurrence of polymorphism.

3.1.4. Dependence on total number of eggs

Occurrence of each case in Fig. 2 is determined by the parameters B and C involved in our model. With some cumbersome and careful calculations about the function φ , we can describe the dependence of the graph shape of φ , that is, of F on the parameters B and C as shown in Fig. 3. For larger values of K_t ; that is, as the total number of eggs per individual gets larger, the polymorphism would be more likely to occur.

In contrast, for sufficiently small values of K_t , when the total number of eggs per individual is sufficiently small, the maximal fitness is realized with $K_b = 0$; that is, when brood-parasitism is not optimal.

Case I_0 : In detail, as seen from Fig. 3, the optimality of brood-parasitism depends only on B and K_t , and does not depend on C : If

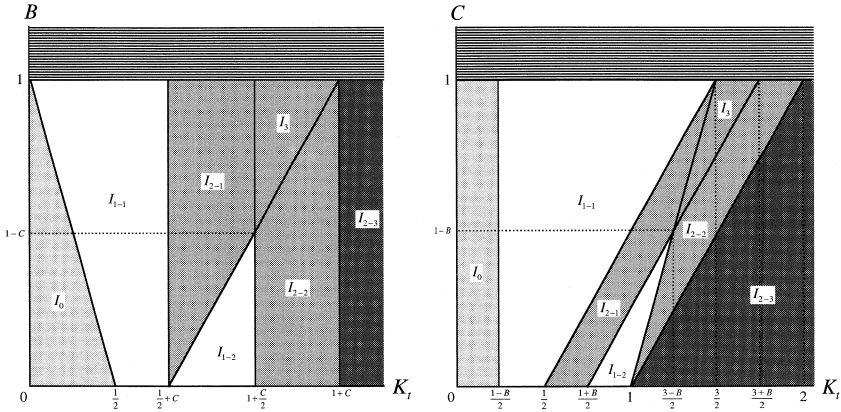


Fig. 3. The parameter dependence of the shape of graph of $F(k_b)$. Positive parameters B and C are not beyond 1 from the assumption (4). Each region corresponds to the category of the shape of graph of $F(k_b)$, shown in Fig. 2. The region I_0 indicates the case when the maximal fitness can be obtained by $k_b = 0$, which is the case when the brood-parasitism is not favoured. Blank regions represent the case where there exists a unique $k_b = k_b^*$ that maximizes the fitness F . Gray regions, except for I_0 , represent the case when there exist more than one local maxima of F for different values of k_b . For the detail explanation, see the main text.

$$K_t \leq \frac{1 - B}{2}, \tag{14}$$

$F(k_b)$ is monotonically decreasing in terms of k_b , corresponding to the case I_0 in Fig. 2. Hence, the optimal number k_b^* of eggs which the parasite lays in the host's nest is zero: $k_b^* = 0$, $F(0) = K_t(1 - K_t)$. In this case, as a result, brood-parasitism cannot spread within the population. The smaller the number of eggs which the parasite lays in the host's nest is, the larger the fitness of the parasite is. The larger b_1 or c_1 is, the wider the range of k_t that satisfies the condition (14). That is, the larger the survival probability of nestlings in their own parents' care is, the wider the range of k_t which satisfies the condition (14).

If $B = 1$, that is, if $b_1 = b_2$, the survival probability of nestlings under the host parent's care with small k_b is almost as same as that of nestlings under their own parent's care. In this case, the fitness gain of the parasite from eggs laid in the host's nest is sufficiently high that parasitism could cause an increase in the parasite's fitness, since the survival probability increases due to the reduction of the number of eggs in the female's own nest.

Case I_{1-1} : Next, if

$$\frac{1 - B}{2} < K_t \leq \frac{1}{2} + C,$$

$F(k_b)$ has the graph of I_{1-1} in Fig. 2 (see also Fig. 3). Then, the optimal number of eggs which parasite lays is given by $K_b^* = \widehat{K}_b$, that is,

$$k_b^* = c_1 \widehat{K}_b = \frac{c_2/c_1}{b_2/b_1 + c_2/c_1} \left(k_t - \frac{1 - b_2/b_1}{2} c_1 \right).$$

For the spread of brood-parasitism within the population, an intermediate optimal number of eggs laid by the parasite in the host’s nest would be required. In this case, since the maximum of $F(k_b)$ is globally unique, the optimal parasite would be uniquely identified as one which lays k_b^* eggs in the host’s nest.

Case I_{1-2} : In contrast, if

$$\frac{1 + B + 2C}{2} \leq K_t \leq 1 + \frac{C}{2},$$

$F(K_b)$ has the graph of I_{1-2} in Fig. 2, with the globally unique maximum at $K_b = K_t - 1/2$, that is, $k_b^* = k_t - c_1/2$. Then the maximal fitness value of F is $b_1 c_1/4$. This is the case similar to the previous one with the globally unique strategy k_b^* to maximize the fitness F .

Case I_{2-1} : If

$$\frac{1}{2} + C < K_t \leq \min \left(1 + \frac{C}{2}, \frac{1 + B + 2C}{2} \right),$$

$F(k_b)$ has the graph of I_{2-1} in Fig. 2, with two local maxima at $K_b = \widehat{K}_b$ and $K_b = K_t - 1/2$. This is a case of possible polymorphism for brood-parasitism. The global maximum at $k_b = k_b^*$ is determined by the parameters B , C , and K_t :

$$k_b^* = \begin{cases} c_1 \widehat{K}_b & \text{for } K_t < \kappa_c, \\ k_t - \frac{c_1}{2} & \text{for } K_t \geq \kappa_c, \end{cases} \tag{15}$$

where

$$\kappa_c = \frac{C + 1 + \sqrt{C(B + C)}}{2}. \tag{16}$$

Cases I_{2-2} and I_{2-3} : If

$$\max \left(1 + \frac{C}{2}, \frac{1 + B + 2C}{2} \right) < K_t, \tag{17}$$

$F(k_b)$ has the graph of I_{2-2} or I_{2-3} in Fig. 2, with two local maxima at $K_b = C/2$ and $K_b = K_t - 1/2$. As already mentioned, in this case, the global maximum is always at $K_b = K_t - 1/2$, and the maximal value of F is $b_1 c_1/4$. Especially, in case of I_{2-3} , when

$$1 + C \leq K_t,$$

there is a range of values of k_b for which fitness is zero between these two maxima. So, the occurrence of polymorphism is significantly suggested,

because such a parameter range would indicate a large cost for the transition between those two strategies represented by $K_b = C/2$ and $K_b = K_t - 1/2$.

Case I_3 : In case of I_3 in Fig. 2, that is, if

$$1 + \frac{C}{2} < K_t < \frac{1 + B + 2C}{2}, \tag{18}$$

there exist three local maxima. From the above-mentioned arguments, one of them, at $K_b = C/2$, cannot become the global maximum. The global maximum is either at $K_b = \widehat{K}_b$ or at $K_b = K_t - 1/2$, which is determined by (15) again.

*3.1.5. Parameter dependence of k_b^**

In Fig. 4, we show the variation of $K_b = K_b^*$, that is, $k_b = k_b^*$, for which the global maximum of the fitness F is realized, in terms of K_t . It is shown that k_b^* is linearly increasing as the total number k_t of eggs per individual gets larger, although the increment has a discontinuous jump at $K_t = \kappa_c$ given by (16). For $K_t < \kappa_c$, K_b^* becomes larger as the parameter C gets larger. In addition, we can prove that for $K_t < (1 + C)/2$, K_b^* becomes larger as the parameter B gets larger, whereas it becomes smaller for $(1 + C)/2 < K_t < \kappa_c$. K_b^* for $K_t > \kappa_c$ is independent of parameters B and C , since it is $K_t - 1/2$.

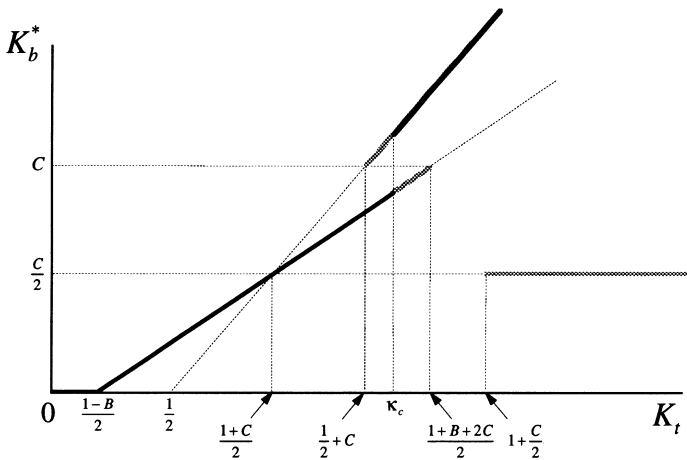


Fig. 4. The value $K_b = K_b^*$ that maximizes the fitness F when $B < 1 - C$. The case when $B \geq 1 - C$ is analogous. The bold lines indicate the value K_b^* corresponding to the global maximum of F . The gray segments indicate the value K_b for the existing local maxima. The value K_b^* has a discontinuity at $K_t = \kappa_c$ given by (16).

3.2. Invasion success of brood-parasitism

From Figs. 3 and 4, we can see that, if condition (14) is satisfied, the optimal strategy for the parasite is represented by $k_b^* = 0$, which means that the brood-parasitism is not adaptive, as mentioned also in the previous section.

Conversely, if the following condition is satisfied,

$$k_t > \frac{c_1}{2} \left(1 - \frac{b_2}{b_1} \right), \tag{19}$$

the invasion of brood-parasitism is successful, because the satisfaction of (19) means that the optimal strategy for the parasite is represented by $\exists k_b^* > 0$. Condition (19) is necessary and sufficient for the successful invasion of brood-parasitism.

Condition (19) for successful invasion could be fulfilled if k_t is sufficiently large and the parasite is sufficiently reproductive, or if c_1 is sufficiently small and the survival probability of nestlings raised by the parasite herself decreases steeply as the number of eggs increases in the same nest, or if b_2/b_1 is sufficiently close to, but less than 1 and the disadvantage of nestlings in the host's nest, compared to those in their own parent's nest, is small in terms of the difference of survival probability.

In the evolutionary process, those parameters c_1 , b_1 , and b_2 could be changed as well as k_t could. Probably, the evolutionary changes of these parameters would be correlated. However, now for given parameters except for k_t , we can consider the optimal clutch size of k_t that maximizes the reproductive success of female when parasitism does not exist within the considered population. This is what is called the 'Lack clutch size' [11]. In this case, the expected reproductive success is given by $k_t P_s(k_t)$. Thus, from (7), we can easily see that the optimal clutch size is given by $k_t = c_1/2$ in this case. So, if we apply this resulting optimal clutch size $k_t = c_1/2$ for (19), we can immediately see that condition (19) is always satisfied, independent of the value of any parameter, as seen also from Figs. 3 and 4. This would mean that, in our model, the brood-parasitism could eventually successfully invade the considered population. However, if the population could not realize the optimal clutch size due to some trade-offs with the other evolutionary factors, the clutch size smaller than the optimal might cause the failure of the invasion of brood-parasitism.

3.3. Optimal parasitism ratio

In this section, we consider the optimal parasitism ratio $\lambda^* = k_b^*/k_t = K_b^*/K_t$, where k_b^* depends on the other parameters, b_1 , b_2 , c_1 , c_2 and k_t as shown in the previous section. In Fig. 5, we show the typical configuration of λ^* against K_t .

Fundamentally λ^* is monotonically increasing as the total number of eggs per individual gets larger. The increment has a discontinuous jump at $K_t = \kappa_c$

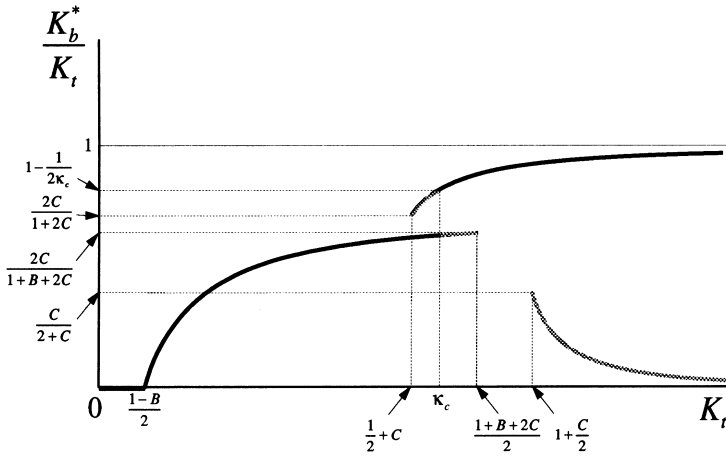


Fig. 5. The optimal parasitism ratio $\lambda^* = K_b^*/K_t = k_b^*/k_t$ when $B < 1 - C$. The case when $B \geq 1 - C$ is analogous. The bold curves indicate the ratio determined by the global maximum of F . The gray partial curves indicate the ratio determined by the local maxima. The ratio is monotonically increasing in terms of K_t with a discrete jump at $K_t = \kappa_c$ given by (16), and asymptotically approaches $C/(B + C)$ for $K_t < \kappa_c$, while does 1 for $K_t > \kappa_c$. See also the corresponding Fig. 4.

given by (16) (see also Fig. 4). As K_t gets larger, the ratio λ^* asymptotically approaches $C/(B + C)$ for $K_t < \kappa_c$, and approaches 1 for $K_t > \kappa_c$.

This result about the monotonically increasing feature of optimal parasitism ratio in terms of the total number of eggs per individual corresponds to that derived for another mathematical model analyzed in Yamauchi [5], although he analyzed a quantitative genetic model to discuss the evolution of intra-specific brood-parasitism, different from our fundamental modelling focusing the optimality of parasitic behaviour.

As with K_b^* mentioned by Fig. 4 in the previous section, also for $K_t < \kappa_c$, λ^* becomes larger as the parameter C gets larger. Also, for $K_t < (1 + C)/2$, λ^* becomes larger as the parameter B gets larger, whereas it becomes smaller for $(1 + C)/2 < K_t < \kappa_c$. λ^* for $K_t > \kappa_c$ is independent of parameters B and C , since it is $1 - 1/2K_t$.

We find that c_1 and c_2 exert significant influence on the optimal parasitism ratio λ^* . We demonstrate it with a numerical example shown as Fig. 6. Fig. 6(a) shows the case when c_1 and c_2 are relatively large, and Fig. 6(b) shows the case when they are relatively small. In the case of Fig. 6(a), the optimal parasitism ratio is around 44% for $k_t = 8.0$. On the other hand, in the case of Fig. 6(b), the optimal parasitism ratio is around 78% for $k_t = 8.0$. In the case of Fig. 6(a), 44% of total number 8.0 of eggs corresponds to around 3.5. Then, we find from Fig. 6(a) that the fitness of these dumped eggs is positive with a positive survival probability. In contrast, in the case of Fig. 6(b), 78% of the total number

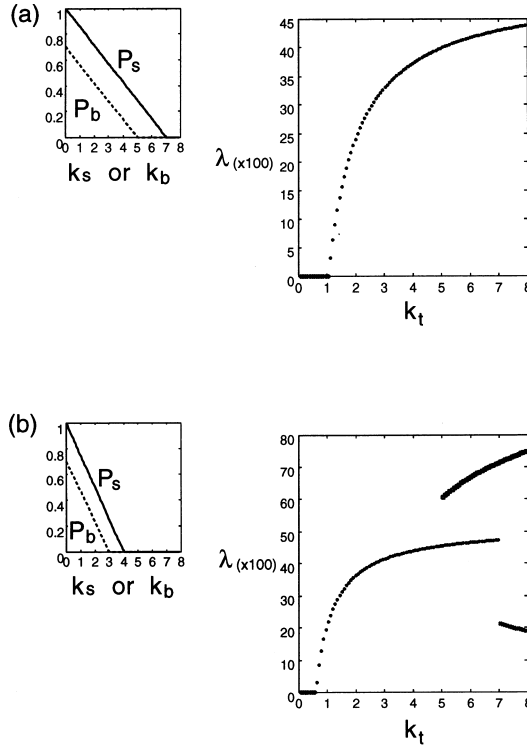


Fig. 6. Numerical example of the parasitism ratio $\lambda = K_b/K_t = k_b/k_t$. See also Fig. 5. For the survival probabilities P_s and P_b : (a) with relatively gradual variations; (b) with relatively steep variations.

8.0 of eggs corresponds to around 6.24, and we find from Fig. 6(b) that the fitness of these dumped eggs is 0 because the survival probability is zero. This result means that there could be a case such that the optimal parasite would tend to desert some eggs in order to raise the expected fitness of eggs in her own nest. We will argue this case in more detail in the next section.

3.4. Parasitism with egg desertion

As mentioned in the previous section, some optimal level of parasitism involves the desertion of some eggs with zero survival probability as a result of optimal parasitic behaviour.

From (7) and (8) ((10) and (11)), too many eggs laid in a nest could cause the total extinction because of zero survival probability. As seen from Fig. 4, if $K_t > \kappa_c$, the globally optimal number of parasitized eggs, K_b^* , is $K_t - 1/2$, and is larger than C . The case is of I_{1-2} or I_{2-1} indicated in Figs. 2 and 3. Then, from

(11), we can see that $P_b = 0$ in this case, while $P_s > 0$ from (10) because $K_b^* = K_t - 1/2$. This is indeed the case mentioned in the previous section: the optimal parasite deserts some eggs (k_b^*) to raise the expected fitness gain via the eggs in her own nest. In other words, such an optimal parasite gains in fitness just from the nestlings raised by herself. This argument is valid also for the case of locally optimal parasitism with $K_b = K_t - 1/2$, which exists when $1/2 + C < K_t < \kappa_c$ as shown in Figs. 3 and 4.

In such a case, the parasite should stop brood-parasitism in order to save the cost of it, because the parasitism makes no contribution to her fitness. To get the same amount of fitness, the parasite should decrease the total number of eggs, and lay no more eggs than the number of eggs hatched and raised by herself.

This argument means a decrease in the total number k_t of eggs per parasite from the viewpoint of the optimal behaviour for the parasite individual. As seen from Fig. 4, this decrease of the total number of eggs could continue until it becomes $1/2 + C$, because the globally or locally optimal parasitism with $K_b = K_t - 1/2$ exists for K_t greater than $1/2 + C$. Once the total number of eggs reaches $1/2 + C$, the optimal parasitism becomes globally unique with $K_b^* = \hat{K}_b$ given by (13), as seen from Fig. 4. Hence, the optimal parasitism must transit to that with $K_b^* = \hat{K}_b$, when both P_s and P_b are positive so that eggs laid both in the host's nest and in the parasite's own nest make a contribution to the parasite's fitness.

On the other hand, from (10), if $K_b^* \leq K_t - 1$, then $P_s = 0$ so that all nestlings raised by the parasite herself would fail to survive. We can see from Fig. 4 that such a case could occur for the locally optimal parasitism with $K_b = C/2$, which could appear in cases of I_{2-2} , I_{2-3} , and I_3 of Figs. 2 and 3. In this case, the parasite gains in fitness just from the nestlings in the host's nest. Since the raising of nestlings certainly requires some cost for the parent, the parasite should not raise the nestlings by herself, and in turn, should not lay more eggs than $C/2$.

This argument means again an decrease in the total number k_t of eggs per parasite from the viewpoint of the optimal behaviour for the parasite. As seen from Figs. 3 and 4, such a decrease of the total number of eggs per parasite causes the transition of parasitism from the locally optimal $K_b = C/2$ to the globally optimal $K_b^* = K_t - 1/2$, when the case changes from I_{2-2} , I_{2-3} , or I_3 to I_{1-2} or I_{2-1} . Then, the situation corresponds to the case mentioned above. Therefore, this argument concludes that the case with the locally optimal parasitism with $K_b = C/2$ would not be stationary, and would be at a transient stage in the evolution of brood-parasitism.

Lastly, we conclude that parasitism with desertion of eggs would be a transient on the way of evolution of the parasitic behaviour, and the behavioural evolution carries the brood-parasitism into such condition that eggs laid both in the host's nest and in the parasite's own nest make a contribution to the

parasite’s fitness, so that the apparent egg desertion mentioned in the above arguments disappears. In other words, to gain a greater fitness, any locally optimal parasitism will disappear, so that the polymorphism will disappear as well, if the cost to reduce the total number of eggs is sufficiently small.

3.5. Optimal total number of eggs

In this section, we consider $F(k_b^*)$ to be a function of the total number of eggs per individual, k_t . Fig. 7 shows the typical relation between $\varphi(K_b^*) = F(k_b^*)/b_1c_1$ and the parameters involved. We find that there always exists the unique total number of eggs, $K_t = K_t^* = (1 + C)/2$, that is,

$$k_t = k_t^* = \frac{c_1 + c_2}{2}, \tag{20}$$

that maximizes the fitness of the optimal parasite which lays k_b^* eggs in the nest of the host. This means that the parasite with the total number k_t^* of eggs would be favoured and would spread within the population, with the optimal behaviour to lay k_b^* eggs in the nest of host.

As already mentioned in the previous section about the invasion success of brood-parasitism, for given parameters except for k_t , we can consider the optimal clutch size of k_t that maximizes the reproductive success of female when parasitism does not exist in the considered population, and it is obtained as $k_t = c_1/2$. Let us call here this size by the ‘Lack clutch size’ [11]. From (20), the optimal total number of eggs per parasitic individual is greater than the Lack clutch size.

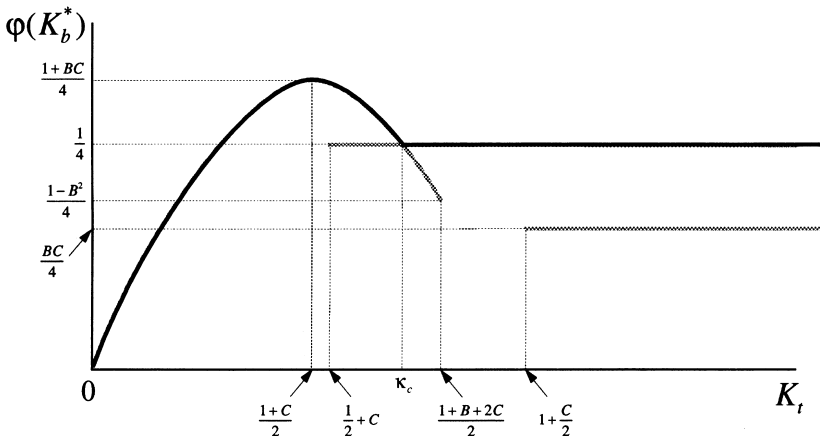


Fig. 7. The maximized fitness $F(k_b^*)$. $\varphi(K_b^*) = F(k_b^*)/b_1c_1$. The case when $B < 1 - C$. The case when $B \geq 1 - C$ is analogous. The bold curves indicate the fitness of the global maximum. The gray segments and curve indicate the fitness of the local maxima. The fitness takes its maximal when $K_t = (1 + C)/2$.

From our results given by Figs. 3 and 4, the maximal fitness realized by $k_t = k_t^*$ is the case of I_{1-1} . Since the optimal number of parasitized eggs is $K_b = \widehat{K}_b$ in the case of I_{1-1} , the best of the optimal parasitisms is uniquely determined by the optimal number k_b^* of parasitized eggs with $k_t = k_t^*$:

$$k_b^* = c_1 \widehat{K}_b \Big|_{K_t=K_t^*} = c_1 \cdot \frac{C}{2} = \frac{c_2}{2}. \quad (21)$$

Then, the optimal parasitism ratio $\lambda^* = k_b^*/k_t^*$ becomes

$$\lambda^* = \frac{c_2}{c_1 + c_2}. \quad (22)$$

Also, simultaneously, the best of the optimal brood-parasitisms involves the optimal number k_s^* of eggs the parasite raises by herself:

$$k_s^* = k_t^* - k_b^* = \frac{c_1}{2}. \quad (23)$$

This argument indicates that the optimal parasitic female lays eggs equal to the Lack clutch size in her own nest. This result is equivalent to that derived for another mathematical model analysed in Yamauchi [5], although he analyzed a quantitative genetic model to discuss the evolution of intra-specific brood-parasitism, different from our fundamental modelling focusing the optimality of parasitic behaviour. Our modelling consideration implies that, without taking account of some quantitative genetic factors into mathematical modelling, some essential results could be derived as some corresponding forms.

With the values k_b^* and k_s^* , the survival probabilities of the parasite's nestlings, respectively, in the host's nest and in the parasite's own nest are determined from (7) and (8) as follows:

$$P_s(k_s^*) = \frac{b_1}{2}, \quad (24)$$

$$P_b(k_b^*) = \frac{b_2}{2}. \quad (25)$$

Moreover, from Fig. 7, the maximum of the maximal fitness with (20) and (21) is

$$F(k_b^*) \Big|_{k_t=k_t^*} = b_1 c_1 \cdot \varphi(K_b^*) \Big|_{K_t=K_t^*} = \frac{b_1 c_1 + b_2 c_2}{4}. \quad (26)$$

From the arguments in the previous section, from the viewpoint of the higher fitness obtained by the brood-parasitism, any case except for I_0 and I_{1-1} would be transient to the case of I_{1-1} . In addition, from Fig. 7, it is clear that the case of I_{1-1} can provide higher fitness than that of I_0 . This means that, if the cost to increase the total number of eggs per parasite individual could be reasonable so as to shift the case of I_0 to I_{1-1} , the population without brood-parasitism in case of I_0 could be vulnerable to the invasion of the

brood-parasitism that increases the fitness gain of parasitic individual. Hence, we can conclude that the evolution of brood-parasitism to maximize the parasite's fitness would tend to reach the parasitic strategy with (20) and (21).

4. Conclusion

We found conditions for the successful invasion of brood-parasitism within a population. If the reproductive capacity per individual is sufficiently high, and the total number of eggs per individual is sufficiently large, brood-parasitism could successfully invade the population and spread. If, on the other hand, the reproductive capacity per individual is rather low and the total number of eggs per individual is very small, brood-parasitism would not be optimal, and would not spread within the population. Our modelling analysis implies that the reproductive capacity critical according to the invasion success depends considerably on the difference in survival probabilities of the parasite's nestlings respectively in the host's nest and in the parasite's own nest.

Our mathematical modelling considerations imply some possibility of the occurrence of polymorphism with regard to the optimal parasitic behaviour: The optimal parasitism ratio with which the favoured parasite individual lays a portion of the total eggs in the host's nest could be different depending on the particular population. Such polymorphism could occur when the total number of eggs per parasite individual is sufficiently large. However, our modelling analysis implies that the brood-parasitism with such possible polymorphism could provide smaller fitness than the case without such polymorphism. That is, the fitness provided by the brood-parasitism with a uniquely determined parasitism ratio would be larger than that provided by the brood-parasitism with some possibility of polymorphism. Especially, by our analysis, such brood-parasitism that provides the larger fitness requires an intermediate number of eggs per parasite individual. So, even if the polymorphism exists, with a reasonably low cost to reduce the number of eggs per parasite individual, the polymorphism of brood-parasitic behaviour would tend to disappear eventually and transit to the unique optimal behaviour that can provide greater fitness.

According to the observations by Gibbons [9] etc., $k_t = 5 - 8$, and $k_b \approx 4$. If the observed brood-parasitism is to be the best possible optimal one, our modelling analysis shows that, from the resulting relationships (20) and (21), $c_1 + c_2 = 10 - 16$, and $c_2 \approx 8$. Hence, $c_1 = 2 - 8$. With our modelling assumption (4), our model requires the condition $c_1 \geq c_2$. Therefore, from our modelling considerations, we can estimate the following: $c_1 \approx 8$ and $c_2 \approx 8$ with $c_1 \geq c_2$. With this estimated value of c_1 , and $k_t \approx 8$, condition (19) for the successful invasion of brood-parasitism is simultaneously satisfied for any b_1 and b_2 which satisfy the assumed condition that $b_1 \geq b_2$.

Our mathematical modelling is different from that by Yamauchi [5,6], in which he analyzed a quantitative genetic model to discuss the evolution of intra-specific brood-parasitism, since our fundamental modelling is focusing the optimality of parasitic behaviour without taking account of some genetic factors, for instance, the cost of parasitism or the evolution of rejective behaviour of host. However, some of our results essentially correspond to his. Thus, we can think that some of our results about the intra-specific brood-parasitism would have a kind of generality related to the fundamental nature of the brood-parasitism.

Our mathematical modelling and arguments are qualitatively different from those of Lyon [10]. This is because the intra-specific brood-parasitism of moorhen that we intuitively referred for our modelling contrasts in its specific nature, for instance, with that of American coots *Fulica americana* reported by Lyon [10], in which every individual is assumed to be parasitic and might become host for the other. So our results could be qualitatively (and carefully) compared to his results, though these two arguments have been carried out for different types of intra-specific brood-parasitisms.

Although our mathematical modelling considerations focused the intra-specific brood-parasitism, we think that our mathematical modelling could be applied to inter-specific brood-parasitism. Some results presented in this paper might be perhaps applicable also to the discussion about the inter-specific brood-parasitism.

We expect that our arguments by a mathematical model can at least intuitively give some perspectives or stimuli for any researches about intra-specific or inter-specific brood-parasitism.

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