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A MATHEMATICAL MODEL OF THE EVOLUTION OF HOST DEFENSIVE BEHAVIOR IN CUCKOO - HOST ASSOCIATIONS

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Abstract. - In order to gain insights into the process of coevolution in brood parasitism, a mathematical model is constructed in term of population dynamics together with population genetics of a rejection gene in a host population. The model analyses show that both the dynamical change in the cuckoo-host association and the establishment of the rejecter gene in the host population crucially depend on the product of two factors, the carrying capacity of the host and the cuckoo's searching efficiency. Based on these results, various quantities at the evolutionary equilibrium state in the cuckoo-host associations are discussed.

Introduction

The cuckoo *Cuculus canorus* does not build a nest and does not rear its chick by itself. Instead, a female cuckoo lays eggs in the nest of several other bird species and lets them rear the chicks. The cuckoo can not obtain reproductive success if the para-sitism is rejected by the host. On the other hand, a parasitized host gets no reproductive success if it accepts the cuckoo egg, because the cuckoo chick ejects the host's eggs and nestlings out of the nest. Therefore, it is thought that the cuckoo has been selected for sophisticated egg mimicry to deceive the host, and the host species have been selected for developing counteradaptation to avoid the parasitism such as an ability to recognize the cuckoo eggs. Although it is believed that the host's rejection behavior has evolved in response to the cuckoo parasitism, what triggers the rejection behavior remains unknown. Since some host populations which are not parasitized at present show high abilities to discriminate the cuckoo parasitism, it is

likely that genetic factors determine the host behavior toward parasitism and the rejection behavior is inherited within one host population.

Recent studies have shown that host species, in general, differ in their abilities to avoid the cuckoo parasitism from population to population even within one host species. A host population with a long history of parasitism seems to have a high ability to reject parasitism, compared with the populations which seem to have no experience of the cuckoo parasitism (Nakamura 1990, Davies & Brooke 1989 , Soler 1991).

Nakamura (1990) compiled the records of the brood parasitism by the cuckoo during the last 60 years at Nagano prefecture located in the central Japan and showed that the parasitic relations between the cuckoo and hosts have changed. Siberian meadow bunting *Emberiza cioides*, which was the main host about 60 years ago, is currently seldom parasitized, while a new host, Azure-winged magpie *Cyanopica cyana*, has become parasitized for these decades. Because Azure-winged magpie did not show rejection behavior at all in the beginning, it has suffered severe parasitism. However, some magpie populations has been establishing the rejection behavior. Magpie population at Azumino, which has been exposed to cuckoo parasitism for about 20 years, shows a rejection rate of 41.7% (rate at which a magpie rejects parasitism) and the magpie at Nagano city with parasitism history of about 15 years shows a rejection rate of 34.7%.

Imanishi (personal communication) recorded temporal changes in the parasitism rate (rate of a nest being parasitized) and rejection rate at Nobeyama height, where the magpie population has been exposed to severe parasitism for about 10 years (Fig. 1). These evidences support the idea that the host rejection behavior establishes in response to the cuckoo parasitism and that the cuckoo-host association can change dynamically within a short period. In order to explore the process of such dynamical phenomena, a mathematical model is constructed.
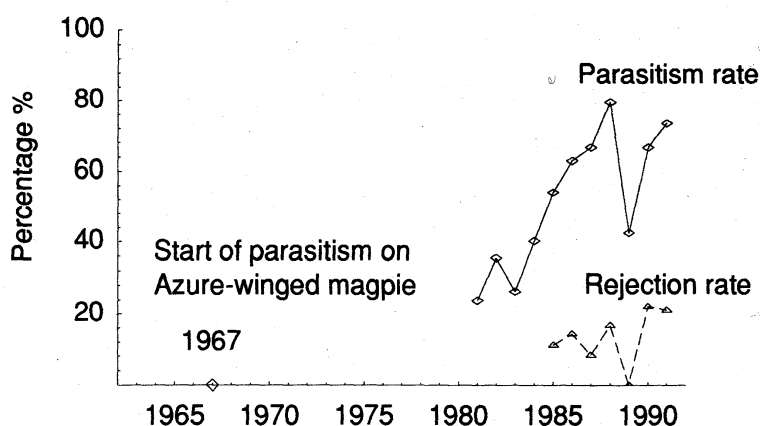
148

Fig. 1. Changes in the parasitism rate on Azure-winged magpie (rectangle) and the rejection rate of naturally deposited cuckoo eggs (triangle) at Nobeyama height recorded by Imanishi. In 1989, a number of cuckoos were captured for research so that the parasitism rate and the rejection rate decreased temporarily.

Assumptions

The cuckoo and majority of its host species are migrants and it is known that they come back to the same area in the next breeding season. We consider population densities of female cuckoo and female host in one locality. The rejection behavior of the host is determined by two alleles at one locus, allele R causing the rejection behavior, allele A causing no rejection behavior and R is dominant over A. Genotypes RR, RA are rejecters and that of AA is an accepter. Let P_t be the population density of female cuckoo and H_t be that of female host in year t. Let x_t, y_t and z_t be the frequencies of RR, RA and AA genotypes in the host population in year t, respectively. Newly born offspring are recruited into adulthood at the end of their first year.

The probability that a given host nest escapes from the cuckoo parasitism is given by the zeroth term of Poisson distribution, $\exp(-a\,P_t)$, where parameter a measures the cuckoo's ability in searching the host nest. The cuckoo parasitism succeeds if both of breeding pair are accepters, which we call an accepter pair, and the parasitism fails if at least one of the pair is a rejecter, which we call rejecter pair. If a cuckoo egg is accepted, it reares and survives to the next breeding season with probability Γ. Γ remains constant even when a nest is parasitized multiply, because only one cuckoo chick usually monopolizes the nest. An adult cuckoo survives to the next breeding season with probability s_P.

A host accepter pair rears f female chicks only if it escapes from parasitism and a rejecter pair rears less chicks of εf by a factor of ε ($\varepsilon <$

1). The parameter ε measures the rejection cost. The host density in the absence of the cuckoo is regulated by availabilities of limited food recourses or territories. An adult host survives to the next breeding season with probability s_H.

In Table 1, 2 and Fig. 2, we summarize the above assumptions.

Table1. Variables and parameters used in this model.

Variables		Parameters			
		Cuckoo		Host	
Female cuckoo density	P_t				
Female host density	H_t	Survival rate	s_P	Survival rate	s_H
Frequency of RR	x_t	Searching efficiency	a	Net breeding rate of	f
RA	y_t	Surviral rate of egg	Γ	accepter pair	
AA	z_t			Rejection cost	ε
				Intra-specific competition	k

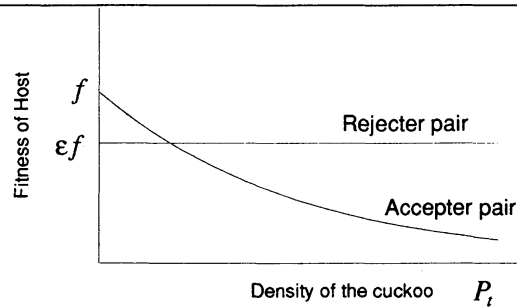| Frequency Female \ Frequency Male		x_t RR	y_t RA	z_t AA
x_t	RR	εf	εf	εf
y_t	RA	εf	εf	εf
z_t	AA	εf	εf	$f e^{-a P_t}$

Table. 2 Breeding rate of the host.

Fig. 2 Fitness of rejecter & accepter pairs

A Model

The cuckoo parasitism succeeds only when she lays an egg in the nest of an accepter pair, whose frequency is z_t^2. Then, the cuckoo density in the next year, $t+1$, is related to P_t, H_t and z_t as follows:

$$P_{t+1} = s_P P_t + \left(1 - e^{-a P_t}\right) z_t^2 H_t \Gamma ,$$ (1-a)

where the first term represents the survivors and the second term the recruitment to adulthood. The parasitism rate is given as

$$\left(1 - e^{-a P_t}\right) z_t^2 .$$

With respect to host dynamics, the density of rejecter pair is $(1 - z_t^2)H_t$, each of which produces εf offspring, while the density of accepter pair is $z_t^2 H_t$, each of which breeds $f \exp(- a P_t)$ offspring, to yield the intrinsic total density of offspring as

$$\left\{\left(1 - z_t^2\right)\varepsilon + z_t^2 e^{-a P_t}\right\} f H_t .$$

Then, the density of host in the next year is obtained as follows:

$$H_{t+1} = \frac{1}{1 + H_t / k}\left[s_H H_t + \left\{\left(1 - z_t^2\right)\varepsilon + z_t^2 e^{-a P_t}\right\} f H_t \right] .$$ (1-b)

The term $1/(1+H_t/k)$ represents the density effect by intra-specific competition and the degree of the density effect is measured by a parameter $1/k$.

Next, we derive equations that relate the frequencies of genotypes in year $t+1$ to those in the previous year. From Table 2, the densities of offspring with genotype RR, RA and AA are derived as follows.

Genotype RR: $(x_t^2 + x_t y_t + y_t^2 / 4)\, \varepsilon f H_t$

Genotype RA: $(x_t y_t + 2x_t z_t + y_t z_t + y_t^2 / 2)\, \varepsilon f H_t$

Genotype AA: $(y_t^2 / 4 + y_t z_t)\, \varepsilon f H_t + z_t^2 f \exp(-a\, P_t)\, H_t$

Then, the frequencies of RR and RA in the next year in the host population are given as

$$x_{t+1} = \frac{s_H\, x_t + \left(x_t^2 + x_t y_t + y_t^2 / 4 \right) \varepsilon f}{s_H + \left(1 - z_t^2 \right) \varepsilon f + z_t^2 f\, e^{-a\, P_t}} \tag{1-c}$$

$$y_{t+1} = \frac{s_H\, y_t + \left(x_t y_t + 2x_t z_t + y_t z_t + y_t^2 / 2 \right) \varepsilon f}{s_H + \left(1 - z_t^2 \right) \varepsilon f + z_t^2 f\, e^{-a\, P_t}} . \tag{1-d}$$

Possible nontrivial equilibria (P^*, H^*, x^*, y^*) of equations (1) are obtained by setting $P_t = P_{t+1}=P^*$, $H_t = H_{t+1}=H^*$, $x_t = x_{t+1}=x^*$ and $y_t = y_{t+1}=y^*$, to get $(P^*, H^*, x^*, y^*) =$

$(0, k\,(f + s_H - 1), 0, 0)$ (2-a)

$(P^\sim, H^\sim, 0, 0)$ (2-b)

$(0, k\,(\varepsilon f + s_H - 1), 1, 0)$ (2-c)

$\left(\frac{1}{a} \log \frac{1}{\varepsilon}, k(\varepsilon f + s_H - 1), \left(1 - D^{\frac{1}{4}}\right)^2, 2\left(D^{\frac{1}{4}} - D^{\frac{1}{2}} \right) \right)$ (2-d)

where $(P^\sim, H^\sim)$ is a unique solution of the following equations

$$H^\sim = \frac{(1 - s_P)\, P^\sim}{\Gamma\left(1 - e^{-a P^\sim}\right)} \quad \text{and} \quad H^\sim = k\left(f\, e^{-a P^\sim} + s_H - 1 \right)$$

and $\quad D = \dfrac{(1 - s_P) \log \frac{1}{\varepsilon}}{a\, k\, \Gamma\,(\varepsilon f + s_H - 1)(1 - \varepsilon)} .$

The population density of the host before parasitism starts, K, is obtained by setting $P_t = 0$ and $x_t = y_t = 0$ in (1-b) as

$K = k\,(f + s_H - 1) .$ (3)

This quantity is the carrying capacity of the host population, i.e., the equilibrium density of the host population before the cuckoo starts parasitism. The value of K will vary from place to place, depending on environmental conditions and host species. Since K is proportional to k, we treat K as a new parameter instead of k. The dynamical properties of (1) are analyzed by linearization around each equilibrium together with

numerical calculations (see Appendix for details). The result shows that the dynamical behaviors are characterized by the product of K and a and there are two critical values for $a\,K$: A_1 and A_2 ($> A_1$) which are defined as

$$A_1 = \frac{1-sp}{\Gamma} \quad \text{and} \quad A_2 = \frac{(1-sp)(f+s_H-1)\log\frac{1}{\varepsilon}}{\Gamma(1-\varepsilon)(\varepsilon f+s_H-1)}.$$

The product $a\,K$ biologically represents the average number of host nests which a female cuckoo parasitizes during a breeding season when the cuckoo density is low. In the following, we summarize the possible cases which are classified by the value of $a\,K$.

Case (i) $0 < a\,K < A_1$

The inequality implies that the death rate of the cuckoo exceeds the birth rate. Thus the system always approaches equilibrium state (2-a), where only the host population sustains itself. The rejecter allele, if it emerges by mutation, does not spread because there are no threat of parasitism.

Case (ii) $A_1 < a\,K < A_2$

The system finally approaches the equilibrium (2-b) or oscillates around it, depending on the parameter values. Thus both populations persist. The rejecter allele, however, does not spread among the population even when the population suffers from parasitism. Therefore, the lack of counter-adaptation does not necessarily imply that the host is a recent host. Note that this case (ii) is possible only when rejection behavior by the host entails some cost ($\varepsilon < 1$), because if the host loses nothing by rejection behavior ($\varepsilon = 1$), critical value A_2 becomes identical to A_1.

Case (iii) $A_2 < a\,K$

Only equilibrium (2-d) is stable and the system always converges to the equilibrium. Both the cuckoo and the host can coexist and the rejecter allele can spread among the host population. Note that the cuckoo can survive only when there is the cost of rejection ($\varepsilon < 1$).

We evaluated several quantities at the stable equilibrium state which seem biologically meaningful. The ratio of the cuckoo density to the host density and the parasitism rate at the equilibrium (P^*/H^* and $(1-\exp(-a\,P^*))\,z^{*2}$, respectively) are illustrated as a function of $a\,K$ (Fig. 3-a). The ratio remains zero for $0 < a\,K < A_1$, then it increases from zero until reaching a maximum $(1-\varepsilon)\Gamma/(1-sP)$ at $a\,K = A_2$. As $a\,K$ becomes larger than A_2, the ratio decreases to zero. The parasitism rate at the equilibrium

shows a pattern similar to the ratio, P^*/H^*, having a maximum $1-\varepsilon$ at $a\,K$ $= A_2$. Because the rejection cost, in general, is thought to be small (ε is close to 1), these results imply that the cuckoo population is scarce compared with the host population and the parasitism rate is very low at the equilibrium state. In Fig. 3-b, the equilibrium frequencies of the rejecter individual and the rejecter pair ($x^* + y^*$ and $1-z^{*2}$, respectively) are illustrated in relation to the value of $a\,K$. When $a\,K$ is greater than A_2, both quantities increase monotonically tending to 1 at $a\,K = \infty$. Except for the extreme $a\,K = \infty$, the host population exhibits a polymorphic blend of rejecter and accepter individuals at the equilibrium state.
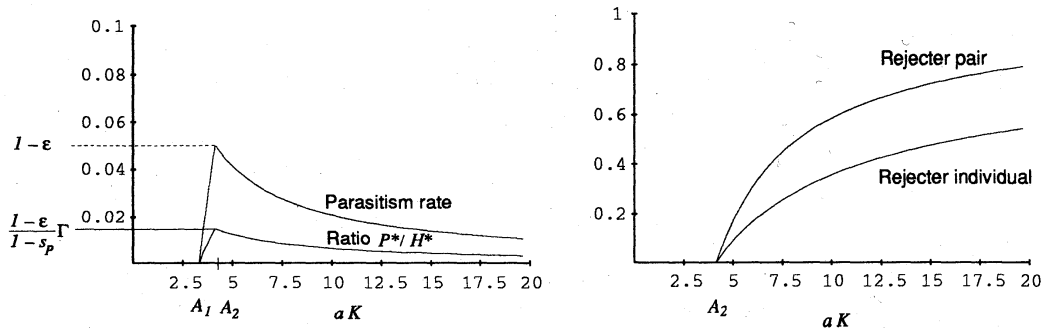

Fig. 3-a (left) The ratio of the cuckoo density to the host density and the parasitism rate at the equilibrium state in relation to $a\,K$. The maximum ratio $(1-\varepsilon)\Gamma/(1-sP)$ and the maximum parasitism rate $1-\varepsilon$ are attained at $a\,K = A_2$. b (right) The equilibrium frequencies of the rejecter individual and rejecter pair in relation to $a\,K$. For $a\,K < A_2$, the rejecter allele does not spread among the host population.

Numerical calculations

Here we choose a set of parameter values s_P, $s_H = 0.5$, $f = 0.7$, $\Gamma = 0.15$, $a = 0.7$, $K = 16$. The rejection cost, ε, is temporarily set to 0.95, because there are few data available for the estimation. These parameter values satisfy condition (iii) $A_2 < a\,K$, in which the rejecter allele spreads among the host. At the initial state, we set $P_0 = 0.01$, $H_0 = K = 16$ and $x_0 = 0$, $y_0 = 0.05$, i.e., a small number of the cuckoo start to parasitize the host population which is maintained at the carrying capacity K and contains a small fraction of the rejecter individuals. In Fig. 4-a, the densities of the cuckoo and the host, and in Fig. 4-b, the parasitism rate and the frequency of rejecter pair are illustrated as a function of time.
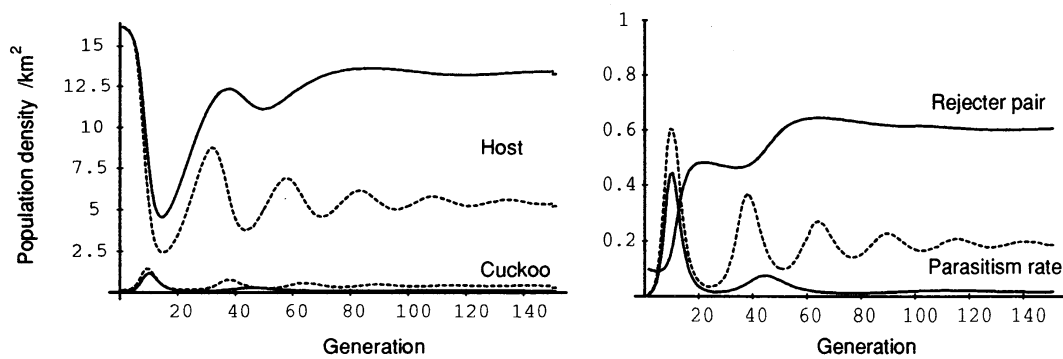
Fig. 4-a (left): Temporal changes in the densities of the cuckoo and the host populations. b (rigth): Temporal changes in the parasitism rate and the frequency of rejecter pair. The dotted lines are the corresponding ones for the case of no genetic variation. Parameters used are: $s_H = 0.5$, $f = 0.7$, $\varepsilon = 0.95$, $K = 16$, $s_P = 0.5$, $\Gamma = 0.15$, $a = 0.7$. The initial state is $P_0 = 0.01$, $H_0 = 16$ and $x_0 = 0$, $y_0 = 0.05$.

For comparison, we include the corresponding case (the dashed curves) in the absence of the rejecter allele ($x_0 = y_0 = 0$). The presence of the rejecter allele leads to an increase in the host density and decrease in the parasitism rate. Frequency of the rejecter pair increases rapidly, eventually reaching 60%, and the rate of increases is accelerated when the parasitism rate begins to decrease. At the equilibrium state, the host density recovers to as much as the level prior to the parasitism, while the cuckoo density and the parasitism rate go down to very low levels.

Discussion

The magpie density prior to parasitism seems to be high and the magpie builds a nest on a tree which is easy to find so that $a K$ could be larger than A_2. Rapid changes in the cuckoo-Azure-winged magpie associations in Japan may correspond to the initial stage of dynamical change. Our model predicts that the magpie population will eventually establish counteradaptation within a short period and the host density will recover to the original level with concomitant reduction in the cuckoo parasitism. Our model could be also applied to the former main host, Siberian meadow bunting. We suggest that the density of the bunting was high and its nests were probably easy to find, so that the bunting has established rejection behavior at a high level, driving the bunting gens cuckoo to decline. More detailed demographic data are needed to strengthen the mathematical formulation.

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Appendix

Stability of the equilibria of (1) are tractable by examining the eigenvalues of Jacobi matrix: an equilibrium is locally stable if the absolute values of eigenvalues of the Jacobi matrix are all less than unity. Using this criterion, we examine the stability properties of all the equilibrium state (2- a~d) with respect to small perturbation. Global stabilities are also studies by extensive numerical calculations and the results show that global stability is assured if each equilibrium is locally stable.

Stability of equilibrium (2-a)

Linearization of difference equation (1) around (2-a) yields the Jacobi matrix whose eigenvalues are given as follows:

$$s_P + k \Gamma a (f + s_H - 1), \quad 1/(f + s_H), \quad s_H/(f + s_H) \quad \text{and} \quad (\varepsilon f + s_H)/(f + s_H)$$

The last two eigenvalues are always positive and less than unity and equilibrium (2-a) is stable if and only if $0 < a K < A_1$. When $K = k(f + s_H - 1) < 0$, the host population goes extinct in the absence of the cuckoo. We do not consider such a biologically meaningless case.

Stability of equilibrium (2-b)

Equilibrium (2-b) can not be given in explicit form. But this equilibrium bifurcates from (2-a) as $a\,K$ increases across A_1. Numerical calculations show that (2-a) is stable or unstable, depending on parameter values. If unstable, the system contains a stable limit cycle.

Stability of equilibrium (2-c)

This equilibrium is unstable and never attained actually. This is because the rejection behavior is always disadvantageous in the absence of the cuckoo.

Stability of equilibrium (2-d)

This is a unique equilibrium which allows positive internal frequencies of the rejecter genotypes $(0 < x^*, y^* < 1)$. Although it is very complicated, the jacobi matrix, M, around (2-d) can be obtained. Eigenvalues of the jacobi matrix are the solutions of the following form:

$$|\lambda\,I - M| = \lambda^4 + a_1\lambda^3 + a_2\lambda^2 + a_3\lambda + a_4 = 0 , \qquad (4)$$

where a_1, a_2, a_3, a_4 are determined by the parameters and the followings are satisfied.

$$a_1, a_3 < 0 \text{ and } a_2, a_4 > 0.$$

To analyze the stability, we transfer the complex space $|\lambda| < 1$ to $\mathrm{Re}(\omega) < 0$ by a transform$\omega = (\lambda + 1)/(\lambda - 1)$. Then the characteristic equation (4) is transformed into the following equation,

$$\omega^4 + b_1\omega^3 + b_2\omega^2 + b_3\omega + b_4 = 0 , \qquad (5)$$

where $b_1 = \dfrac{4 + 2\,a_1 - 2\,a_3 - 4\,a_4}{1 + a_1 + a_2 + a_3 + a_4}$ $b_2 = \dfrac{6 - 2\,a_2 + 6\,a_4}{1 + a_1 + a_2 + a_3 + a_4}$

$b_3 = \dfrac{4 - 2\,a_1 + 2\,a_3 - 4\,a_4}{1 + a_1 + a_2 + a_3 + a_4}$ $b_4 = \dfrac{1 - a_1 + a_2 - a_3 + a_4}{1 + a_1 + a_2 + a_3 + a_4}$

and $1 + a_1 + a_2 + a_3 + a_4 > 0$ for $A_2 < a\,K$.

We make use of the Routh-Hurwitz condition, which assures for all the solution of (5) to have negative real parts. The Routh-Hurwitz criteria are as follows.

(a) $b_1 > 0$ (b) $\begin{vmatrix} b_1 & b_3 \\ 1 & b_2 \end{vmatrix} > 0$ (c) $\begin{vmatrix} b_1 & b_3 & 0 \\ 1 & b_2 & b_4 \\ 0 & b_1 & b_3 \end{vmatrix} > 0$ and (d) $b4 > 0$ (6)

It can be proved that condition (6- d) is satisfied when $A_2 < a\,K$. Further mathematical analyses together with numerical calculation show that conditions (6- a, b, c) are satisfied for biologically reasonable ranges of parameter values.