Mathematical modelling for intra-specific brood-parasitism: coexistence between parasite and non-parasite

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Abstract

In this paper, we consider an aspect of the intra-specific brood-parasitism with a mathematical modelling. As in case of moorhen *Gallinula chloropus*, the case dealt with in this paper in such that just a part of the whole population has the parasitising behaviour against the individuals belonging to another part of non-parasite subpopulation that does not have such behaviour. Analysing the expected fitness gain from the brood-parasitism, we consider the condition in order that parasite individuals coexist with non-parasite ones within a population. From the mathematical modelling analysis, it is shown that the stable equilibrium frequency of parasite individuals within a population, if exists, depends on the difference among individuals in terms of the individual quality reflected to the survival probability of bred offsprings. © 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 (for instance, see Refs. [1,2]). There are two categories of such nest parasitism. One is inter-specific brood-parasitism in which eggs are laid in the nest of different species, and another is intra-specific brood-parasitism in which eggs are laid in the nest of the other individual 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 at an intermediate stage in the evolution toward inter-specific brood-parasitism, and Yamauchi [5,6] discussed their opinions from some theoretical points of view. Takasu et al. [7] analysed a mathematical model of population dynamics between parasite and host, and discussed the evolution of such behaviour that host refuses the eggs laid by the parasite.

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

The moorhen inhabits all over the world except for Australia. Its breeding season is generally from April to August or September. On the average, the female lays just one egg a day, and the expected clutch size per female is generally from five to eight. But the number of eggs in some nests could be significantly larger than it. We could consider that some female birds which are not the owner of the nest lays eggs in such a nest. Three evidences would indicate that more than one female have laid eggs in a nest [1]: (i) More than one egg were 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. [8,1,9]

Field work by Gibbons [9] was conducted in 1982, 1983 and 1984 at the Wildfowl Trust's Peakirk Waterfowl Gardens in Cambridgeshire. Gibbons [9] found that the number of moorhen nests in which more than two females lay eggs is 31 of 128 investigated nests. There could be two types of phenomena that more than one bird lay eggs in the same nest. First is *the cooperative nesting*. Moorhen is generally monogynous and its pair cooperates in defending the breeding territory. Gibbons [9] reported that 10% of pairs consisted of a group of one male and some females. 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 of totally 97 breeding territories, females consisted of mothers and daughters.

Second is the *brood-parasitism*. In the investigation by Gibbons [9], 59 out of 75 females laid eggs only in their own nests. 11 females laid eggs in both their own nest and another. Four females laid eggs in her own nest and the other two, and one female did in her own and the other five. That is, roughly saying, about 20% females out of 75 were parasites, and about 70% of parasites laid eggs only in a certain unique nest of host. Therefore, in our modelling, we assume that parasitic individuals are related to the host's nests different from each other, that is, with one-to-one relationship. In addition, Gibbons [9] reported that 97 clutches out of 128 were laid by only one female, 20 clutches laid by two, 9 clutches laid by three, and 2 clutches laid by four. That is, about 65% out of 128 parasitised nests were parasitised by only one parasite. So, we again assume in our modelling that the parasitisation for each non-parasitic individual's nest could not occur by more than one parasitic individual, that is, with one-to-one relationship.

The averaged number of such parasite's eggs laid in the other nest was four. The parasitised nest was in the territory defended by the other pair. In case of moorhen, after parasitic female had laid eggs in the nest of a host in an earlier period of breeding season, it constructed its own nest and turned to lay eggs in it. On the other hand, the host did not remove eggs laid by parasites, and brought them up as well as or better than her own. However, the expected survival rate of parasitised eggs could be regarded as lower than that of host's ones. The reasons are as follows: Parasitic females dumped their eggs when some period had passed after the host had initiated her clutch. Therefore, those parasitised eggs hatch in general later than the eggs of host does, so that the parasite's fledglings are expected to be subordinate in the physical strength in comparison with those of the host own. And the parasite's eggs dumped in the later period of host's hatching are deserted because host does not hatch eggs after the fledglings of host's own have left the nest. From this argument, we could consider that the parasitised eggs are in a disadvantageous condition for their survival.

In this paper, we consider a mathematical modelling for the intra-specific brood-parasitism with regard to the coexistence between parasitic and non-parasitic individuals within a population. From the viewpoint of natural selection, only the individuals that could adapt themselves to the environment could persist within a population. A cuckoo lays eggs only in the nest of others. A hen lays eggs only in her nest. We could consider that such consequent behaviour is to gain the possibly highest fitness. Why and how parasitic and non-parasitic individuals could coexist in the population of moorhen? In our mathematical modelling consideration, we focus the existence of the stationary ratio of parasitic individuals within a population.

2. Modelling assumptions

In this paper, we consider the mathematical modelling with the following assumptions: The whole population consists of parasitic and non-parasitic

subpopulations, of which the non-parasite might become the host for the brood-parasitism by the parasite. The parasite does not parasitise the nest of any other parasite. For each non-parasitic individual, the parasitisation by more than one parasite could not occur in the considered breeding season. Each parasite makes its parasitisation for a specific non-parasite, and does not utilise more than one non-parasite, that is, each parasitic individual is related to its host's nest different from the other's, that is, with one-to-one relationship.

Now, k_s and k_b are respectively the number of eggs laid by the parasite in its own nest and that in the nest of host. And let k_t denote the total number of eggs the bird lays, that is, the clutch size per parasitic individual. Then, the relation among k_s, k_b and k_t is

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

In our modelling consideration, for mathematical simplification, host and parasite bear the common total number of eggs. We could regard the total number k_t of eggs and/or the number k_b of parasitised eggs as the parasite's reproductive strategy, and try to discuss the optimal strategy. However, in this paper, we will not analyse our model from such viewpoint. (As for a mathematical modelling consideration from such a viewpoint, we have already accomplished it and will publish the work elsewhere sooner or later.) Instead, each individual is assumed to have such a strategy as to be able to select alternatively the behaviour as non-parasite or parasite. In order to clarify such a viewpoint, we consider that the above-mentioned numbers k_t and k_b are given. Thus, we will discuss the possibility of coexistence between non-parasitic and parasitic individuals with a stationary population frequency in the considered population with a given set of k_t and k_b. As clearly indicated in the following sections, since the expected fitness of each individual is significantly influenced by the population frequency of parasites or non-parasites within the considered population, the selection of behaviour as non-parasite or parasite considerably affects the fitness of the selector.

Now, we assume the *rank among females*, in terms of the breeding capacity, for instance, to discover foods or bring up their fledglings. Such qualitative difference among females is to be reflected to the survival probability of fledglings in the nests. The survival probability of the fledglings with their own mother of rank l is assumed to be given by

$$P_{l,s}(k_s) = \mu^{l-1}e^{-\alpha k_s} \quad (l = 1, 2, \ldots), \tag{2}$$

while that with the host mother of rank l is assumed to be given by

$$P_{l,b}(k_b) = \mu^{l-1}e^{-\beta k_b} \quad (l = 1, 2, \ldots), \tag{3}$$

where μ, α and β are constants such that $0 < \mu \leqslant 1$ and $0 \leqslant \alpha \leqslant \beta$. These survival probability functions are under such hypothetical condition that the total number of eggs in the nest of the female with rank l would be just k_s for Eq. (2) or k_b for Eq. (3), and indicate that the survival probability of the fledgling

decreases as the number of *kin* eggs in the same nest gets larger. This is because the larger the number of kin eggs in the same nest, the less the expected amount of food per fledgling. In case of $P_{l,b}$, it gives the survival probability per fledgling with the total number of eggs just k_b, provided that no eggs of any other mother existed in the nest. The effect of another mother's eggs on the survival probability in the same nest, which is the case for the host's nest, will be introduced as another factor defined below. The condition $\alpha \leqslant \beta$ means that the survival probability with its own mother's care is not less than that with the host mother's care, if the ranks for those mothers would be equivalent. So $P_{l,s}(k) \leqslant P_{l,b}(k)$ for any $k \geqslant 0$. If a parasite could select the host of the rank higher than its own, the survival probability of the parasite's fledglings might be greater for those with the host than with their own mother. The case with $\mu = 1$ corresponds to when there is no qualitative difference among females. In this case, the survival probability of fledglings is independent of which their mother is their own or the host.

Besides, we assume that, the more is the number of eggs which have less relatedness with the considered egg in the same nest, the lower the survival probability of the egg is. Let $\sigma(x)$ denote the factor of such effect as to reduce the survival probability given by Eq. (2) or Eq. (3), where x is the number of eggs which have less relatedness in the same nest, that is, the number of host's eggs for the parasitised egg or that of parasite's eggs for the host's one. So $\sigma(x)$ is monotonically decreasing function of x, given in our modelling by

$$\sigma(x) = \mathrm{e}^{-\gamma x}, \tag{4}$$

where γ is a non-negative constant. Without eggs with the less relatedness, that is, when $x = 0$, this effect does not exist so that $\sigma(0) = 1$.

3. Females without qualitative difference

In this section, we consider the case when every females have no qualitative difference, that is, when $\mu = 1$ in Eqs. (2) and (3) and let $P_{l,s}(k_s) = P_s(k_s)$; $P_{l,b}(k_b) = P_b(k_b)$ for any l. We consider the fitnesses W_p and W_h which are respectively the expected fitness for the parasitic individual and that for the nonparasitic one. We consider in this paper that the fitness for mother is defined by the expected number of survived eggs. Moreover, the success of parasitisation of one egg is assumed to be independent of the success or the failure of any other parasitisation. In this case, W_p is given as follows (Appendix A)

$$W_p = k_s P_s(k_s) + \sum_{i=0}^{k_b} \left\{ \binom{k_b}{i} \eta^i (1-\eta)^{k_b - i} \, i \, P_b(i) \sigma(k_t) \right\}, \tag{5}$$

where η is the probability that the parasite succeeds in parasitising one egg to its host. For the second term, as described in Appendix A, we now assume that,

when the parasite fails to parasitise an egg, the egg is lost from the clutch. The first term of Eq. (5) is the expected fitness gain from the fledglings under the care of its own mother which is a parasite. The second term is the expected fitness gain from the fledglings under the host mother's care. If we introduced the parasitism also to the parasite's nest, W_p must be considerably modified, although such case would be contrary to some observations at least for moorhen [9].

On the other hand, W_h is given as follows (Appendix A)

$$W_h = \left(1 - \frac{Q}{1 - Q}\right) k_t \, P_s(k_t) + \frac{Q}{1 - Q} k_t,$$

$$P_s(k_t) \sum_{i=0}^{k_b} \left\{ \binom{k_b}{i} \eta^i (1 - \eta)^{k_b - i} \sigma(i) \right\}, \tag{6}$$

where Q denotes the proportion of parasitic individuals in the considered female population. As we assume that each parasitic individual can partner with a host individual different from hosts for the other parasites, that is, with one-to-one relationship, we will consider our model only with the following range of the parameter Q

$$0 \leqslant Q \leqslant \tfrac{1}{2}. \tag{7}$$

This is a confinement for our modelling analysis. If we eliminated the assumption of one-to-one relationship between parasite and host, Q could be beyond 1/2. However, in such case, the fitness W_h could not be given by Eq. (6), and would require some considerable modification of Eq. (6), with some account of multi-parasitism.

The parasitic individual is assumed to select at random a non-parasite as its host. The first term of Eq. (6) denotes the expected fitness gain in the case when the non-parasitic individual could avoid being parasitised. The second term denotes the expected fitness gain in the case when the non-parasitic individual is parasitised and becomes host for a parasite.

If non-parasites stationarily coexist with parasites in the considered population, we could suppose that the fitness of the non-parasite is equal to that of the parasite

$$W_h = W_p.$$

This equation should determine the stationary frequency $Q = Q^*$ of parasites in the population. With the mathematical argument described in Appendix B, however, in the case when there is not any qualitative difference among females in the breeding capacity, we can obtain the following result:

Proposition 1. *Without any qualitative difference among females in terms of the breeding capacity, there could exist no stable equilibrium parasite frequency in a fixed population.*

From the argument in Appendix B, our mathematical modelling consideration concludes that, if the total number (k_t) of eggs laid per female is suffi-

ciently small, for instance, under some unfavourable habitat condition, the parasites would eventually disappear from the population, whereas if the total number of eggs laid per female is sufficiently large under some favourable habitat condition, the frequency of parasites would gradually increase within the population. The discussion for the latter case is out of the present framework of our mathematical modelling with the confinement Eq. (7). It may be suggested that such case would lead to the evolution of multi-parasitism.

From this result, within the framework of our modelling, we could consider that the population with a parasitic subpopulation might be on the way of evolution, that is, the frequency of parasitic individuals might be still changing.

4. Females with qualitative difference

At first, we suppose that the female population consists only of non-parasites at the initial phase, and then at a moment the female of rank l changes to behave as a parasite. Should she remain to behave as a parasite, if all the females of rank higher than l are kept as non-parasites and if the number of parasitic females of rank lower than l increases? Provided that parasitic individual selects its host at random from non-parasitic individuals, the higher the rank of host individual is, the more is the fitness gain for the parasitic individual.

We assume that the total number of females is $2N$ (For the case of $2N + 1$, the following result can be proved valid, too.) If the number of parasites of rank lower than l is $q (\leqslant 2N - l)$, the expected fitness gain $W_{l,\mathrm{p}}$ for the female of rank l when it would remain to behave as a parasite is

$$
W_{l,\mathrm{p}} = k_\mathrm{s} P_{l,\mathrm{s}}(k_\mathrm{s}) + \sum_{\substack{i=1 \\ i \notin \{l, x_1, x_2, \dots, x_q\}}}^{2N} \left\{ \frac{1}{2N - (q+1)} \sum_{j=0}^{k_\mathrm{b}} \binom{k_\mathrm{b}}{j} \eta^j \right.
$$
$$
\left. \times (1 - \eta)^{k_\mathrm{b} - j} j P_{i,\mathrm{b}}(j) \sigma(k_\mathrm{t}) \right\},
\tag{8}
$$

where $\{x_1, x_2, \dots, x_q\}$ is the ranks of parasitic females lower than l (for the modelling derivation, see Appendix C). In contrast, in this case, the expected fitness gain $W_{l,\mathrm{h}}$ for the female of rank l when it would change to a non-parasite is

$$
W_{l,\mathrm{h}} = \left(1 - \frac{q}{2N - q}\right) k_\mathrm{t} P_{l,\mathrm{s}}(k_\mathrm{t}) + \frac{q}{2N - q} k_\mathrm{t} P_{l,\mathrm{s}}(k_\mathrm{t})
$$
$$
\times \sum_{i=0}^{k_\mathrm{b}} \binom{k_\mathrm{b}}{i} \eta^i (1 - \eta)^{k_\mathrm{b} - i} \sigma(i).
\tag{9}
$$

By comparing $W_{l,\mathrm{p}}$ to $W_{l,\mathrm{h}}$ in the above, we can obtain the following result (for the argument, see Appendix D):

Proposition 2. *If all the females of rank higher than l are non-parasites, the parasitic female of rank l remains to be parasite even though the number of parasites of rank lower than l increases.*

This means in other words that the behavioural choice by the highest rank of parasite is not affected by the number of parasites of the lower rank.

Next, we suppose such a configuration of non-parasites and parasites that the higher ranks from 1 to m of females are non-parasitic, and the lower than m are parasitic. For this configuration, let us further suppose the following:

$$W_{m,h} > W_{m,p},$$

$$W_{m+1,h} < W_{m+1,p}. \tag{10}$$

Would some females change their behaviours from non-parasite or parasite to another? With mathematical arguments described in Appendix E, we can obtain the following result:

Proposition 3. *Once established is such a configuration that the females of rank higher than $m + 1$ are all non-parasites and those of rank lower than m are all parasites, as long as the female of rank m remains to be non-parasite and that of rank $m + 1$ does to be parasite, any other non-parasite remains to be non-parasite and any other parasite does to be parasite, that is, the configuration could be stationarily stable.*

In this result, we use the term 'stationarily stable' for the configuration as to mean that, in the stationarily stable configuration, any change of behaviour of any individual decreases the expected fitness for the individual which changes the behaviour.

Now, we consider the existence of stationary proportion of parasites in the population. Is it possible to determine such a unique m as to satisfy Eq. (10)? We assume again that the total number of females is $2N$ (For the case of $2N + 1$, the following result can be proved valid, too). At first, we consider the case when all the females of rank higher than $2N - 1$ are just non-parasites. We focus the females of rank $2N - 1$ and of rank $2N$. Following three cases are possible:

(i) $W_{2N-1,h} > W_{2N-1,p},   W_{2N,h} > W_{2N,p}.$

(ii) $W_{2N-1,h} > W_{2N-1,p},   W_{2N,h} < W_{2N,p}.$

(iii) $W_{2N-1,h} < W_{2N-1,p},   W_{2N,h} < W_{2N,p}.$

In case of (i), both females of rank $2N - 1$ and of rank $2N$ behave as non-parasite. In this case, from Proposition 2, non-parasites occupy the population so that there is no parasite within the considered population. So, formally $m = 2N$ for the case (i). In case of (ii), the female of rank $2N - 1$ behaves as a non-parasite and that of rank $2N$ does as a parasite. Therefore, $m = 2N - 1$. In case of (iii), both females of rank $2N - 1$ and $2N$ behave as parasite. In this

case, we turn to focus the females of rank $2N - 2$ and of rank $2N - 1$. In such case, the following two cases are to be considered:

$$W_{2N-2,h} > W_{2N-2,p}, \quad W_{2N-1,h} < W_{2N-1,p}.$$

$$W_{2N-1,h} < W_{2N-1,p}, \quad W_{2N,h} < W_{2N,p}.$$

In the former case, $m = 2N - 2$. In the latter case, we turn to consider the females of rank $2N - 3$ and of rank $2N - 2$ in the same way. Along this procedure of arguments, we can obtain the following result (for details, see Appendix F) given in Proposition 4.

Proposition 4. *If the following condition is satisfied, there is the unique m to define such configuration that all the females of rank higher than $m + 1$ are non-parasites and those of rank lower than m are parasites:*

$$\tilde{\mu}_N \leqslant \mu \leqslant \tilde{\mu}_{2N} \quad \zeta > \varphi,$$

where

$$\zeta = (\eta e^{-\gamma} + 1 - \eta)^{k_b} k_t e^{-\alpha k_t} - k_s e^{-\alpha k_s};$$

$$\varphi = e^{-\beta k_t} \eta e^{-\beta} (\eta e^{-\gamma} + 1 - \eta)^{k_b - 1} k_b,$$

and $\tilde{\mu}_N$ and $\tilde{\mu}_{2N}$ are defined by

$$\frac{\tilde{\mu}_N^{N-1}(N-1)(1-\tilde{\mu}_N)}{1-\tilde{\mu}_N^{N-1}} = \varphi; \qquad \frac{\tilde{\mu}_{2N}^{2N-1}(2N-1)(1-\tilde{\mu}_{2N})}{1-\tilde{\mu}_{2N}^{2N-1}} = \varphi.$$

To confirm this analytical result, we carried out some numerical calculations directly with Eqs. (8) and (9) (a numerical result is given as Fig. 1). All numerical calculations are set with such initial configuration that there are only non-parasitic individuals. The numerical calculations are not aimed to show the process of inheritance of behaviour, instead, are aimed to search and get numerically the stationarily stable configuration. For any set of parameters we applied for the numerical calculations, the configuration numerically converges to such type that all the females of higher than a rank are non-parasites and those of lower than it are parasites. We remark that, since the behavioural choice is determined by the *expected* fitness, it could occur occasionally in the numerical calculations that the whole population is occupied by parasites (see Fig. 1, at a step after 300). From our modelling assumption of one-to-one relationship between parasite and host, the population ratio of parasitic individuals cannot be beyond 50%. The numerical result in Fig. 1 that contains some configurations contradictory to this assumption is due to the behavioural choice determined by just the expected fitness instead of the rank of actually selected host, that is given by Eqs. (8) and (9) summed up all non-parasitic individuals including the possible hosts for another parasite.
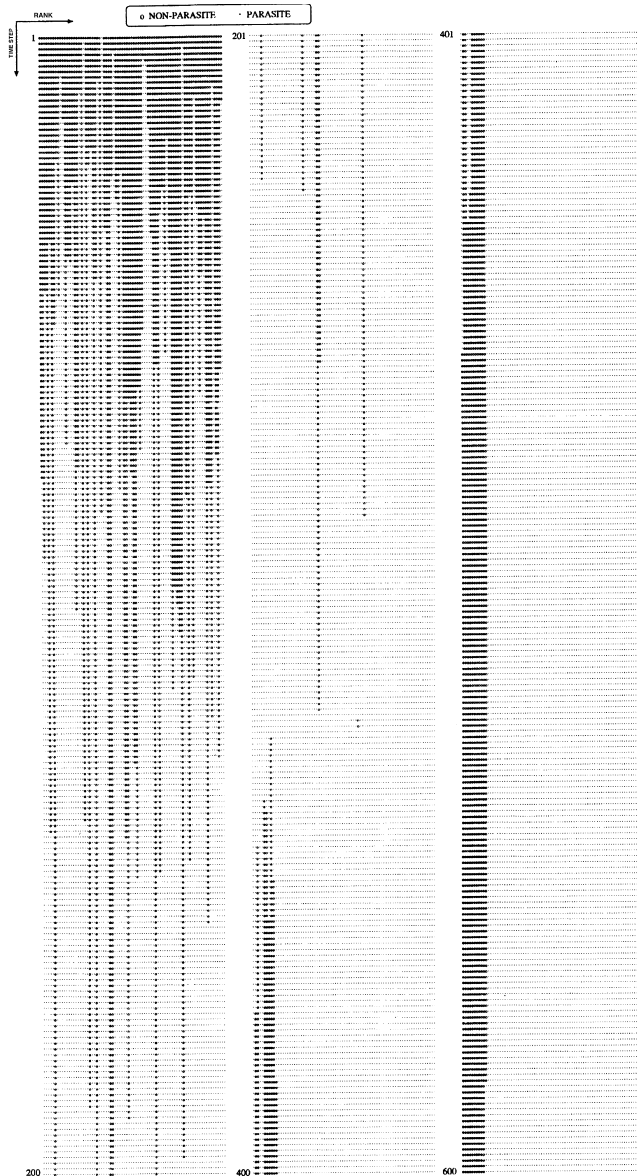
Fig. 1. Numerical calculation of the configuration change. At the initial, every individuals are non-parasites (○) without any parasite (·). The rank is higher for the individual located at left. An individual is randomly selected at each time step, and the behavioral choice is estimated according to the expected fitnesses given by Eqs. (8) and (9). The configuration reaches the stationary state at time step 585. $\mu = 0.5$; $\alpha = 1.0$; $\beta = 2.0$; $\eta = 0.5$; $\gamma = 0.9$; $k_t = 10$; $k_b = 4$; the fixed total population $= 80$.

5. Conclusion

Field work by Gibbons [9] implied that only a portion of females in a population involving the intra-specific brood-parasitism, about 20% in the case of observed moorhen at the Wildfowl Trust's Peakirk Waterfowl Gardens in Cambridgeshire, would behave as the intra-specific brood-parasites (parasitic females), while another portion of females (non-parasitic females) would not. In our mathematical modelling consideration, we focused the existence and the uniqueness of the stationary ratio of parasitic females within a population. Especially, our modelling analysis showed that the existence of such a stationary ratio of parasitic females required an appropriate difference among females in terms of the breeding capacity. That is, within the framework of our modelling analysis, only when the survival probability of offsprings significantly and appropriately depends on which female they are bred by, the intra-specific parasitism with the coexistence between parasitic and non-parasitic females would stationarily exist within the population. If the difference among females is non-significant with respect to the survival probability of offsprings, the ratio of parasitic females within the population would be changing to a certain next stage of evolutionary process which could not be involved in our modelling, or alternatively, if the difference among females is sufficiently strong, the intra-specific brood-parasitism would be excluded from the population due to the natural selection, because the result from our modelling analysis implies that, in such case, the intra-specific brood-parasitism would make the fitness of any female reduce.

With a population of females ranked in terms of the breeding capacity related to the survival probability of offsprings, we found a stable stationary configuration of parasitic females in the ranked population (Proposition 3): the stable stationary configuration consists of non-parasitic females with the higher breeding capacity and parasitic ones with the lower. Provided that the lower rank would be of the younger female, this result indicates that the younger female would have the stronger tendency to behave as parasite than the older.

From the result of Proposition 4, the above-mentioned stationary configuration could be realised only for an intermediate range of parameter μ that represents the degree of the difference of breeding capacity among females. Hence, neither little difference nor extreme one of breeding capacity among females would sustain the stationary coexistence between parasitic and non-parasitic individuals with a *stationary* ratio in the population.

From Proposition 2, the behavioural choice by the highest rank of parasite is not affected by the number of parasites of the lower rank. Therefore, with the result by Proposition 3, we could suggest the following transient process for the invasion of brood-parasitism into the considered population (for a numerical example, see Fig. 1): Suppose such initial population that consists of only non-parasitic females, that is, without any parasitic behaviour while those females

could be ranked in terms of the breeding capacity relative to the fitness. At first, a female of certain rank takes somehow the strategy to behave as parasite, and gets the higher fitness. Then the descendants with parasitic behaviour increase the frequency within the population. On the way of the frequency variation from generation to generation, the configuration of parasitic females within the ranking would fluctuate. Configuration of parasitic females within the ranking at each generation determines the optimality of the parasitic behaviour for each parasitic female in it. Hence, such configuration-dependent optimality of the parasitic behaviour significantly drives the variation of configuration itself through generations. With such a self-organising dynamic change of the configuration, it eventually approaches the stationary configuration with a certain frequency of parasitic females (as given by the result of Proposition 4). Since the optimality of parasitic behaviour must be significantly affected by the frequency of parasites within the population, the configuration of parasitic females within the ranking might have a variation from generation to generation while such variation would be small enough not to change significantly the stationary (or quasi-stationary) frequency of parasites within the population.

In this paper, the individual of each rank is assumed to choose the behaviour in terms of whether it behaves as non-parasite or parasite, using the expected fitness in each case. Since the relationship between parasite and host is assumed at first to be one-to-one, the population ratio of parasitic individuals could not be beyond 50%. However, as long as the decision on the behavioural choice is assumed to be done according to the expected fitness, the ratio could become beyond 50% in our mathematical modelling (see Fig. 1). So it will be interesting to make an improved mathematical modelling explicitly involved such one-to-one relationship between parasite and host, and discuss the existence and the uniqueness of the population ratio of parasitic individuals.

Acknowledgements

Appendix A. Fitnesses of parasite and non-parasite with the qualitatively even females

We assume that the total number of individuals is n in the considered population. Let Q denote the proportion of parasites in the population. The

expected number of parasites is given by Qn and that of non-parasites is by $(1 - Q)n$. Each parasite tries to lay k_b eggs in the nest of its host.

First, we derive the fitness of parasite. The success probability for the parasite to lay one egg in the nest of its host is now given by a constant η. Then, the case when parasite succeeds in laying j eggs of k_b in the nest of its host occurs with the probability

$$\binom{k_b}{j}\eta^j(1 - \eta)^{k_b - j} \quad (j = 0, 1, 2, \ldots, k_b), \tag{A.1}$$

taking account of which of k_b eggs are succeeded in being laid in the nest of host.

Lastly, the expected fitness gain for the parasite from those eggs laid in the nest of host is summed up over the number of parasite's eggs successfully laid in the nest of host as follows:

$$\sum_{j=0}^{k_b}\binom{k_b}{j}\eta^j(1 - \eta)^{k_b - j}j\,P_b(j)\sigma(k_t). \tag{A.2}$$

On the other hand, the expected fitness gain for the parasite from the eggs laid in her own nest is $k_s P_s(k_s)$. Therefore, the whole expected fitness gain W_p for the parasite is now obtained as Eq. (5).

Next, we derive the fitness of non-parasite. The number of cases concerning to which non-parasitic Qn individuals out of $(1 - Q)n$ become hosts is given by

$$\binom{(1 - Q)n}{Qn}.$$

The number of cases when a non-parasitic individual does not become host and Qn non-parasitic individuals out of $(1 - Q)n - 1$ become hosts is

$$\binom{(1 - Q)n - 1}{Qn}.$$

Hence, the probability that a non-parasitic individual does not become host is given by

$$\frac{\binom{(1 - Q)n - 1}{Qn}}{\binom{(1 - Q)n}{Qn}} = \frac{1 - 2Q}{1 - Q}.$$

The expected fitness gain for such a non-parasitic individual is given by $k_t P_s(k_t)$. The case when host is laid j eggs by its parasite occurs with the probability

$$\binom{k_b}{j}\eta^j(1 - \eta)^{k_b - j}. \tag{A.3}$$

Lastly, the expected fitness gain for the host is given as follows

$$\sum_{j=0}^{k_\mathrm{b}} \binom{k_\mathrm{b}}{j} \eta^j (1-\eta)^{k_\mathrm{b}-j} k_\mathrm{t} P_\mathrm{s}(k_\mathrm{t}) \sigma(j). \tag{A.4}$$

Therefore, taking account of the probability that a non-parasite would become host for a parasite, the whole expected fitness gain W_h for the non-parasite is obtained as Eq. (6).

Appendix B. Non-existence of stable parasite frequency with qualitatively even females

In this appendix, we prove Proposition 1 for the case when there is not any qualitative difference among females in the breeding capacity. Now, we introduce the ratio of the parasitised eggs k_b to the clutch size k_t of parasitic individual: $\rho \equiv k_\mathrm{b}/k_\mathrm{t}$. Then the relation $W_\mathrm{h} = W_\mathrm{p}$ brings the following equation from Eqs. (5) and (6):

$$(1-\rho)\mathrm{e}^{\alpha\rho k_\mathrm{t}} + \frac{\eta \mathrm{e}^{-\beta}\rho}{\eta \mathrm{e}^{-\beta}+1-\eta}\{\mathrm{e}^{\alpha-\gamma}(\eta\mathrm{e}^{-\beta}+1-\eta)^\rho\}^{k_\mathrm{t}}$$

$$= \frac{1}{1-Q}\{(1-2Q)+Q(\eta\mathrm{e}^{-\gamma}+1-\eta)^{\rho k_\mathrm{t}}\}. \tag{B.1}$$

Let $f(k_\mathrm{t})$ denote the left-hand side of Eq. (B.1) and $g(k_\mathrm{t})$ the right-hand side. Depending on the parameters, there are some different relations between $f(k_\mathrm{t})$ and $g(k_\mathrm{t})$ (see Fig. 2). In every case,

$$f(k_\mathrm{t}) < g(k_\mathrm{t}) \Longleftrightarrow W_\mathrm{p} < W_\mathrm{h};$$

$$f(k_\mathrm{t}) > g(k_\mathrm{t}) \Longleftrightarrow W_\mathrm{p} > W_\mathrm{h}.$$

Now we argue the case of (a − 1) in Fig. 2. In the case,

$$\exists k_\mathrm{t}^* \quad \text{s.t.} \quad f(k_\mathrm{t}^*) = g(k_\mathrm{t}^*).$$

We suppose a certain $k_\mathrm{t} < k_\mathrm{t}^*$, when $g(k_\mathrm{t}) > f(k_\mathrm{t})$. Then $W_\mathrm{h} > W_\mathrm{p}$, so that the parasite frequency Q could be expected to decrease, from the viewpoint of optimality in terms of the expected fitness gain. $f(k_\mathrm{t})$ is independent of Q, whereas $g(k_\mathrm{t})$ is monotonically decreasing function of Q. Thus, $g(k_\mathrm{t})$ increases for any k_t as Q decreases. So the relation between $f(k_\mathrm{t})$ and $g(k_\mathrm{t})$ remains such that $g(k_\mathrm{t}) > f(k_\mathrm{t})$, that is, $W_\mathrm{h} > W_\mathrm{p}$. Therefore, we could expect that $Q \to 0$ eventually. Next we suppose a certain $k_\mathrm{t} > k_\mathrm{t}^*$. Since $W_\mathrm{h} < W_\mathrm{p}$ in this case, Q could be expected to increase eventually. Then, W_h decreases and the relation between $f(k_\mathrm{t})$ and $g(k_\mathrm{t})$ remains such that $g(k_\mathrm{t}) < f(k_\mathrm{t})$, that is, $W_\mathrm{h} < W_\mathrm{p}$. In this case, we can just conclude that Q asymptotically increases. From this argument for the case of (a − 1) in Fig. 2 from the viewpoint of optimality in terms of the expected fitness gain, it is shown that the relation
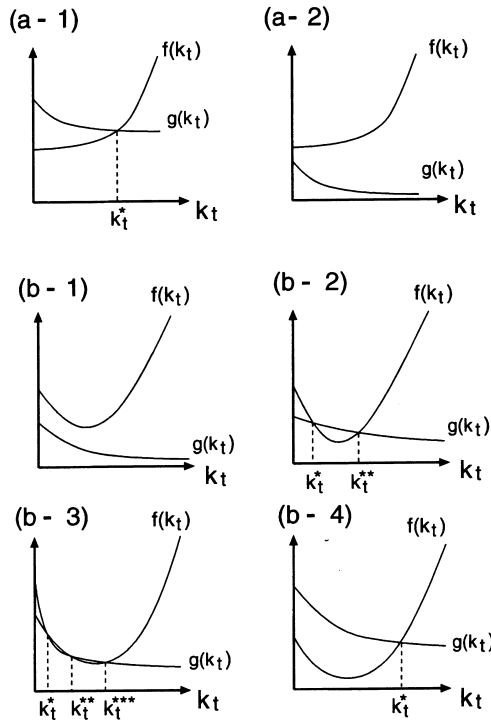
Fig. 2. Possible relations between $f(k_t)$ and $g(k_t)$.

between W_h and W_p could not change. Therefore, the equilibrium frequency $Q = Q^*$ satisfying Eq. (B.1) is unstable even if it exists.

Analogous arguments can be applied for the other cases indicated by the other figures in Fig. 2. Consequently, it can be shown that there is not any stable equilibrium frequency $Q = Q^*$ satisfying Eq. (B.1).

Appendix C. Fitnesses of parasite and non-parasite with qualitatively different females

Suppose that there are m non-parasites and n parasites within the population. First, we derive the fitness of the parasite. Parasite selects and pairs host at random. Hence, the probability that a parasite lays eggs in the nest of the host of rank $l(1 \leqslant l \leqslant m)$ is obtained by $1/m$. The expected fitness gain for the parasite from the eggs laid in the nest of host is

$$\sum_{l=1}^{m} \left\{ \frac{1}{m} \sum_{j=0}^{k_b} \binom{k_b}{j} \eta^j (1 - \eta)^{k_b - j} j \, P_{l,b}(j) \sigma(k_t) \right\},$$ (C.1)

where the average in terms of l is taken over ranks of all hosts according to which non-parasitic individuals become hosts. In addition to the above expected fitness gain for the parasite of rank i, the expected fitness gain from the eggs laid in her own nest is now given by $k_s P_{i,s}(k_s)$. Therefore, the whole expected fitness gain $W_{i,p}$ for the parasite of rank i is now obtained as follows:

$$W_{i,p} = k_s P_{i,s}(k_s) + \sum_{l=1}^{m} \left\{ \frac{1}{m} \sum_{j=0}^{k_b} \binom{k_b}{j} \eta^j (1-\eta)^{k_b-j} j\, P_{l,b}(j) \sigma(k_t) \right\}. \qquad (C.2)$$

Next, we consider the fitness of host. The probability that a specific non-parasite becomes host for a parasite is given by n/m. When the non-parasite of rank i could avoid becoming host, the expected fitness gain for such non-parasite is $k_t P_{i,s}(k_t)$. On the other hand, when the non-parasite of rank i becomes host for a parasite, the expected fitness gain for the host is

$$\sum_{j=0}^{k_b} \binom{k_b}{j} \eta^j (1-\eta)^{k_b-j} k_t P_{i,s}(k_t) \sigma(j), \qquad (C.3)$$

taking account of how many parasite's eggs could be successfully parasitised. Lastly, the whole expected fitness gain for the non-parasite of rank i is obtained as follows:

$$W_{i,h} = \left(1 - \frac{n}{m}\right) k_t P_{i,s}(k_t) + \frac{n}{m} k_t P_{i,s}(k_t) \sum_{j=0}^{k_b} \binom{k_b}{j} \eta^j (1-\eta)^{k_b-j} \sigma(j). \qquad (C.4)$$

Appendix D. Proof for Proposition 2

In this appendix for Proposition 2, we consider how the expected fitness gain for the female of rank l changes when the number of parasites of rank lower than l increases. Now suppose the total number $2N$ of females in the population. In our modelling argument, we assume the following: $N + 1 \leqslant l \leqslant 2N$. We can carry out the following argument in the same way also when the number of females is $2N + 1$.

At first, we consider the fitness gain for the female of rank l which behaves as a non-parasite. Let q denote the number of parasites in the population except for the female of rank l. Then, from Eqs. (2), (3) and (6), the expected fitness gain $W_{l,h}$ for the considered female of rank l is obtained as follows. If $q = 0$,

$$W_{l,h} = k_t \mu^{l-1} e^{-\alpha k_t}, \qquad (D.1)$$

and otherwise,

$$W_{l,h} = \left(1 - \frac{1}{2N-q}\right) k_t \mu^{l-1} e^{-\alpha k_t}$$

$$+ \frac{1}{2N-q} k_t \mu^{l-1} e^{-\alpha k_t} \sum_{i=0}^{k_b} \binom{k_b}{i} \eta^i (1-\eta)^{k_b-i} \sigma(i). \qquad (D.2)$$

Eq. (D.2) can be rewritten as follows:

$$W_{l,\mathrm{h}} = k_{\mathrm{t}}\mu^{l-1}\mathrm{e}^{-\alpha k_{\mathrm{t}}} - \frac{1}{2N-q}k_{\mathrm{t}}\mu^{l-1}\mathrm{e}^{-\alpha k_{\mathrm{t}}}\left\{1 - \sum_{i=0}^{k_{\mathrm{b}}}\binom{k_{\mathrm{b}}}{i}\eta^i(1-\eta)^{k_{\mathrm{b}}-i}\sigma(i)\right\}.$$

(D.3)

Therefore, we find from Eq. (D.3) that $W_{l,\mathrm{h}}$ is monotonically decreasing in terms of the number q of parasites. That is, the larger the number of parasites, the less the expected fitness gain for the non-parasite.

Next, we consider the expected fitness gain for the female of rank l which behaves as a parasite. Let Λ_q denote the set of ranks for the other q parasites,

$$\Lambda_q = \{x_1, x_2, \ldots, x_q\},$$

where $x_i (i = 1, 2, \ldots, q)$ is the rank of the ith parasite, different from l.

Now, we assume the following:

$$l + 1 \leqslant x_i \leqslant 2N \quad \text{for } i = 1, 2, \ldots, q.$$

Since the number of the parasites including the female of rank l is $q + 1$, $W_{l,\mathrm{p}}$ is given from some calculation with Eqs. (2)–(4) and (8) by

$$W_{l,\mathrm{p}} = k_{\mathrm{s}}\mu^{l-1}\mathrm{e}^{-\alpha k_{\mathrm{s}}} + \frac{1}{2N-(q+1)}\eta\mathrm{e}^{-\beta}U^{k_{\mathrm{b}}-1}k_{\mathrm{b}}\mathrm{e}^{-\gamma}k_{\mathrm{t}}\left(\sum_{i=1}^{l-1}\mu^{i-1} + \sum_{\substack{i=l+1\\i\notin\Lambda_q}}^{2N}\mu^{i-1}\right),$$

(D.4)

where $U = \eta\mathrm{e}^{-\beta} + 1 - \eta$. If one additional female of rank lower than l would become parasite and the total number of parasites would increase to $q + 2$, $W_{l,\mathrm{p}}$ becomes

$$W_{l,\mathrm{p}} = k_{\mathrm{s}}\mu^{l-1}\mathrm{e}^{-\alpha k_{\mathrm{s}}} + \frac{1}{2N-(q+2)}\eta\mathrm{e}^{-\beta}U^{k_{\mathrm{b}}-1}k_{\mathrm{b}}\mathrm{e}^{-\gamma}k_{\mathrm{t}}\left(\sum_{i=1}^{l-1}\mu^{i-1} + \sum_{\substack{i=l+1\\i\notin\Lambda_{q+1}}}^{2N}\mu^{i-1}\right).$$

(D.5)

Comparing Eq. (D.5) to Eq. (D.4), we find that only the second term of Eq. (D.4) is different from that of Eq. (D.5). We consider the ratio $E(\mu)$ of the second term of the Eq. (D.4) to that of Eq. (D.5)

$$E(\mu) = \frac{2N-(q+2)}{2N-(q+1)}\left(1 + \frac{\mu^{x_{q+1}-1}}{\sum_{i=1}^{l-1}\mu^{i-1} + \sum_{\substack{i=l+1\\i\notin\Lambda_{q+1}}}^{2N}\mu^{i-1}}\right).$$

(D.6)

With the following argument, we will prove that $E(\mu) < 1$.

Now we define $f(\mu)$ by

$$f(\mu) = \frac{\mu^{x_{q+1}-1}}{\sum\limits_{i=1}^{l-1}\mu^{i-1} + \sum\limits_{\substack{i=l+1 \\ i\notin \Lambda_{q+1}}}^{2N}\mu^{i-1}}. \tag{D.7}$$

Then,

$$\frac{df}{d\mu} = \frac{(x_{q+1}-1)\mu^{x_{q+1}-2}\left(\sum\limits_{i=1}^{l-1}\mu^{i-1} + \sum\limits_{\substack{i=l+1 \\ i\notin \Lambda_{q+1}}}^{2N}\mu^{i-1}\right)}{\left(\sum\limits_{i=1}^{l-1}\mu^{i-1} + \sum\limits_{\substack{i=l+1 \\ i\notin \Lambda_{q+1}}}^{2N}\mu^{i-1}\right)^2}$$

$$-\frac{\mu^{x_{q+1}-1}\left(\sum\limits_{i=2}^{l-1}(i-1)\mu^{i-1} + \sum\limits_{\substack{i=l+1 \\ i\notin \Lambda_{q+1}}}^{2N}(i-1)\mu^{i-1}\right)}{\left(\sum\limits_{i=1}^{l-1}\mu^{i-1} + \sum\limits_{\substack{i=l+1 \\ i\notin \Lambda_{q+1}}}^{2N}\mu^{i-1}\right)^2}. \tag{D.8}$$

The numerator of Eq. (D.8) is rewritten as follows:

$$x_{q+1} - 1 + \sum\limits_{i=2}^{l-1}(x_{q+1}-i)\mu^{i-1} + \sum\limits_{\substack{i=l+1 \\ i\notin \Lambda_{q+1}}}^{2N}(x_{q+1}-i)\mu^{i-1}. \tag{D.9}$$

It can be easily shown that, when $x_{q+1} = l + 1$, Eq. (D.9) takes its minimum and

$$x_{q+1} - 1 + \sum\limits_{i=2}^{l-1}(l+1-i)\mu^{i-1} + \sum\limits_{\substack{i=l+1 \\ i\notin \Lambda_{q+1}}}^{2N}(l+1-i)\mu^{i-1}$$

$$> x_{q+1} - 1 + \sum\limits_{i=2}^{l-1}(l+1-i)\mu^{i-1} + \sum\limits_{i=l+1}^{2N}(l+1-i)\mu^{i-1}. \tag{D.10}$$

The sums of the right-hand side of Eq. (D.10) become

$$\sum\limits_{i=3}^{2l-2N+1}(l+1-i)\mu^{i-1} + (l-1)\mu - \mu^{l-1}$$

$$+ \sum\limits_{i=l+2}^{2l-2N+1}(2N-i+1)\mu^{i+l-2N-1}(1-\mu^{4N-2i+2}) > 0$$

for $\forall \mu < 1$.

Therefore, we find that $df/d\mu > 0$ for $\forall \mu < 1$. Hence, $f(\mu)$ is monotonically increasing function of μ, and

$$f(1) = \frac{1}{2N - (q+2)}. \tag{D.11}$$

Thus, we can immediately find that

$$1 + f(\mu) < \frac{2N - (q+1)}{2N - (q+2)} \quad \text{for } \forall \mu < 1, \tag{D.12}$$

so that $E(\mu) < 1$ from Eq. (D.6). Consequently, we find that

$$\mu < 1 \Rightarrow E(\mu) < 1. \tag{D.13}$$

This implies that, the larger the number of parasites of rank lower than l that is the highest rank of present parasites, the larger the expected fitness of the parasite of rank l. These arguments prove Proposition 2.

Appendix E. Proof for Proposition 3

In this appendix for Proposition 3, we consider the stability of such a configuration of non-parasites and parasites that the higher ranks from 1 to m of females are of non-parasite, and the lower than m are of parasite. At first, the following inequality is supposed to be hold for the non-parasite of rank m

$$W_{m,\mathrm{h}} > W_{m,\mathrm{p}}, \tag{E.1}$$

which now becomes

$$\left(1 - \frac{n}{m}\right)\mu^{m-1}k_\mathrm{t}\mathrm{e}^{-\alpha k_\mathrm{t}} + \frac{n}{m}\mu^{m-1}k_\mathrm{t}\mathrm{e}^{-\alpha k_\mathrm{t}}V^{k_\mathrm{b}}$$
$$> k_\mathrm{s}\mu^{m-1}\mathrm{e}^{-\alpha k_\mathrm{s}} + \frac{1}{m-1}\frac{1-\mu^{m-1}}{1-\mu}\eta\mathrm{e}^{-\beta}U^{k_\mathrm{b}-1}k_\mathrm{b}\mathrm{e}^{-\gamma k_\mathrm{t}}, \tag{E.2}$$

where

$$U = \eta\mathrm{e}^{-\beta} + 1 - \eta;$$

$$V = \eta\mathrm{e}^{-\gamma} + 1 - \eta.$$

The expected fitness function for the female of rank $m-1$ in the case when it would remain to be non-parasite is given by

$$W_{m-1,\mathrm{h}} = \left(1 - \frac{n}{m}\right)\mu^{m-2}k_\mathrm{t}\mathrm{e}^{-\alpha k_\mathrm{t}} + \frac{n}{m}\mu^{m-2}k_\mathrm{t}\mathrm{e}^{-\alpha k_\mathrm{t}}V^{k_\mathrm{b}}. \tag{E.3}$$

In contrast, the fitness in the case when it would change to behave as a parasite is

$$W_{m-1,\mathrm{p}} = k_\mathrm{s}\mu^{m-2}\mathrm{e}^{-\alpha k_\mathrm{s}} + \frac{1}{m-1}\eta\mathrm{e}^{-\beta}U^{k_\mathrm{b}-1}k_\mathrm{b}\mathrm{e}^{-\gamma k_\mathrm{t}}\frac{1-\mu^{m-2}+\mu^{m-1}-\mu^m}{1-\mu}. \tag{E.4}$$

We multiply μ^{-1} to both sides of Eq. (E.2), and obtain

$$W_{m-1,\mathrm{h}} - W_{m-1,\mathrm{p}}$$

$$> \frac{1}{m-1} \frac{\mu^{-1} - \mu^{m-2}}{1-\mu} \eta \mathrm{e}^{-\beta} U^{k_\mathrm{b}-1} k_\mathrm{b} \mathrm{e}^{-\gamma k_\mathrm{t}} - \frac{1}{m-1} \eta \mathrm{e}^{-\beta} U^{k_\mathrm{b}-1} k_\mathrm{b} \mathrm{e}^{-\gamma k_\mathrm{t}}$$

$$\times \frac{1 - \mu^{m-2} + \mu^{m-1} - \mu^m}{1-\mu}. \tag{E.5}$$

From the following inequality

$$\mu^{-1} - \mu^{m-2} - (1 - \mu_{m-2} + \mu_{m-1} - \mu^m) = \mu^{-1}(1-\mu)(1-\mu^m) \geqslant 0,$$

we can easily prove the non-negativeness of the right-hand side of Eq. (E.5). With this argument, we can obtain the following result:

$$W_{m-1,\mathrm{h}} > W_{m-1,\mathrm{p}}. \tag{E.6}$$

Consequently, we have got the proof for the following:

$$W_{m,\mathrm{h}} > W_{m,\mathrm{p}} \Rightarrow W_{m-1,\mathrm{h}} > W_{m-1,\mathrm{p}}. \tag{E.7}$$

This means that the female of rank $m-1$ remains to be non-parasite as long as the female of rank m is non-parasite. With the mathematical induction, provided that the female of rank m is non-parasite, we can prove that the female of rank higher than m must remain to be non-parasite in the same way.

Next, we consider the females of rank lower than m. Suppose that the following inequality is hold for the parasite of rank $m + 1$.

$$W_{m+1,\mathrm{h}} < W_{m+1,\mathrm{p}}, \tag{E.8}$$

that is,

$$\left(1 - \frac{n-1}{m+1}\right) k_\mathrm{t} \mu^m \mathrm{e}^{-\alpha k_\mathrm{t}} + \left(1 - \frac{n-1}{m+1}\right) \mu^m V^{k_\mathrm{b}-1} k_\mathrm{b} \mathrm{e}^{-\gamma k_\mathrm{t}}$$

$$< k_\mathrm{s} \mu^m \mathrm{e}^{-\alpha k_\mathrm{s}} + \frac{1}{m} \frac{1-\mu^m}{1-\mu} \eta \mathrm{e}^{-\beta} U^{k_\mathrm{b}-1} \mathrm{e}^{-\gamma k_\mathrm{t}}. \tag{E.9}$$

The expected fitness function for the female of rank $m + 2$ in the case when it would remain to be parasite is given by

$$W_{m+2,\mathrm{p}} = k_\mathrm{s} \mu^{m+1} \mathrm{e}^{-\alpha k_\mathrm{s}} + \frac{1}{m} \frac{1-\mu^m}{1-\mu} \eta \mathrm{e}^{-\beta} U^{k_\mathrm{b}-1} k_\mathrm{b} \mathrm{e}^{-\gamma k_\mathrm{t}}. \tag{E.10}$$

On the other hand, the expected fitness gain in the case when it would change to a non-parasite is

$$W_{m+2,\mathrm{h}} = \left(1 - \frac{n-1}{m+1}\right) k_\mathrm{t} \mu^{m+1} \mathrm{e}^{-\alpha k_\mathrm{t}} + \frac{n-1}{m+1} \mu^{m+1} V^{k_\mathrm{b}} k_\mathrm{t} \mathrm{e}^{-\alpha k_\mathrm{t}}. \tag{E.11}$$

We multiply μ to both sides of Eq. (E.9), and obtain the following from Eq. (E.11):

$$W_{m+2,\mathrm{h}} < W_{m+2,\mathrm{p}} - \frac{1}{m}(1-\mu^m) \eta \mathrm{e}^{-\beta} U^{k_\mathrm{b}-1} k_\mathrm{b} \mathrm{e}^{-\gamma k_\mathrm{t}} \leqslant W_{m+2,\mathrm{p}}. \tag{E.12}$$

Therefore, it is proved that

$$W_{m+1,\mathrm{h}} < W_{m+1,\mathrm{p}} \Rightarrow W_{m+2,\mathrm{h}} < W_{m+2,\mathrm{p}}. \tag{E.13}$$

With the mathematical induction, provided that the female of rank $m+1$ is parasite, we can prove that the female of rank lower than $m+1$ must remain to be parasite in the same way. These arguments prove Proposition 3.

Appendix F. Proof for Proposition 4

In this appendix for Proposition 4, we show the condition for the existence and the uniqueness of m such that $W_{m-1,\mathrm{p}} < W_{m-1,\mathrm{h}}$ and $W_{m,\mathrm{p}} > W_{m,\mathrm{h}}$. Provided that the configuration of non-parasites and parasites is such that the females of rank higher than $m+1$ are all non-parasites and those of rank lower than m are all parasites, how is the critical rank m determined?

Now we consider the whole population consisting of only non-parasites, and the number is $2N$. The following argument can be carried out in the same way for the case when the total number of females is $2N+1$.

At first, we consider the expected fitness gain for the female of rank $2N$. When the female is non-parasite, the expected fitness gain $W_{2N,\mathrm{h}}$ is given by

$$W_{2N,\mathrm{h}} = k_{\mathrm{t}} \mu^{2N-1} \mathrm{e}^{-\alpha k_{\mathrm{t}}}. \tag{F.1}$$

Next, we consider the expected fitness gain for the female when she would become parasite. The expected fitness gain from the eggs laid in the nest of host depends on the rank of randomly selected host individual and is now given as follows (see Appendix C)

$$\sum_{i=1}^{2N-1} \frac{1}{2N-1} \left\{ \sum_{j=0}^{k_{\mathrm{b}}} \binom{k_{\mathrm{b}}}{j} \eta^j (1-\eta)^{k_{\mathrm{b}}-j} j \mu^{i-1} \mathrm{e}^{-\beta j} \mathrm{e}^{-\gamma k_{\mathrm{t}}} \right\}. \tag{F.2}$$

So the totally expected fitness gain for the parasite of rank $2N$ is now given by

$$W_{2N,\mathrm{p}} = k_{\mathrm{s}} \mu^{2N-1} \mathrm{e}^{-\alpha k_{\mathrm{s}}} + \frac{1}{2N-1} \frac{1-\mu^{2N-1}}{1-\mu} \mathrm{e}^{-\gamma k_{\mathrm{t}}} \eta \mathrm{e}^{-\beta} U^{k_{\mathrm{b}}-1} k_{\mathrm{b}}, \tag{F.3}$$

where $U = \eta \mathrm{e}^{-\beta} + 1 - \eta$. We consider that the female of rank $2N$ tends to behave as parasite if and only if $W_{2N,\mathrm{p}} > W_{2N,\mathrm{h}}$.

Now we suppose that the females of rank lower than $2N-i+1$ ($i = 2, 3, \ldots, N+1$) are all parasites. We focus the fitness of the female of rank $2N-i+1$. From Eqs. (8) and (9), the inequality

$$W_{2N-i+1,\mathrm{h}} < W_{2N-i+1,\mathrm{p}} \tag{F.4}$$

is equivalent to the following inequality

$$g_{2N-i+1}(\mu) \equiv \mu^{2N-i} \{ (2N-i) \zeta_{2N-i+1}(1-\mu) + \varphi \} < \varphi, \tag{F.5}$$

where

$$\zeta_{2N-i+1} = \left\{ 1 - (1 - V^{k_{\mathrm{b}}}) \frac{i-1}{2N-i+1} \right\} k_{\mathrm{t}} \mathrm{e}^{-\alpha k_{\mathrm{t}}} - k_{\mathrm{s}} \mathrm{e}^{-\alpha k_{\mathrm{s}}};$$

$$V = \eta e^{-\gamma} + 1 - \eta;$$

$$\varphi = e^{-\gamma k_t} \eta e^{-\beta} U^{k_b-1} k_b.$$

If one of the following four conditions is satisfied, the inequality (F.5) is true for $\forall \mu \ (0 < \mu < 1)$:

$$\zeta_{2N-i+1} > 0, \quad \zeta_{2N-i+1} \leqslant \varphi \qquad \text{(Fig. 3(a))}$$

$$\zeta_{2N-i+1} < 0, \quad (2N-i)\zeta_{2N-i+1} > \varphi \quad \text{(Fig. 3(c))}$$

$$\zeta_{2N-i+1} < 0, \quad (2N-i)\zeta_{2N-i+1} \leqslant \varphi \quad \text{(Fig. 3(d))}$$

$$\zeta_{2N-i+1} = 0, \qquad\qquad\qquad\qquad\quad \text{(Fig. 3(d))}.$$

In this case, the female of rank $2N - i + 1$ would tend to behave as a parasite.

If $\zeta_{2N-i+1} > 0$ and $\zeta_{2N-i+1} > \varphi$, there is a certain $\tilde{\mu}_{2N-i+1}(< 1)$ such that $g_{2N-i+1}(\tilde{\mu}_{2N-i+1}) = \varphi$ (see Fig. 3(b)). Then

$$0 < \mu < \tilde{\mu}_{2N-i+1} \Rightarrow W_{2N-i+1,h} < W_{2N-i+1,p};$$

$$\mu = \tilde{\mu}_{2N-i+1} \Rightarrow W_{2N-i+1,h} = W_{2N-i+1,p};$$

$$\tilde{\mu}_{2N-i+1} < \mu < 1 \Rightarrow W_{2N-i+1,h} > W_{2N-i+1,p}.$$

Thus, $\tilde{\mu}_{2N-i+1}$ gives such a range of μ that the female of rank $2N - i + 1$ behaves as parasite.

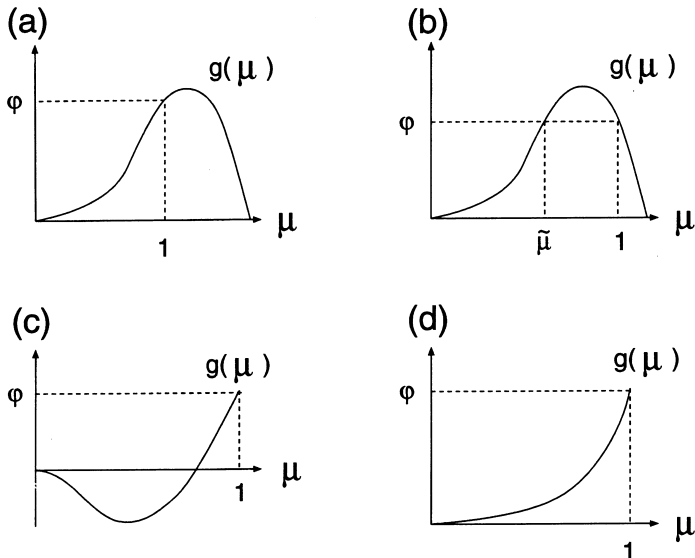We can make the same argument for the female of rank $2N - i$. The inequality

Fig. 3. Possible relations between φ and $g(\mu)$. For details, see text.

$$W_{2N-i,\text{h}} < W_{2N-i,\text{p}} \tag{F.6}$$

is equivalent to the following:

$$g_{2N-i}(\mu) = \mu^{2N-i-1}\{(2N - i - 1)\zeta_{2N-i}(1 - \mu) + \varphi\} < \varphi, \tag{F.7}$$

where

$$\zeta_{2N-i} = \left\{1 - (1 - V^{k_\text{b}})\frac{i}{2N - i}\right\}k_\text{t}\text{e}^{-\alpha k_\text{t}} - k_\text{s}\text{e}^{-\alpha k_\text{s}}. \tag{F.8}$$

We find that Eq. (F.6) is true when $\zeta_{2N-i} \leqslant 0$ or when $\zeta_{2N-i} > 0$ and $\zeta_{2N-i} \leqslant \varphi$. If $\zeta_{2N-i+1} > 0$ and $\zeta_{2N-i+1} > \varphi$, there is a certain $\tilde{\mu}_{2N-i}$ (< 1) such that $g_{2N-i}(\tilde{\mu}_{2N-i}) = \varphi$. Lastly, it is shown that

$$0 < \mu < \tilde{\mu}_{2N-i} \Rightarrow W_{2N-i,\text{h}} < W_{2N-i,\text{p}};$$

$$\mu = \tilde{\mu}_{2N-i} \Rightarrow W_{2N-i,\text{h}} = W_{2N-i,\text{p}};$$

$$\tilde{\mu}_{2N-i} < \mu < 1 \Rightarrow W_{2N-i,\text{h}} > W_{2N-i,\text{p}}.$$

From these arguments, we can find that the necessary condition for the existence of m is $\zeta_N > \varphi$. The reason why this condition is necessary for the existence of m is as follows: We can easily find that $\zeta_{2N-i} \leqslant \zeta_{2N-i+1}$. Thus, if the inequality that $\zeta_x \leqslant \varphi$ is true for a certain rank x, the inequality that $\zeta_y \leqslant \varphi$ is always true for any rank y higher than x, that is, from 1 to $x - 1$. This means that any female of rank higher than x tends to behave as parasite and the number of parasites increases. Therefore, for the existence of m, the condition $\zeta_N > \varphi$ is necessary.

Now, we consider the relation between $\tilde{\mu}_{2N-i+1}$ and $\tilde{\mu}_{2N-i}$. We can find that $\tilde{\mu}_{2N-i} < \tilde{\mu}_{2N-i+1}$ if the following inequality is satisfied.

$$g_{2N-i}(\tilde{\mu}_{2N-i+1}) > \varphi. \tag{F.9}$$

On the other hand, we get the following equation from the definition of $\tilde{\mu}_{2N-i+1}$:

$$\frac{\tilde{\mu}_{2N-i+1}^{2N-i}(2N - i)(1 - \tilde{\mu}_{2N-i+1})}{1 - \tilde{\mu}_{2N-i+1}^{2N-i}} = \varphi. \tag{F.10}$$

Therefore, from Eqs. (F.7) and (F.10), the inequality (F.9) is lead to the following:

$$\tilde{\mu}_{2N-i+1}^{2N-i-1}(2N - i - 1)(1 - \tilde{\mu}_{2N-i+1})\zeta_{2N-i}$$

$$> \frac{\tilde{\mu}_{2N-i+1}^{2N-i}(1 - \tilde{\mu}_{2N-i+1})(2N - i)}{1 - \tilde{\mu}_{2N-i+1}^{2N-i}}(1 - \tilde{\mu}_{2N-i+1}^{2N-i-1})\zeta_{2N-i+1}$$

$$> \frac{\tilde{\mu}_{2N-i+1}^{2N-i}(1 - \tilde{\mu}_{2N-i+1})(2N - i)}{1 - \tilde{\mu}_{2N-i+1}^{2N-i}}(1 - \tilde{\mu}_{2N-i+1}^{2N-i-1})\zeta_{2N-i}, \tag{F.11}$$

where we used the relation $\zeta_{2N-i} \leqslant \zeta_{2N-i+1}$ for $i = 1, 2, \ldots, N - 1$. The obtained inequality (F.11) is rewritten as follows:

$$\frac{2N - i - 1}{2N - i} > \frac{\tilde{\mu}_{2N-i+1}}{1 - \tilde{\mu}_{2N-i+1}^{2N-i}} (1 - \tilde{\mu}_{2N-i+1}^{2N-i-1}). \tag{F.12}$$

Now, we define the following function of x:

$$Q(x) = \frac{x}{1 - x^{2N-i}} (1 - x^{2N-i-1}), \tag{F.13}$$

and can easily show that $Q(x)$ is monotonically increasing function of x $(0 < x < 1)$. Since $Q(0) = 0$ and

$$\lim_{x \to 1} \frac{x(1 - x^{2N-i-1})}{1 - x^{2N-i}} = \frac{2N - i - 1}{2N - i}, \tag{F.14}$$

we can prove that Eq. (F.12) is true for $\forall \tilde{\mu}_{2N-i+1}$ $(0 < \tilde{\mu}_{2N-i+1} < 1)$, so that Eq. (F.9) is true. Consequently, we find that $\tilde{\mu}_{2N-i} < \tilde{\mu}_{2N-i+1}$ for $\forall \tilde{\mu}_{2N-i+1}$ $(0 < \tilde{\mu}_{2N-i+1} < 1)$. That is, the higher the rank of the female is, the narrower the range of μ which satisfies the condition for the female to behave as parasite.

From the above arguments, if there exists m such that $W_{m-1,p} < W_{m-1,h}$ and $W_{m,p} > W_{m,h}(N < m \leqslant 2N)$, the following condition must be satisfied:

$$\zeta_N > \varphi, \quad \tilde{\mu}_{m-1} \leqslant \mu < \tilde{\mu}_m. \tag{F.15}$$

Therefore, lastly, since $\tilde{\mu}_N \leqslant \tilde{\mu}_m \leqslant \tilde{\mu}_{2N}$ for $N \leqslant m \leqslant 2N$, if the following conditions are satisfied, there exists the unique m such that $W_{m-1,p} < W_{m-1,h}$ and $W_{m,p} > W_{m,h}(N < m \leqslant 2N)$:

$$\zeta_N > \varphi, \quad \tilde{\mu}_N \leqslant \mu < \tilde{\mu}_{2N}. \tag{F.16}$$

These arguments prove Proposition 4.

References

[1] Y. Yom-Tov, Intraspecific nest parasitism in birds, Biol. Rev. 55 (1980) 93.

[2] F.C. Rohwer, S. Freeman, The distribution of conspecific nest parasitism in birds, Can. J. Zool. 70 (1992) 1859.

[3] W.J. Hamilton, G.H. Orians, Evolution of brood parasitism in altricial birds, Condor 67 (1965) 361.

[4] R.P. Payne, The ecology of brood parasitism in birds, Ann. Rev. Ecol. Sys. 8 (1977) 1.

[5] A. Yamauchi, Theory of intraspecific nest parasitism in birds, Anim. Behav. 46 (1993) 335.

[6] A. Yamauchi, Theory of evolution of nest parasitism in birds, Am. Natural 145 (1995) 434.

[7] F. Takasu, K. Kawasaki, H. Nakamura, J.E. Cohen, N. Shigesada, Modeling the population dynamics of a cuckoo-host association and the evolution of host defenses, Am. Natural 142 (1993) 819.

[8] N.A. Wood, The breeding behaviour and biology of the moorhen, Br. Birds 67 (1974) 104.

[9] D.W. Gibbons, Brood parasitism and cooperative nesting in the moorhen, gallinula chloropus, Behav. Ecol. Sociobiol. 19 (1986) 221.