

MODELING THE POPULATION DYNAMICS OF A CUCKOO-HOST ASSOCIATION AND THE EVOLUTION OF HOST DEFENSES

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Abstract.—Cuckoo parasitism in Nagano Prefecture in Japan has shown dramatic changes in the parasitism rate, host usage by the cuckoo, and defensive behavior of hosts during the past 60 yr. To gain insights into these phenomena, we model the population dynamics of a cuckoo-host association together with the population genetics of a rejecter gene in the host population. Analysis shows that both the dynamical change in the host-parasite association and the establishment of the host's counteradaptation crucially depend on the product of two factors, the carrying capacity of the host and cuckoo's searching efficiency. When the product is less than a critical value, the host population cannot evolve a counteradaptation even if parasitized by the cuckoo. Hence, the lack of counteradaptation does not necessarily imply that the host population only recently has become parasitized. As the product becomes larger, the rejection behavior will be eventually established at higher levels in the host population. In this case, the spreading of rejection behavior is very fast, which suggests that the cuckoo-host association reaches an equilibrium state within a relatively short period. These results make possible new interpretations of several circumstances reported about cuckoo-host associations.

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 nests of other bird species and lets them rear her chicks. The cuckoo cannot reproduce successfully if the parasitism 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. How to cheat a host is, therefore, of crucial importance for the cuckoo, and how to avoid parasitism is crucial for the host. As a result of the interaction, it is expected that the cuckoo has been selected for sophisticated egg mimicry to deceive its host and host species have been selected for counteradaptations to avoid the parasitism, such as an ability to recognize the cuckoo eggs and aggressive behaviors toward the cuckoo.

More than 100 species have been recorded as hosts of the cuckoo (Wyllie 1981). Some host species have a great ability to discriminate against cuckoo eggs, while other species show no rejection behavior. The degree of rejection behavior differs from species to species and from population to population even within one host

species. Host populations with a long history of parasitism show relatively high abilities to reject parasitism and are more aggressive toward the cuckoo, compared with populations that seem to have no experience of the cuckoo parasitism (Davies and Brooke 1989a, 1989b; Soler and Møller 1990; Briskie et al. 1992; H. Nakamura, S. Kubota, and R. Suzuki, unpublished manuscript). Although it is believed that the host's rejection behavior has evolved in response to the cuckoo parasitism, what triggers the host rejection behavior remains unknown. Some host populations that are not parasitized at present show high abilities to discriminate cuckoo eggs and aggressive behavior toward stuffed cuckoos (Briskie et al. 1992; H. Nakamura, S. Kubota, and R. Suzuki, unpublished manuscript). Therefore, it is likely that genetic factors determine the host behavior toward parasitism, and the rejection behavior is inherited within one host population.

Nakamura (1990) compiled the records of brood parasitism by the cuckoo *C. canorus* during the last 60 yr in Nagano Prefecture, central Japan. He found that the parasitic relation between the cuckoo and its hosts in Nagano Prefecture, where cuckoos live widely from the bottom of basins (280–400 m) to the subalpine zone (less than 1,800 m), shows some dynamic characteristics, to wit, a large number of major host species, a high frequency of parasitism exceeding 20%, and recent changes in host usage. Six species, bull-headed shrike (*Lanius bucephalus*), brown shrike (*Lanius cristatus*), Siberian meadow bunting (*Emberiza cioides*), great reed warbler (*Acrocephalus arundinaceus*), grey-headed bunting (*Emberiza fucata*), and black-face bunting (*Emberiza spodocephala*), have been the main hosts. The number of major host species is large compared with those in England and in continental Europe.

Recently, however, the main hosts have been changing (Nakamura 1990). The Siberian meadow bunting has become a rare host, although it is still the most abundant species. It seems that the bunting has established a strong egg-discrimination ability during the past 60 yr, causing the cuckoo's parasitism to be unsuccessful. On the other hand, the azure-winged magpie, *Cyanopica cyana*, has been emerging as a new major host of the cuckoo, since the magpie was first observed in mid-1960s (Hosono 1969). About 50 yr ago, the distributions of the cuckoo and the azure-winged magpie were mostly separated altitudinally: azure-winged magpies lived below 1,000 m and the cuckoos were distributed from 700 m to 1,600 m. In the mid-1960s, the range of the magpie started to expand into the higher area and that of the cuckoo toward the lower area, and the overlapping area has since been increasing monotonically. In the mid-1970s, the cuckoo spread to the Nagano basin (280 m), while the magpie ascended to 1,450 m. At present, cuckoo parasitism on the magpie has expanded almost over the entire breeding range of the magpie. As a result, the cuckoos that parasitize the magpie have increased in number so much that multiple egg laying by cuckoos within a nest is often observed (Yamagishi and Fujioka 1986; Nakamura 1990).

Typical data of parasitism on azure-winged magpie were taken at the Kawana-kajima village near Nagano city, where few cuckoos were observed in the mid-1960s. During the past two decades, the population density of the cuckoo reached about two individuals/km², while the density of azure-winged magpie declined from 16 to five/km². Meanwhile, the parasitism rate increased from 0% to 30%.

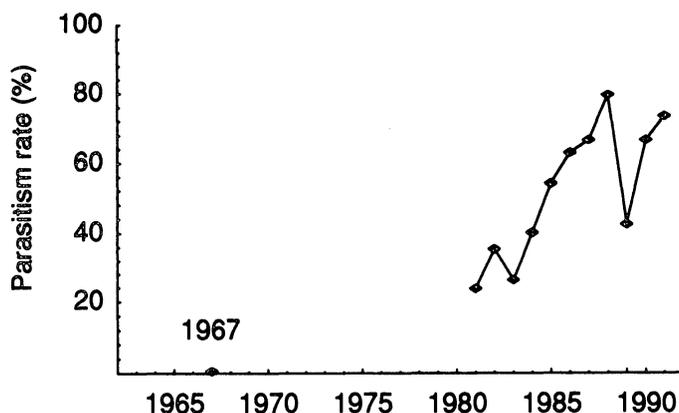


FIG. 1.—Temporal changes in the parasitism rate on azure-winged magpie (*diamond*) at Nobeyama Heights recorded by S. Imanishi. The magpie was observed at Nobeyama Heights in 1967 for the first time (Hosono 1969). No observation was made from 1968 to 1980. In 1989, a number of cuckoos were captured for research so that parasitism rate decreased temporarily.

Another dramatic example was observed at Nobeyama Heights by S. Imanishi (personal communication; see fig. 1). In this region, the magpies were first observed in 1967. After a period of no observation, the frequency of cuckoo parasitism increased from 23% to 80% during the last 10 yr. It was verified that this particular magpie population lacked defensive behaviors against cuckoo's parasitism until recently, thus allowing such extensive parasitism. The magpie population at Nobeyama, however, recently began to develop counteradaptations such as ejection of cuckoo eggs or desertion of parasitized nests. Some other magpie populations with a longer history of parasitism show higher rates of rejection of cuckoo's eggs. For example, the magpie population at Azumino has been exposed to cuckoo parasitism for about 20 yr and its rejection rate reaches 41.7%. The magpie at Nagano has been parasitized for about 15 yr and shows a rejection rate of 34.7%. All these observations support the idea that the egg discrimination ability of the magpie increases with the duration of exposure to the parasitism. A similar change in the cuckoo-host association was observed in Spain (Soler 1990; Soler and Møller 1990).

May and Robinson (1985) modeled the population dynamics of a host-brood parasite association, which has a stable equilibrium state for reasonable estimates of the demographic parameters. Their model did not involve the evolutionary processes of egg mimicry or host defense. On the other hand, Rothstein (1975), Kelly (1987), and Brooker et al. (1990) investigated the evolution of a host's defensive ability or a cuckoo's egg mimicry on the basis of population genetics. They evaluated the time taken for the spreading of such counterresponses. Rothstein suggested that, under parasitic pressure from cowbirds, some host species that had suitable mutations by chance rapidly evolved to be rejecters and explained why a host species with intermediate rates of rejection of cowbird eggs is scarce. Kelly and Brooker et al. dealt with models including the population

genetics of rejection and egg mimicry. In these analyses, the population dynamics of host and parasite are almost unchanged during the evolutionary process so that the parasitism rate remains constant and the rejecter gene is finally fixed.

In this article, we present a mathematical model that incorporates both the population dynamics of the cuckoo-host association as originally introduced by May and Robinson and the evolution of defensive behavior of the host and explore the mechanisms of dynamical changes in brood parasitism.

MODELING ONE CUCKOO GENS AND ONE HOST ASSOCIATION

The cuckoo and the majority of its host species are migrants, and it is known that they tend to come back to the same area in the next breeding season. Hence, population densities of the cuckoo and host in one locality are considered throughout this article. There are several strains of female cuckoo called *gentes* (singular, *gens*), which lay eggs of distinct color and pattern (Brooke and Davies 1988). A female cuckoo lays eggs of the same color and pattern throughout her life and is thought to specialize on a particular host species (Chance 1940; Baker 1942; Wyllie 1981). It is likely that egg colors and patterns are inherited from a mother cuckoo by her daughter and the mating partner does not influence the egg type. Choosing a correct host is possibly assured by imprinting of the cuckoo chicks on the foster host, and in adulthood the cuckoo returns to choose the same host species (Brooke and Davies 1991; Davies and Brooke 1991). By assuming the maternal inheritance of egg properties and chick imprinting, we treat each *gens* as an independent species with respect to host usage and egg properties.

It is likely that the host's antiparasite behavior is determined by genetic factors. The rejection behavior of the host is thought to entail some costs, reducing the host's reproductive success (Rothstein 1977; May and Robinson 1985; Davies and Brooke 1988; Rohwer et al. 1989; Røskaft et al. 1990; Moksnes et al. 1991; Marchetti 1992). The rejection cost in general will be small and may possibly be different among host species. We consider the association of one cuckoo *gens* and one host population with a genetically determined rejection behavior, in which rejecter individuals have less breeding success.

Let P_t be the population density of the female cuckoo and H_t be that of the female host in year t . We assume that the sex ratio is kept at unity and that the newborn offspring of both the cuckoo and host are recruited into the adult population at the end of their first year. A female cuckoo lays one egg in the host nest if she finds the nest, and with probability Γ a female cuckoo chick grows up from a parasitized nest and survives to the next breeding season. Even if a host nest is parasitized multiply by cuckoo eggs, Γ remains constant because only one cuckoo chick usually monopolizes the nest. The adult female cuckoo survives to the next season with a constant survival rate of s_p .

Assume that the host response to parasitism is determined by two alleles at a single autosomal locus, allele R and A ; allele R causes rejection behavior and allele A does not. We further assume that allele R is dominant over allele A and that random mating occurs in the host population. 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

($x_t + y_t + z_t = 1$). In bird breeding, usually both the male and the female incubate cooperatively. Here we assume that the cuckoo parasitism succeeds if both of the breeding pair are acceptor individuals, which we call an acceptor pair, and parasitism is rejected if at least one of the pair is a rejecter individual, which we refer to as a rejecter pair.

In the absence of the cuckoo, an acceptor pair raises f female offspring, while a rejecter pair raises ϵf female offspring, which is less by a factor of ϵ ($\epsilon < 1$). Parameter ϵ measures the cost of rejection, and the value is generally less than but close to one.

To model the parasitic behavior of the cuckoo, we assume that the cuckoo female searches independently and randomly with a searching efficiency measured by a parameter a (called the area of discovery by Nicholson and Bailey [1935]). Then the probability that a host nest escapes from parasitism is given by the zeroth term of a Poisson distribution (see May and Robinson 1985) as e^{-aP_t} . Parameter a will vary from host species to species. If a host builds a nest on an open tree that the cuckoo can find easily, the value of a will be large. Conversely, if a host nest is hidden in heavy bushes, the value of a will be small. Note that this function counts all cases of parasitism including multiple egg laying by the cuckoo.

Under this assumption, the number of female offspring from an acceptor pair that survive to the next breeding season is given by fe^{-aP_t} . On the other hand, a rejecter pair produces a constant ϵf female offspring, irrespective of whether parasitized or not. The female cuckoo usually removes one of the host eggs when she lays an egg. Thus, strictly speaking, a rejecter pair has less breeding success once parasitized than a rejecter pair that escapes from parasitism. However, this difference will be negligibly small, because competition within a host clutch is weakened by the loss of one egg. Therefore, it is thought that almost the same number of fledglings will be reared by a rejecter pair irrespective of the presence or absence of parasitism. In figure 2, we show the fitnesses of rejecter and acceptor pairs as a function of cuckoo density, P_t .

Cuckoo parasitism is successful in the nest of an acceptor pair, of which the frequency is z_t^2 . Thus, the population density of the cuckoo in the next year, P_{t+1} , is

$$P_{t+1} = s_p P_t + (1 - e^{-aP_t}) z_t^2 H_t \Gamma, \tag{1a}$$

where the first term of the right side represents the density of adult survivors and the second term represents the newly recruited yearlings. In the framework of this model, the parasitism rate is given as

$$(1 - e^{-aP_t}) z_t^2.$$

Next, we consider the dynamics of the host population. The density of rejecter pairs is $(1 - z_t^2) H_t$, each of which produces ϵf offspring, while the density of acceptor pairs is $z_t^2 H_t$, each of which breeds fe^{-aP_t} offspring. Thus the total density of offspring is

$$[(1 - z_t^2) \epsilon + z_t^2 e^{-aP_t}] f H_t.$$

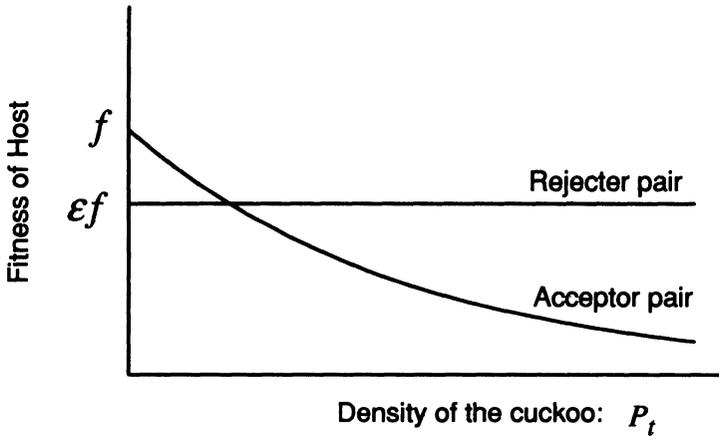


FIG. 2.—The average numbers of female offspring that survive to the next breeding season from a nest of acceptor and rejecter pairs, respectively. When the cuckoo density, P_t , is low, the acceptor pair produces more offspring than the rejecter pair. The rejecter pair has more advantages with larger P_t , because the rejecter pair can avoid a reproductive loss by rejecting the cuckoo eggs.

The host density in the absence of the cuckoo is generally regulated by the availability of limited food resources or territories. Taking into account this effect, we have the following equation for the host density in the next year:

$$H_{t+1} = \frac{1}{1 + H_t/k} \{s_H H_t + [(1 - z_t^2) \epsilon + z_t^2 e^{-aP_t}] f H_t\}, \quad (1b)$$

where s_H represents the intrinsic survival rate of an adult host to the next breeding season and the factor $1/(1 + H_t/k)$ represents the density effect of intraspecific competition on the host population; the degree of the density effect is measured by a parameter $1/k$.

The densities of offspring with genotypes RR , RA , and AA are derived as follows:

$$\text{Genotype } RR: (x_t^2 + x_t y_t + y_t^2/4) \epsilon f H_t;$$

$$\text{Genotype } RA: (x_t y_t + 2x_t z_t + y_t z_t + y_t^2/2) \epsilon f H_t;$$

$$\text{Genotype } AA: (y_t^2/4 + y_t z_t) \epsilon f H_t + z_t^2 f \exp(-aP_t) H_t.$$

Then the frequencies of RR and RA in the next year, x_{t+1} and y_{t+1} , are given as

$$x_{t+1} = \frac{s_H x_t + (x_t^2 + x_t y_t + y_t^2/4) \epsilon f}{s_H + (1 - z_t^2) \epsilon f + z_t^2 f e^{-aP_t}} \quad (1c)$$

and

$$y_{t+1} = \frac{s_H y_t + (x_t y_t + 2x_t z_t + y_t z_t + y_t^2/2) \epsilon f}{s_H + (1 - z_t^2) \epsilon f + z_t^2 f e^{-aP_t}}. \quad (1d)$$

Analyses and Results

Equations (1) constitute our model. 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

$$(P^*, H^*, x^*, y^*) = \begin{cases} (0, k(f + s_H - 1), 0, 0) & (2a) \\ (\tilde{P}, \tilde{H}, 0, 0) & (2b) \\ (0, k(\epsilon f + s_H - 1), 1, 0) & (2c) \\ \left(\frac{1}{a} \log \frac{1}{\epsilon}, k(\epsilon f + s_H - 1), (1 - D^{1/4})^2, 2(D^{1/4} - D^{1/2}) \right), & (2d) \end{cases}$$

where (\tilde{P}, \tilde{H}) is the unique solution of the following equations:

$$\tilde{H} = \frac{(1 - s_P)\tilde{P}}{\Gamma(1 - e^{-a\tilde{P}})} \text{ and } \tilde{H} = k(fe^{-a\tilde{P}} + s_H - 1),$$

and

$$D = \frac{(1 - s_P) \log \frac{1}{\epsilon}}{ak\Gamma(\epsilon f + s_H - 1)(1 - \epsilon)}.$$

The equilibrium population density of the host before parasitism begins, K , is obtained by setting $P_t = 0$ and $x_t = y_t = 0$ in equation (1b). Then

$$K = k(f + s_H - 1). \tag{3}$$

This quantity corresponds to the carrying capacity of the host population. 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 . When $K < 0$ ($f + s_H - 1 < 0$), the host population becomes extinct because the birth rate f is less than the death rate $1 - s_H$. When $\epsilon f + s_H - 1 < 0$, the rejecter individuals, if any, decrease to zero spontaneously for the same reason. We preclude these cases in the following analyses.

The dynamical properties of equations (1) are analyzed by standard methods (see Appendix for details) together with numerical calculations. The result shows that the dynamical behaviors are characterized by the product of K and a ; the product aK biologically indicates the average number of host nests that a female cuckoo parasitizes during a breeding season when a few cuckoos start parasitism on a naive host, because when P_t is very small,

$$\frac{(1 - e^{-aP_t})K}{P_t} \sim aK.$$

The physical dimensions of aK are host/parasite. There are two critical values of aK : A_1 and A_2 ($> A_1$), which are defined as

$$A_1 = \frac{1 - s_P}{\Gamma}$$

and

$$A_2 = \frac{(1 - s_p)(f + s_H - 1) \log \frac{1}{\epsilon}}{\Gamma(1 - \epsilon)(\epsilon f + s_H - 1)}.$$

The dynamical properties are classified into the following three cases, depending on the value of aK relative to A_1 and A_2 .

Case 1. $0 < aK < A_1$.—The inequality implies that the death rate of the cuckoo ($1 - s_p$) exceeds the birth rate $aK\Gamma$. Thus the system always approaches equilibrium state (2a), where only the host population sustains itself. The rejecter allele, if it emerges by mutation, does not spread because there is no threat of parasitism.

Case 2. $A_1 < aK < A_2$.—The system approaches equilibrium (2b) or oscillates around it, depending on the parameter values. Both populations persist. The rejecter allele does not spread in the host population even when the population suffers from parasitism. Therefore, the lack of counteradaptation does not necessarily imply that the host is a recent host. Case 2 is possible only when rejection behavior by the host entails some cost ($\epsilon < 1$), because, if the host loses nothing by rejection behavior ($\epsilon = 1$), the critical value A_2 becomes identical to A_1 .

Case 3. $A_2 < aK$.—The system approaches equilibrium (2d) or oscillates around it, depending on the parameter values (see Appendix for parameter values generating an oscillation). Both the cuckoo and the host can coexist, and the rejecter allele, once introduced, can spread in the host population. The cuckoo can survive only when there is cost of rejection ($\epsilon < 1$). Thus, the cost of rejection is totally responsible for the existence of the cuckoo: if the host loses nothing by rejection behavior, the cuckoo can enjoy parasitism only for a certain period and is driven to extinction as the host establishes its counteradaptation. Note that the rejecter allele does not go to fixation for a finite value of aK .

First, we evaluate several quantities at the stable equilibrium state of equations (1). We calculate the ratio of the cuckoo density to the host density and the parasitism rate at the equilibrium (P^*/H^* and $(1 - \exp(-aP^*))z^{*2}$, respectively). These are illustrated as a function of aK in figure 3A. The ratio remains zero for $0 < aK < A_1$, then increases from zero to reach a maximum $(1 - \epsilon)\Gamma/(1 - s_p)$ at $aK = A_2$. As aK becomes larger than A_2 , the ratio decreases, tending to zero. The parasitism rate at the equilibrium shows a pattern similar to the ratio, P^*/H^* , having a maximum $1 - \epsilon$ at $aK = A_2$. Because the rejection cost, in general, is thought to be small (ϵ is close to one), these results imply that the parasitism rate at the equilibrium state is very low and that the cuckoo population is scarce at the equilibrium state compared with the host population, if $\Gamma/(1 - s_p) \leq 1$. In figure 3B the equilibrium frequencies of the rejecter individuals and rejecter pairs ($x^* + y^*$ and $1 - z^{*2}$, respectively) are illustrated in relation to the value of aK . When aK is greater than A_2 , both quantities increase monotonically, tending to one at $aK = \infty$. Except for the extreme $aK = \infty$, the host population exhibits a polymorphic blend of rejecter and acceptor individuals at equilibrium.

Now we estimate the parameter values for real cuckoo-host associations and show temporal changes of various quantities, such as population densities of the

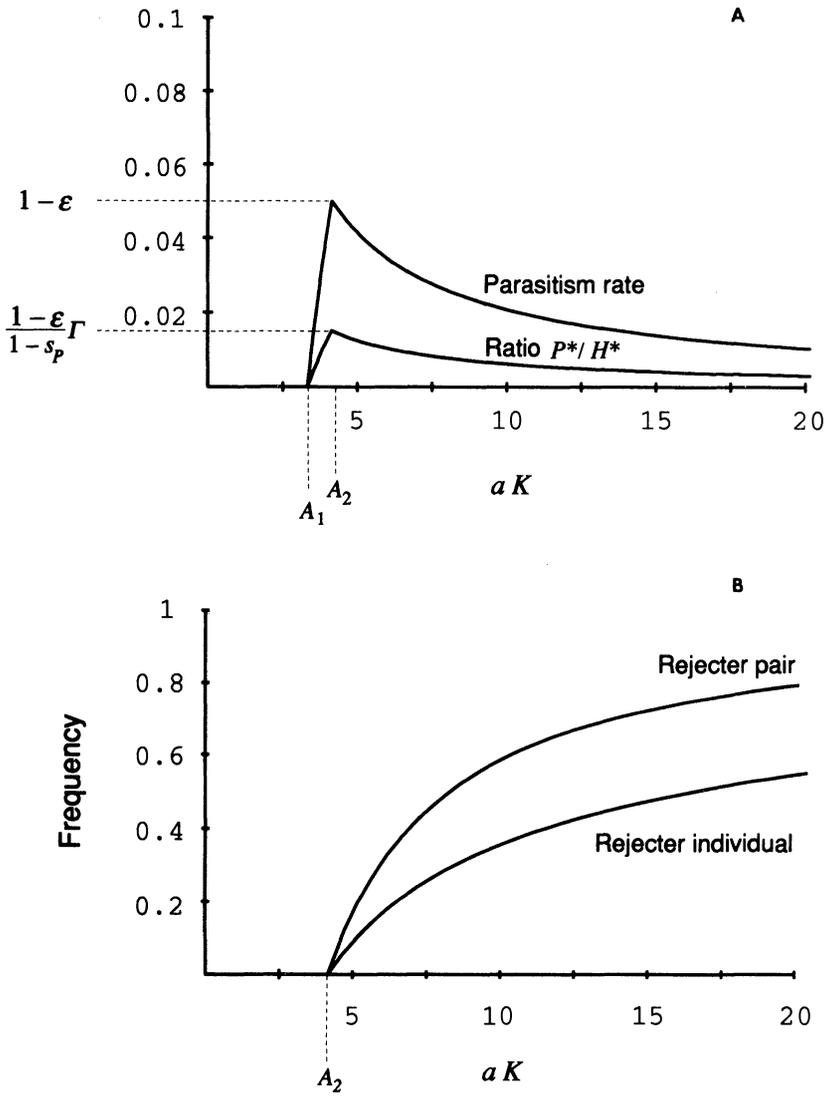


FIG. 3.—A, The ratio of the cuckoo density to the host density and the parasitism rate at equilibrium in relation to aK . The maximum ratio $(1 - \epsilon) \Gamma / (1 - s_p)$ and the maximum parasitism rate $1 - \epsilon$ are attained at $aK = A_2$. B, The equilibrium frequencies of rejecter individuals and rejecter pairs in relation to aK . For $aK < A_2$, the rejecter allele does not spread in the host population. Parameters are set as $s_p = s_H = 0.5$, $\Gamma = 0.15$, $f = 0.7$, and $\epsilon = 0.95$.

cuckoo and host, parasitism rate, and so on. For the cuckoo and azure-winged magpie association, we estimated the ranges of s_P , s_H , f , and Γ , as follows:

$$\begin{aligned} s_P &= 0.2 \sim 0.5, \\ s_H &= 0.2 \sim 0.5, \\ f &= 0.5 \sim 1, \end{aligned} \tag{4}$$

and

$$\Gamma = 0.15.$$

The carrying capacity K is directly estimated from field data before parasitism starts. For example, at Kawanakajima village, $K \sim 8$ females/km², and, at Chikuma River near Nagano city, $K \sim 15$ females/km². The value of a is most difficult to estimate and one might evaluate it from the equilibrium densities H^* and P^* given in expression (2d) (see also *Parameter Estimation*). Here we choose a set of parameter values: $s_P = s_H = 0.5$, $f = 0.7$, $\Gamma = 0.15$, $a = 0.7$, $K = 16$. Rejection cost, ϵ , is temporarily set to 0.95, because there are few data available for the estimation (but see Marchetti 1992). These parameter values satisfy condition 3, that is, $A_2 < aK$, in which the rejecter allele becomes established in the host population. As the initial state, we set $P_0 = 0.01$, $H_0 = K = 16$, and $x_0 = 0$, $y_0 = 0.05$, that is, a few cuckoos start to parasitize the host population, which is maintained at the carrying capacity K and contains a small fraction of rejecter individuals. In figure 4A and B, densities of the cuckoo and the host and the parasitism rate and the frequency of rejecter pairs, respectively, are illustrated as a function of time. For comparison, we include the corresponding curves (the *dashed curves*) in the absence of the rejecter allele ($x_0 = y_0 = 0$). All the curves except the frequency of the rejecter pairs exhibit damped oscillations, eventually converging to the equilibrium state. The presence of the rejecter allele leads to an increase in the host density and a decrease in the parasitism rate. At the equilibrium state finally attained, the host density recovers as far as the level prior to the parasitism, while the cuckoo density and the parasitism rate go down to very low levels. The frequency of rejecter pairs increases rapidly, eventually reaching 60%, and the rate of increase is accelerated when the parasitism rate begins to decrease. Further numerical analyses show that, as the product aK increases, damped oscillations with larger amplitudes are induced at the early stage, but the characteristics of the damped oscillations as seen in figure 4 are maintained for a wide range of parameter values of equations (4).

In addition to the parameter values, the initial frequency of rejecter individuals also affects sensitively the dynamical behavior at the early stage. As the initial frequencies x_0 and y_0 increase, the amplitude of the oscillation is reduced, as shown in figure 5A and B.

When the rejecter allele is allowed to spread, how fast does it increase in the host population? We evaluated the time taken for rejecter pairs to increase to half of the equilibrium frequency as a function of aK , starting from the initial frequency $x_0 = 0$, and $y_0 = 10^{-5}$. Since the number of individuals of azure-winged magpie in Nagano Prefecture was estimated as $\sim 10^4$ (Nakamura 1990), $y_0 = 10^{-5}$ would be sufficiently small to evaluate the spreading time. The results illustrated

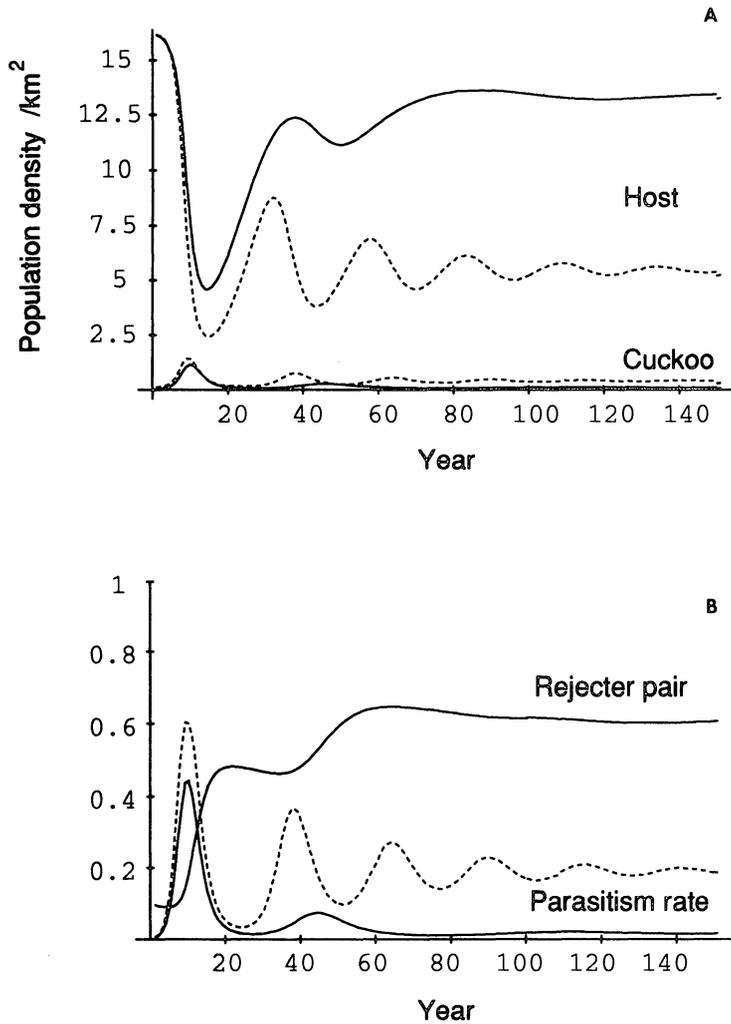


FIG. 4.—*A*, Temporal changes in the densities of the cuckoo and host populations. *B*, The temporal changes in parasitism rate and frequency of rejecter pairs. The *dotted lines* correspond to the case of no genetic variation ($x_0 = y_0 = 0$). The frequency of rejecter pairs is $1 - z_r^2$. Parameters used are $s_H = 0.5$, $f = 0.7$, $\epsilon = 0.95$, $K = 16$, $s_p = 0.5$, $\Gamma = 0.15$, and $a = 0.7$. The initial state is $P_0 = 0.01$, $H_0 = 16$, $x_0 = 0$, and $y_0 = 0.05$, when the rejecter allele is present, and $P_0 = 0.01$, $H_0 = 16$, $x_0 = 0$, and $y_0 = 0$, when the rejecter allele is absent.

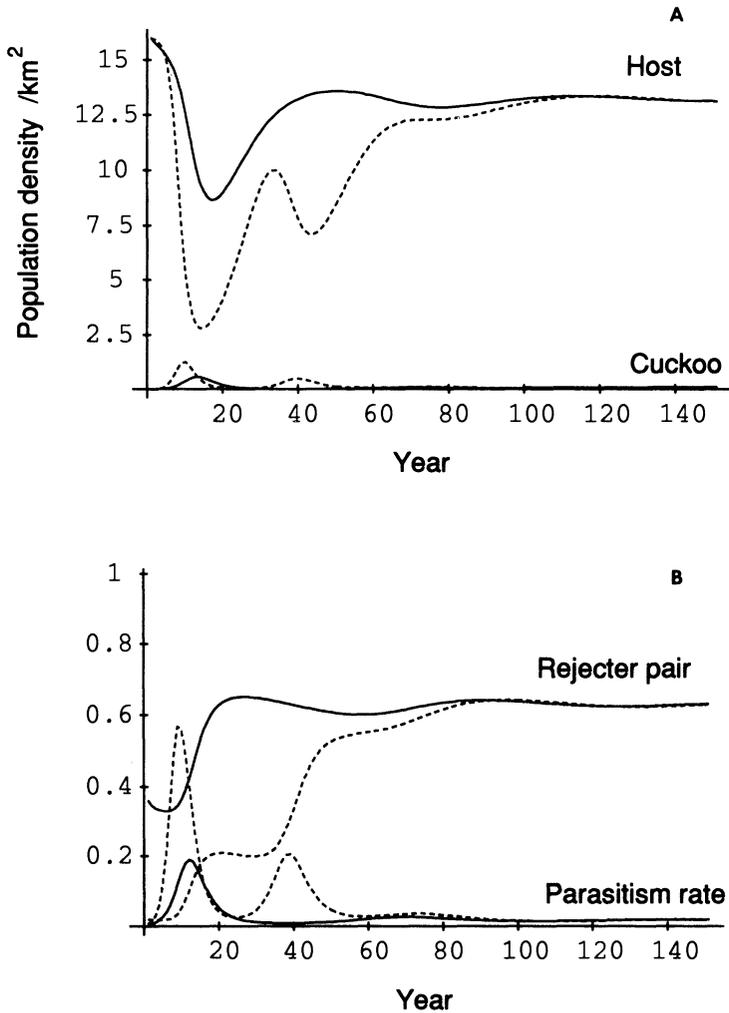


FIG. 5.—Comparison of the dynamics starting from different initial frequencies of the rejecter allele. *A*, Changes in population densities of the cuckoo and host. *B*, Changes in the parasitism rate and frequency of rejecter pairs. The *dotted lines* and the *solid lines* show $x_0 = 0, y_0 = 0.01$, and $x_0 = 0, y_0 = 0.2$, respectively. Parameter values and other initial conditions are the same as in fig. 4.

in figure 6 show that the rejecter allele can spread rapidly. For example, when ϵ is 0.95 and aK is 12, the frequency of rejecter pairs increases to 30% in about 150 yr and eventually reaches 60% at the equilibrium (see fig. 3*B*). On the other hand, if aK is small and hence the equilibrium frequency is small, it takes several hundred years for the rejecter pair frequency to increase to half of the equilibrium frequency. As the cost of rejection decreases (ϵ becomes closer to 1), the rejecter allele spreads faster.

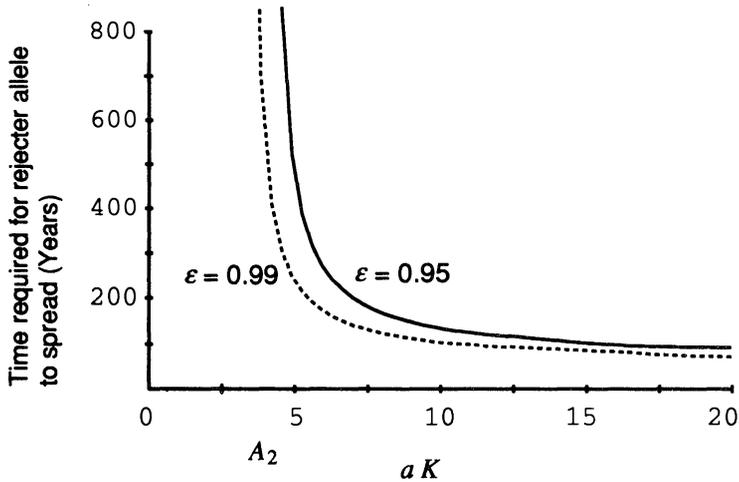


FIG. 6.—The time until the frequency of retractor pairs reaches half of the equilibrium as a function of aK with $\epsilon = 0.95$ (solid line) and 0.99 (dotted line). As aK becomes close to A_2 (note that A_2 depends on ϵ), it takes more time to reach half of the equilibrium frequency. As the rejection cost decreases (ϵ closer to 1), the retractor allele spreads faster. Parameters used are the same as in fig. 4. The initial condition is $P_0 = 10^{-4}$, $H_0 = K$, $x_0 = 0$, and $y_0 = 10^{-5}$; $A_2 = 4.14$ for $\epsilon = 0.95$ and 3.47 for $\epsilon = 0.99$.

The cuckoo density at the equilibrium state, $(1/a) \log(1/\epsilon)$, is kept at a low level if ϵ is close to one, so that the cuckoo may be driven extinct by a stochastic effect. Once freed from the pressure of parasitism, the retractor allele becomes disadvantageous and its frequency gradually decreases. We evaluated the time taken for retractor pairs to decrease from the equilibrium to half of the equilibrium in relation to aK (fig. 7). The duration during which retractor pairs persist in the host population becomes longer as the rejection cost decreases. These results may explain why some host populations that are not at present parasitized show a highly established counteradaptation.

Parameter Estimation

These analyses of our model show that the dynamical behavior of the association of one cuckoo gens and one host can be classified by the product of the host's carrying capacity and the cuckoo's searching efficiency. The host's carrying capacity, $K = k (f + s_H - 1)$, that is, the host population density before the parasitism starts, could be estimated from the accumulated literature of the past. If a host population has established a counteradaptation, the population density should reach the equilibrium density, $k (\epsilon f + s_H - 1)$, which is nearly equal to K because ϵ should be close to unity. Thus, we may substitute the equilibrium host density for the carrying capacity K . In this way, K is evaluated to be eight females/km² at Kawanakajima village and 15 females/km² at Nagano city, as noted before. On the other hand, the searching efficiency, a , which comprises the cuckoo's overall performance in searching for host nests, will probably vary depending on the host species: the shape and site of the nest and also the

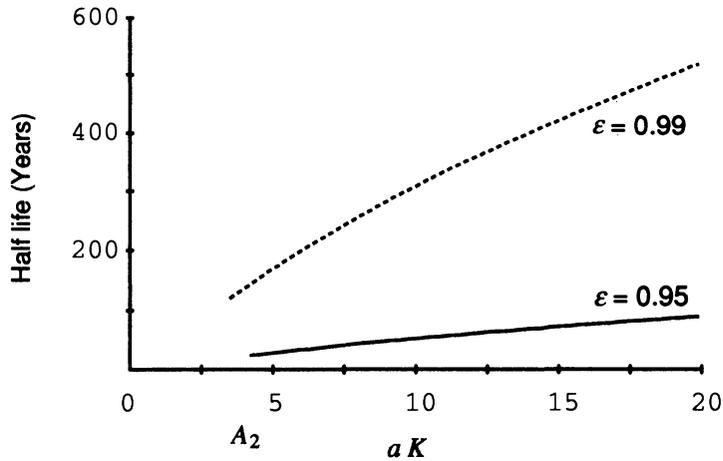


FIG. 7.—Half-life, or time taken for the frequency of rejecter pairs to decrease from the equilibrium to half of the equilibrium level, in relation to aK . Parameters except the rejection cost are the same as in fig. 4.

singing behavior of the host will determine the degree of the cuckoo's attention. This value is difficult to estimate quantitatively for each host species. However, the value could be estimated from the value of aK , which we can measure by counting parasitized nests per cuckoo in a recently parasitized host population.

The dynamical behavior depends also on the other parameter values: s_H , s_P , f , and Γ . These parameters are determined by what proportions of the host and parasite populations survive to the next breeding season and are generally difficult to estimate precisely. More experiments and data are needed to strengthen the mathematical formulation and analysis.

The dynamics of the initial transient stage are greatly influenced by the initial frequency of the rejecter allele in the host population (see fig. 5). Different changes in the cuckoo-azure-winged magpie associations in three localities in Japan may be attributed to the different initial proportions of rejecter individuals. Few field data are available to estimate the initial state. More attention should be paid to geographical differences with distinct parasitism histories to clarify the cuckoo-host associations.

DISCUSSION

Cuckoo-Host Associations: Continuing Arms Race or Equilibrium?

Davies and Brooke (1989a, 1989b) suggested that the various degrees of egg discrimination observed in different host species represent different stages of a continuing arms race between the cuckoo and its hosts (see also Dawkins and Krebs 1979; Harvey and Partridge 1988). On the other hand, Rohwer and Spaw (1988), Lotem et al. (1992), and H. Nakamura, S. Kubota, and R. Suzuki (unpublished manuscript) introduced the concept of an evolutionary equilibrium, in

which the variation of rejection behaviors within a host species depends on the balance between the parasitic burden to acceptors and the cost of rejection to rejecters (see also May and Robinson 1985).

We have shown that various degrees of host counteradaptation are possible at the evolutionary equilibrium state, depending on the host population density and the cuckoo's searching efficiency. When aK is less than A_2 , the host population cannot evolve a counteradaptation. This seems to be the first mathematical result to show that even at equilibrium the host may not evolve a counteradaptation against cuckoo parasitism.

As mentioned in the first section, the parasitism rate of the azure-winged magpie in Japan changed rapidly. The magpie density prior to parasitism was high and the magpie builds a nest on a tree that is easy to find so that aK could be larger than A_2 . Thus, our model suggests that the magpie population at Nobeyama Height as shown in figure 1 has just reached the initial peak of the parasitism rate, which will probably decline in the coming decade. It is also predicted that the magpie population will establish a counteradaptation within a short period and the host density will recover to the original level with a concomitant reduction in the cuckoo parasitism (see figs. 4, 6). If the magpie is clever enough to avoid a rejection cost (if $\epsilon = 1$), the magpie gens cuckoo will be driven to extinction as the magpie develops its counteradaptation. These arguments may apply to the changes of parasitic relations in Spain (Soler and Møller 1990).

Our model could also be applied to the Siberian meadow bunting *Emberiza cioides*, which was the former major host 60 yr ago in central Japan. At present the bunting is seldom parasitized because the host is counteradapted as a result of the past severe parasitism (Nakamura 1990). We suggest that the density of the bunting was high and its nest was probably easy to find, so that the bunting has established rejection behavior at a high level, driving the bunting gens cuckoo to decline.

The dunnoek *Prunella modularis*, one of the main hosts in England, is known for the lack of counteradaptation, although the host has been a victim of cuckoo parasitism for more than 600 yr (Davies and Brooke 1989b, 1991). Davies and Brooke suggested that the dunnoek is still in the process of establishing counteradaptation under the low parasitism rate (2%), because it takes thousands of years for the rejecter allele to spread fully under a low parasitism rate (Kelly 1987; Davies and Brooke 1989b). This explanation, however, is based on models in which the parasitism rate is assumed to be less than a certain constant upper limit, which may underestimate the parasitism pressure.

Our model suggests that the rejection allele, even if present, cannot spread in a population if aK is smaller than a critical value A_2 . Thus, the value of aK for the dunnoek could be smaller than or nearly equal to A_2 so that the rejecter allele is prevented from spreading or, even if the rejecter allele is allowed to spread, the equilibrium frequency is maintained at a very low level. If the equilibrium frequency is kept at a low level, it takes several hundred years for the rejecter allele to reach half of the equilibrium level (see fig. 6). Therefore, we suppose that the dunnoek's rejection behavior will not spread beyond the present low level; that is, the dunnoek is near the equilibrium state. The dunnoek is a common

bird and its density seems relatively high. But if its nests are concealed well or located in places the cuckoo cannot access easily, the value of a will be small. More detailed demographic data on local host densities and the cuckoo's searching efficiency will clarify this problem.

It was shown that the time taken for the rejecter allele to spread depends on the value of aK (fig. 6). A host population with a high aK suffers severe parasitism early and rapidly establishes a high level of counteradaptation. In contrast, a host with a small aK does not suffer severe parasitism and it takes more time to establish a low level of counteradaptation. Therefore, it is suggested that the various degrees of counteradaptation observed in hosts do not necessarily imply that each host is in a different stage of a continuing arms race.

Although the equilibrium state will be eventually attained within several hundred years, the arms race may possibly continue if a cuckoo strain with better mimicry or if new means of counteradaptation such as chick discrimination by the host emerge in the association. However, since new characteristics seem to appear only on the evolutionary time scale, most associations of the cuckoo and host are thought to have nearly reached an equilibrium state unless dynamical changes in the parasitism rate or the population density are actually observed.

Our model describes the trajectory of a single cuckoo gens and a single host species in a single locality over a time period long enough to permit spreading of a rejecter gene in the host population but short enough to exclude evolution of better mimicry in the cuckoo population. In reality, the species of host and cuckoo may have many different local populations, and the trajectory of brood parasitism in the single locality considered here may be substantially affected by other interactions in other localities. Nevertheless, as a first approximation, it is sensible to study the trajectory of a single locality in isolation. By studying a single locality, we are able to show that evolutionary arms races are not necessary to explain the current states and recent dynamic changes of cuckoo-host associations.

FURTHER MODELING NEEDED

Egg Mimicry by the Cuckoo and the Cost of Rejection

A local cuckoo population may contain several gentes, or strains, with different species of primary hosts. A female of each gens lays eggs of specific color and pattern, which mimic the host egg to some extent. The host-specific traits of the cuckoo egg are thought to have evolved to counter the host's rejection behavior. Field experiments show that a host (of some, but not all, species) tends to accept an egg of good mimicry but to reject one of poor mimicry (Davies and Brooke 1989a; Higuchi 1989; H. Nakamura, S. Kubota and R. Suzuki, unpublished manuscript).

In this article, we considered a system in which individual hosts of the rejecter genotype can always reject parasitism. However, if a cuckoo egg is mimetic enough to deceive the host, it will be accepted by a rejecter pair with some probability. Such a case could be analyzed by extending the present model to

include the probabilistic rejection of parasitism. For a rejecter host, the task of detecting a cuckoo egg is analogous to the detection of a disease by a diagnostic test and can be described by two similar parameters, namely, sensitivity and specificity. The rejecter's sensitivity is the conditional probability of rejecting an egg, given that the egg is a cuckoo egg. The rejecter's specificity is the conditional probability of not rejecting an egg, given that the egg is an egg laid by the host. If the sensitivity and specificity are assumed to be independent of the parasitism rate, then the unconditional probability that a rejecter host will reject one of its own eggs will increase as the parasitism rate decreases. This prediction is consistent with the suggestion by H. Nakamura, S. Kubota, and R. Suzuki (unpublished manuscript) that the rejection cost increases as the parasitism rate decreases. In the framework of our model, ϵ would be a monotonically increasing function of the parasitism rate rather than a constant as at present.

Host's Age Structure and the Timing of Breeding

Lotem et al. (1992) observed that great reed warblers that breed in the middle of the breeding season have a notably higher rate of acceptance of cuckoo eggs than pairs that breed either early or late and that midseason breeders are much more likely to have juvenile feathers than early or late breeders. This apparent ontogenetic shift in the warbler's rejection behavior could be due to learning, imitation, or developmental changes in perceptual abilities. It is not known whether other species of hosts change their rejection behavior in the same way as they age.

For a host with such characteristics, it might be helpful to replace the single dynamical variable for the adult host density with two dynamical variables, one for younger breeders and another for mature breeders (May and Robinson 1985). Such a model would have a qualitatively interesting autoregulatory feature. If the host population were growing rapidly, it would be expected to have more juveniles and therefore to have a higher fraction of breeders who are vulnerable to cuckoo parasitism. By contrast, if the host population were stationary or declining, it would be expected to have more mature adults and therefore to have a lower fraction of breeders who are vulnerable to cuckoo parasitism. Quantitative modeling is required to determine the quantitative consequences of age structure associated with age-specific vulnerability to parasitism.

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APPENDIX

STABILITY ANALYSES

The local stability of the equilibria of equations (1) can be determined from the eigenvalues of the Jacobi matrix: an equilibrium is locally stable if the absolute values of eigenvalues of the Jacobi matrix are all less than unity. This condition holds if the Jury criteria (see Murray 1989) are satisfied. Using the Jury criteria, we examine the stability of the equilibrium states (2a)–(2d) with respect to small perturbations. Extensive numerical calculations suggest that global stability is assured if an equilibrium is locally stable.

STABILITY OF EQUILIBRIUM (2a)

Linearization of the difference equations (1) around equilibrium (2a) yields the Jacobi matrix whose eigenvalues are

$$s_p + k\Gamma a(f + s_H - 1), 1/(f + s_H), s_H/(f + s_H), \text{ and } (\epsilon f + s_H)/(f + s_H).$$

The last two eigenvalues are always positive and less than unity, and equilibrium (2a) is positive and stable if and only if $0 < aK < A_1$, where $K = k(f + s_H - 1)$ and $A_1 = (1 - s_p)/\Gamma$.

STABILITY OF EQUILIBRIUM (2b)

Equilibrium (2b) cannot be given in an explicit form. This equilibrium bifurcates from equilibrium (2a) as aK increases across A_1 . Numerical calculations show that equilibrium (2b) is stable or unstable depending on parameter values. If unstable, the system apparently contains a stable limit cycle. Parameter values causing such limit cycles are discussed below in connection with the local stability of equilibrium (2d).

STABILITY OF EQUILIBRIUM (2c)

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

STABILITY OF EQUILIBRIUM (2d)

When $aK > A_2$, equation (2d) describes the unique equilibrium that allows positive internal frequencies of the rejecter genotypes ($0 < x^*, y^* < 1$). Although it is very complicated, the Jacobi matrix, M , around equilibrium (2d) can be obtained. The eigenvalues of the Jacobi matrix are the solutions of

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

where a_1, a_2, a_3 , and a_4 depend on five parameters, f, s_H, s_p, k , and ϵ , but not on Γ and a . The stability of equilibrium (2d) is examined by the Jury criteria. In figure A1, we show the parameter region projected in (f, s_H) space, in which equilibrium (2d) could be unstable. That is, for parameter sets within the dark region, equilibrium (2d) becomes unstable at least for some value s_p and k in $A_2 < aK < \infty$. The unstable region becomes smaller and ultimately vanishes as ϵ approaches one (i.e., the rejection cost decreases to zero). Thus, we may say that the internal equilibrium (2d) is stable for a wide range of parameter values.

We show how the stability property of the system changes with k , when other parameters have values in the dark region in figure A1: $f = 0.7, s_H = 0.339, s_p = 0.5, \epsilon = 0.95, a = 0.7$, and $\Gamma = 0.15$. In this case, the two critical values are $A_1 = 3.33, A_2 = 33.34$, and equilibrium (2d) is unstable for $A_2 < aK < 54.6$, resulting in a limit cycle, and equilibrium

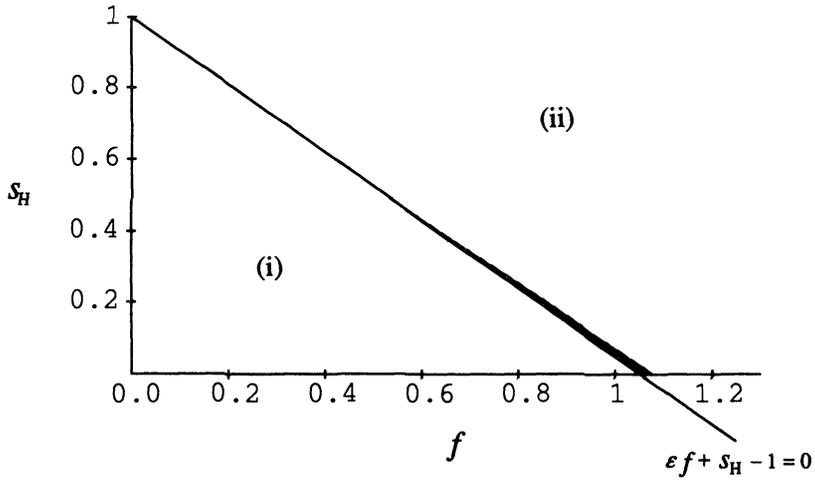


FIG. A1.—Unstable region projected in (f, s_H) space for $\epsilon = 0.95$. Equilibrium (2d) is stable in region *ii* and unstable in the *dark region* for some value of s_p and k . In region *i*, equilibrium (2d) becomes unfeasible ($y^* < 0$).

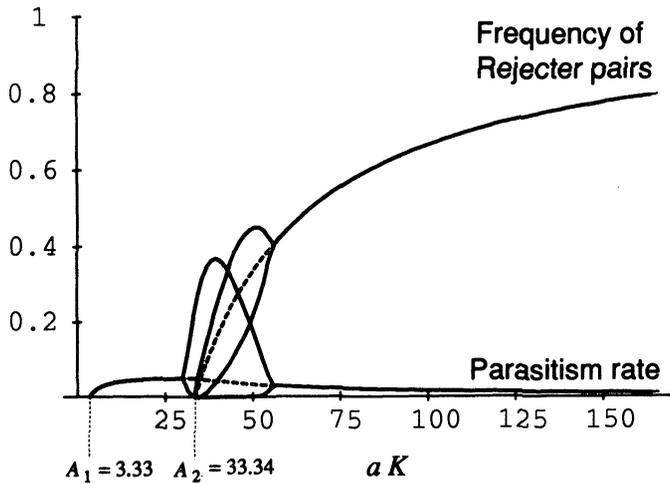


FIG. A2.—The stability property of equilibria (2b) and (2d) in relation to aK , in terms of the parasitism rate and the frequency of rejecter pairs. The *solid single lines* represent the stable equilibrium state, and the *dotted lines* indicate the unstable equilibrium state, and the *bifurcated solid curves* represent the upper and lower bounds of the limit cycle. Parameters are $\epsilon = 0.95$, $f = 0.7$, $s_H = 0.339$, $s_p = 0.5$, $a = 0.7$, and $\Gamma = 0.15$.

(2d) is stable for $54.6 < aK$. On the other hand, when aK is lower than A_2 , equilibrium (2b) becomes feasible instead of equilibrium (2d). Numerical calculation shows that, if equilibrium (2d) is unstable at aK close to A_2 , then equilibrium (2b) is also unstable for a finite interval of aK below A_2 . In general, a pattern like figure A2 that bifurcates around A_2 appears, if the parameters lie in the unstable region in figure A1.

We did not anticipate the existence of a region in parameter space in which the equilibrium (2d) is unstable. In this region, trajectories apparently oscillate periodically around the equilibrium (2d). Numerical calculations suggest that the presence or absence of apparently periodic cycling is very sensitive to the survival probability of the host. If one thinks of the host's survival probability as an external driving force determined by environmental conditions analogous to a wind blowing across a bridge or skyscraper, then the model's susceptibility to apparently cyclical behavior is qualitatively reminiscent of the existence of resonant frequencies when some mechanical structures are subjected to certain external forcing.

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