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Co-evolutionary dynamics of egg appearance in avian brood parasitism

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ABSTRACT

In avian brood parasitism, interactions between parasites and their hosts lead to a co-evolutionary process called an arms race. Field studies have shown that many host species have evolved an ability to recognize and reject parasite eggs that look unlike their own and that some parasites lay eggs of sophisticated mimicry. Egg appearance is a crucial factor that determines the reproductive success both of the parasites and their hosts in the arms race. The appearance of eggs, however, is a quantitative trait and the variation within a population could critically affect the dynamics of the arms race; parasite individuals that lay eggs more similar to those of the host are more likely to reproduce successfully, whereas host individuals that lay eggs more unlike those of the parasite have a better chance of rejecting parasitism and reproducing, which would de-stabilize the parasites' good mimicry. To explore the arms race for egg appearance, I constructed a model described by an integro-difference equation. The temporal change of the 'distributions' of egg appearance along a continuous spectrum was analysed both for the parasite and host populations. The model analyses show that (1) a conventional view of an arms race – 'parasites chasing their hosts escaping from the parasites' – is realized in the early stage of the dynamics, but (2) the distributions of egg appearance finally converge to discrete point-distributions (polymorphism) even when any continuous distributions are used as the initial state. The latter might be relevant to the maintenance of polymorphism of egg appearance. Based on the model analysis, I discuss the implications of this model for general (co)evolutionary processes for quantitative traits and suggest a new modelling framework to account for such processes.

Keywords: arms race, avian brood parasitism, co-evolution, egg appearance, ideal free evolution, quantitative trait.

INTRODUCTION

Brood parasites exploit parental care of their hosts and usually reduce the hosts' reproductive success. It is therefore expected that the hosts will evolve some adaptation to reduce the reproductive damage caused by parasitism, such as an ability to recognize and reject

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parasite eggs, which, in turn, should select for the parasites' counter-adaptation, such as egg mimicry. Field studies have shown that some host species have evolved an ability to recognize and reject parasite eggs that look unlike their own (Rothstein, 1975; Davies and Brooke, 1989; Moksnes and Røskaft, 1989; Brown *et al.*, 1990; Soler, 1990; Soler and Møller, 1990; Moksnes *et al.*, 1993) and that there are various degrees of egg mimicry by the Common Cuckoo *Cuculus canorus*, one of the most extensively studied avian brood parasites (Brooke and Davies, 1988; Davies and Brooke, 1988; Higuchi, 1989, 1998; Moksnes, 1992). Avian brood parasitism is an excellent system for studying the co-evolutionary arms race, where parasites are selected to exploit their hosts more efficiently, while the hosts evolve to escape the reproductive loss caused by the parasites (Dawkins and Krebs, 1979; Rothstein, 1990; Rothstein and Robinson, 1998; Davies, 2000).

In the co-evolutionary process, the appearance of eggs seems to be crucial because acceptance or rejection of parasitism by the host generally depends on differences in appearance of the host and parasite eggs (Victoria, 1972; Brooke and Davies, 1988; Higuchi, 1989, 1998; Moksnes *et al.*, 1993). Recent field studies have demonstrated that the pattern of the distribution of egg appearance within a cuckoo host population is correlated to the history of parasitism (Øien *et al.*, 1995; Soler and Møller, 1996; Stokke *et al.*, 1999). This suggests that parasitic interactions act as selective agents for the co-evolution of egg appearance.

Egg appearance is a quantitative phenotypic trait composed of many characteristics, including background colour and coverage of spots, and it usually exhibits a continuous spectrum within a population. Assuming within-population variation in egg appearance, the consequence of the arms race is open to question because, even if a parasite has evolved very good mimicry, host individuals that lay eggs more dissimilar to those of the parasite can reproduce more and hence the parasite's good mimicry is easily destabilized.

Kelly (1987) presented a mathematical model to determine the rate of spread of hypothetical genes responsible for egg mimicry by parasites and rejection behaviour by hosts. But the classification of parasitic eggs as simply a 'good' or 'poor' match to those of the host misses the essence of the co-evolutionary process, because egg appearance is a quantitative trait and this binary classification is unlikely to be justified. Takasu (1998b) presented a model to explore the arms race between a parasite and its host population, where the degree of egg mimicry was more realistically given by a parameter measuring the probability of acceptance. The model, however, ignores the within-population variation of egg appearance and it cannot fully explore the co-evolutionary process of egg appearance as a quantitative trait. Rodríguez-Gironés and Lotem (1999) presented a model for recognition and learning based on signal-detection theory, but did not analyse co-evolution of egg appearance.

The aim of this study was to examine the co-evolutionary dynamics of a parasite and its host population focusing on egg appearance as a quantitative trait. I constructed a model described by an integro-difference equation to analyse the co-evolutionary change of the 'distributions' of egg appearance. Although the model itself targets avian brood parasitism, the modelling framework can easily be applied to general co-evolutionary processes of host–parasite interactions and others. Previous studies have adopted integro-difference equations for the dynamics of quantitative traits (cf. Slatkin, 1980; Taper and Case, 1985, 1992; Maynard Smith and Brown, 1986; Doebeli, 1996a,b, 1997; Sasaki and Godfray, 1999). Because of the difficulty of an analytic treatment, however, most of these were based on numerical analyses and there remains room to advance theoretical exploration of this type of modelling. In this paper, I show that the dynamics in the early stage can be analytically traced under some circumstances and that the rate of the co-evolutionary change of egg appearance can be estimated from ecological parameters, such as survival and breeding rate. I also show that the distributions of egg appearance finally converge to discrete point-distributions (polymorphism) both for the parasite and host populations, even if continuous initial distributions are used. Based on the model analysis, I discuss the implications of my results.

THE MODEL

Consider a parasite population that parasitizes a host population. Let $P(x)$ be the density of parasite females that lay eggs of appearance x, and let $H(x)$ be that of host females laying eggs of x. Egg appearance in general is a multidimensional trait. In this model, for the sake of simplicity, the appearance is assumed to be a one-dimensional trait on an arbitrary scale within a certain range L ($x \in [-L/2, L/2]$) that both the parasite and host populations share in common. Extension to a multidimensional trait is straightforward but is not dealt with here.

The mechanism of genetic inheritance of egg appearance in birds is unclear, but it has been suggested that independent female lines exist in a bird population, each producing eggs of a distinct appearance directly inherited by daughters (Gibbs *et al.*, 2000). It is possible that a sex-linked gene on the W chromosome controls the appearance (Brooke and Davies, 1988; Marchetti *et al.*, 1998; but see Gibbs *et al.*, 1996; Davies, 2000; Gosler *et al.*, 2000). I assume that the appearance is transmitted asexually to offspring with no effect on mating. I also assume that the sex ratio is 1:1 and that all females share the same ecological characteristics except egg appearance. Relaxation of this assumption, such that the reproductive output is maximized at some particular egg appearance, is addressed later.

Let $A(x, y)$ be the probability that a parasite egg of appearance x, laid in the nest of a host female that lays eggs of appearance y, is accepted. Hereafter, $A(x, y)$ is referred to as the acceptance probability function. Field experiments have demonstrated that host individuals able to reject unlike parasitic eggs tend to accept if the parasitic eggs are mimetic to their own (Victoria, 1972; Brooke and Davies, 1988; Higuchi, 1989, 1998; Moksnes *et al.*, 1993). Thus, the acceptance probability can reasonably be assumed to be a decreasing function of the absolute difference in appearance, $A(x, y) = A(|x - y|)$. If there is no difference in appearance ($x = y$), the parasite egg will look identical to those of the host and it will always be accepted, $A(0) = 1$. In the following analysis, I adopt the following function as the acceptance probability:

$$A(x, y) = \exp[-\gamma(x - y)^2]$$

where the parameter γ measures the sensitivity of the hosts to discriminate against unlike eggs. The greater the value of γ, the less tolerant hosts are to unlike parasitic eggs. The amount of tolerance is measured by the width of the function, defined as $w = 1/\sqrt{\gamma}$.

The probability of a host nest being parasitized by any parasite is given as follows, using the zero-th term of the Poisson distribution (May and Robinson, 1985; Takasu *et al.*, 1993; Takasu, 1998a,b) with the mean amount of parasitism being proportional to the total parasite density:

$$1 - \exp[-a \int P(x)\mathrm{d}x]$$

where a is the search efficiency of the parasites. In all cases, the domain of the integration is set to $x \in [-L/2, L/2]$ unless otherwise stated. Here I assume that the conditional probability of a host nest being parasitized by a specific parasite of egg type x is proportional to its density $P(x)$. The density of the parasites of egg type x in the following year, $P'(x)$, is then obtained as the sum of the adult survivors to the following year and the newly recruited yearlings that fledged from the nests of host y with probability $A(x, y)$, summed over all possible y, as

$$P'(x) = s_P P(x) + (1 - \exp[-a \int P(x)\mathrm{d}x]) \frac{P(x)}{\int P(x)\mathrm{d}x} \int H(y)A(x, y)\mathrm{d}y\Gamma \tag{1}$$

where s_P and Γ are the survival rates of adult parasites and of parasitic eggs after acceptance of parasitism, respectively. Here I have assumed implicitly that only one parasite egg survives in a host nest even if the nest was parasitized more than once (as in the case of cuckoo parasitism) and that no particular parasite trait is preferred at this stage.

The density of the hosts of egg type x in the following year, $H'(x)$, is derived in the same way. The number of the host yearlings of egg type x that fledged from an unparasitized nest, W_{NP}, is given as

$$W_{NP} = f \exp[-a \int P(x)\mathrm{d}x]$$

where f is the reproductive success of the host in the absence of parasitism and exp[*] is the probability of a host nest escaping any parasitism. The number of yearlings of egg type x from a parasitized nest, W_P, is given as the product of the reproductive success of the host in the absence of parasitism, the probability of the nest being parasitized by a parasite y, and the probability of rejecting the parasitism $1 - A(x, y)$, summed over all possible y, to give

$$W_P = f(1 - \exp[-a \int P(x)\mathrm{d}x]) \frac{\int P(y)\{1 - A(x, y)\}\mathrm{d}y}{\int P(x)\mathrm{d}x}$$

The total density of the host population is generally regulated by a density-dependent effect in the absence of parasitism. Then, the density of the hosts x in the following year is obtained as follows:

$$H'(x) = \frac{k}{k + \int H(x)\mathrm{d}x} [s_H + W_{NP} + W_P]H(x) \tag{2}$$

where the first term on the right outside the square brackets represents the density-dependent effect ($1/k$ measures the intensity of the density-dependent effect) and s_H is the survival rate of adult hosts. Here I also assume that the density-dependent effect is independent of host egg appearance. I discuss relaxation of this assumption later.

The integro-difference equations (1) and (2) constitute the model that describes the temporal change of the distributions of egg appearance, $P(x)$ and $H(x)$, for $x \in [-L/2, L/2]$ starting from some initial distributions. We can reduce the number of parameters by rescaling $x \to x/L$, $aLP(x) \to P(x)$, $aL\Gamma H(x) \to H(x)$, $ak\Gamma \to k$, and $\gamma L^2 \to \gamma$. This means that we can set $L = 1$, $a = 1$ and $\Gamma = 1$ without loss of generality to examine the qualitative behaviour of the model.

ANALYSES AND RESULTS

Monomorphic case

First, I analyse the special case when both the parasite and host populations are monomorphic. In this case, within-population variation is zero and both populations are homogeneous. The distributions $P(x)$ and $H(x)$ are given as

$$P(x) = P\delta(x - m_{\mathrm{P}}) \qquad H(x) = H\delta(x - m_{\mathrm{H}}) \tag{3}$$

where P and H are the total densities and m_{P} and m_{H} are the egg appearances of the parasite and host populations, respectively. $\delta(x)$ is the delta function that represents a monomorphic point distribution. Without loss of generality, I assume $m_{\mathrm{P}} < m_{\mathrm{H}}$.

By substituting (3) into (1) and (2) and integrating with respect to x, we obtain the following conventional population dynamics that relates the total densities of parasites and hosts (P and H) to those in the following year (P' and H'):

$$P' = s_{\mathrm{P}}P + (1 - \mathrm{e}^{-P})H\mathrm{e}^{-\gamma d^2} \tag{4}$$

$$H' = \frac{k}{k+H}[s_{\mathrm{H}} + f\mathrm{e}^{-P} + f(1 - \mathrm{e}^{-P})(1 - \mathrm{e}^{-\gamma d^2})]H \tag{5}$$

where d is the distance between the egg appearances ($d = m_{\mathrm{H}} - m_{\mathrm{P}} > 0$).

The behaviour of the monomorphic dynamics (4) and (5) can be readily analysed. There exists a critical threshold d_{C}, defined as

$$d_{\mathrm{C}} = \sqrt{\frac{1}{\gamma}\log\left[\frac{k(f + s_{\mathrm{H}} - 1)}{1 - s_{\mathrm{P}}}\right]}$$

which is proportional to the width of the acceptance probability function w. If $d \geq d_{\mathrm{C}}$, the population dynamics converges to the equilibrium state in which the parasites go extinct and only the hosts survive: $P \to 0$, $H \to k\ (f + s_{\mathrm{H}} - 1)$. In contrast, if $d < d_{\mathrm{C}}$, the dynamics converges to the equilibrium state in which both the parasites and hosts co-exist: $P \to P^*$, $H \to H^*$, where (P^*, H^*) is the unique internal equilibrium of (4) and (5). A monomorphic parasite population of poor mimicry beyond the threshold ($d \geq d_{\mathrm{C}}$) cannot reproduce enough and goes extinct. On the other hand, a parasite population of good mimicry ($d < d_{\mathrm{C}}$) can reproduce enough to sustain the population. This monomorphic case corresponds to a conventional population dynamics in which the (co)evolutionary change of a trait in focus is controlled by a parameter and the condition of a new trait to invade and replace the existing population is analysed (e.g. Takasu, 1998b). In the next sub-section, I relax the monomorphic constraint and introduce within-population variation to examine how the distributions $P(x)$ and $H(x)$ shift with time.

Co-evolution of egg appearance

Let $P(x)$ and $H(x)$ be distributed around some population means with certain variances. Note that each trait x is assumed to reproduce asexually and no genetic structure is considered in this model. Co-evolution of egg appearance is defined in terms of the temporal change of the distributions $P(x)$ and $H(x)$.

The integro-difference equations (1) and (2) allow only a limited analytical treatment, and the following analyses in part are carried out by numerical calculation. As will become clear, however, we can explore the dynamics analytically by focusing on the population means and variances of egg appearance if initial distributions are given proportional to normal.

Assume that the initial distributions $P_0(x)$ and $H_0(x)$ are given proportional to normal distributions with mean m_P and m_H and variance σ_P^2 and σ_H^2, respectively, as follows:

$$P_0(x) = PN(m_P, \sigma_P^2) \qquad H_0(x) = HN(m_H, \sigma_H^2)$$

where $N(m, \sigma^2)$ is a normal distribution with mean m and variance σ^2, and P and H are the initial total densities of the parasite and host populations, respectively. This would be reasonable if new traits are created by random mutation from an existing monomorphic trait. Without loss of generality, we set $m_P = 0$ and $m_H = d > 0$ as the initial state. If the initial variances, σ_P^2 and σ_H^2, are sufficiently small, we can approximate that the range of the trait space L is infinite and, by integrating (1) and (2) for $x \in [-\infty, \infty]$, we obtain the total densities, P' and H', and the population means of egg appearance, m'_P and m'_H, in the following year as functions of those in the previous year (P, H, m_P, m_H, σ_P^2 and σ_H^2) as follows (see Appendix):

$$P' = \int P'(x)\mathrm{d}x = s_P P + (1 - \mathrm{e}^{-P})HC \tag{6}$$

$$H' = \int H'(x)\mathrm{d}x = \frac{kH}{k+H}[f + s_H - f(1 - \mathrm{e}^{-P})C] \tag{7}$$

$$m'_P = \Delta m_P = \frac{2(1 - \mathrm{e}^{-P})H\gamma d\sigma_P^2 C}{\{1 + 2\gamma(\sigma_P^2 + \sigma_H^2)\}\ \{s_P P + (1 - \mathrm{e}^{-P})HC\}} \tag{8}$$

$$m'_H = d + \Delta m_H = d + \frac{2(1 - \mathrm{e}^{-P})f\gamma d\sigma_H^2 C}{\{1 + 2\gamma(\sigma_P^2 + \sigma_H^2)\}\{f + s_H - f(1 - \mathrm{e}^{-P})C\}} \tag{9}$$

where

$$C = \frac{1}{\sqrt{1 + 2\gamma(\sigma_P^2 + \sigma_H^2)}} \exp\left[\frac{-\gamma d^2}{1 + 2\gamma(\sigma_P^2 + \sigma_H^2)}\right]$$

and d is the difference between the means of the parasite and host populations in the previous year ($d = m_H - m_P$). In the same way, we can derive the variances of egg appearance in the following year, σ'^2_P and σ'^2_H, as functions of P, H, m_P, m_H, σ_P^2 and σ_H^2 (the expressions are too lengthy to be listed here; see the Appendix for their full expression):

$$\sigma'^2_P = F_P\,(P, H, m_P, m_H, \sigma_P^2, \sigma_H^2) \tag{10}$$

$$\sigma'^2_H = F_H\,(P, H, m_P, m_H, \sigma_P^2, \sigma_H^2) \tag{11}$$

In the strictest sense, the distributions in the following year, $P'(x)$ and $H'(x)$ given by equations (1) and (2), are no more normally distributed if the initial distributions are proportional to normal, because the reproductive successes of the parasites and hosts are not uniformly constant depending on trait x. Numerical analyses, however, show that $P'(x)$ and $H'(x)$ can be approximately represented as normal again if the initial variances are sufficiently small ($\sigma_P^2, \sigma_H^2 \ll 1$). This provides an analytical tool to explore the full dynamics (1) and (2) by an approximated method, which I refer to as normal distribution approximation. In this approximation, the set of equations (6)–(11) describes an approximated dynamics of the full dynamics under the restriction that the distributions $P(x)$ and $H(x)$ are fixed proportional to normal. Note that the full dynamics (1) and (2) itself does not require the normality of the distributions. With the approximated dynamics, however, we can explore the temporal change of the distributions of egg appearance in more detail, as shown below.

Figure 1 illustrates a typical example of the temporal change of $P(x)$ and $H(x)$ of the full dynamics (1) and (2), starting from initial distributions set proportional to normal. We see that the distributions $P(x)$ and $H(x)$ retain almost the same shape and the parasites run after the hosts. Figure 2 shows the corresponding temporal change of the total densities, P and H, the population means of egg appearance, m_P and m_H, and the variances, σ_P^2 and σ_H^2, calculated from the full dynamics (1) and (2), together with those calculated from the normal distribution approximation (6)–(11). As shown, the approximated dynamics provides a very good fit to the original full dynamics in the early stage of the dynamics.

We can see the early dynamics in more detail by focusing on the distance between the mean egg appearances of the parasite and host populations, $d = m_H - m_P$. When the change in the distance per year is positive ($\Delta d = \Delta m_H - \Delta m_P > 0$), the hosts run away from the parasites. Otherwise ($\Delta d < 0$), the parasites catch up with the hosts. It is not straightforward to see the sign of Δd from (8) and (9). But if the variances are effectively small ($\sigma_P^2, \sigma_H^2 \ll 1$) and we assume that co-evolution starts from the non-trivial monomorphic equilibrium [the total densities P and H are given equal to the non-trivial equilibrium P^* and H^* of the monomorphic dynamics (4) and (5)], Δd is reduced as follows by ignoring the higher orders of the variances (see Appendix):

$$\Delta d = \Delta m_H - \Delta m_P = 2\left[\frac{k(f + s_H - 1) - H^*}{H^* + k}\sigma_H^2 - (1 - s_P)\sigma_P^2\right]\gamma d \qquad (12)$$

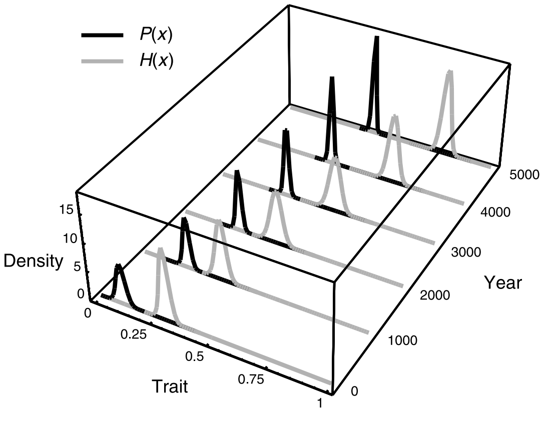

Fig. 1. Temporal change in the density distributions $P(x)$ and $H(x)$, when the sensitivity of the hosts against unlike eggs is not high, $\gamma = 2$. Initial distributions are set proportional to the normal distribution $N(m, \sigma^2)$. Black lines = parasite, grey lines = host. Parameters used are $f = 0.7$, $s_H = 0.5$, $k = 100$, $s_P = 0.5$, $a = 1.0$, $\Gamma = 1.0$, $\gamma = 2$. Initial distributions are $P_0(x) = P_0 N(m_P, \sigma_P^2)$, $H_0(x) = HN(m_H, \sigma_H^2)$, where $m_P = 0.1$, $m_H = 0.3$ and $\sigma_P = 0.02$, $\sigma_H = 0.02$. The total densities, P_0 and H_0, are set to the non-trivial equilibrium value of the corresponding monomorphic case $d = 0.2$; that is, $P_0 = 0.3560$, $H_0 = 0.6438$.

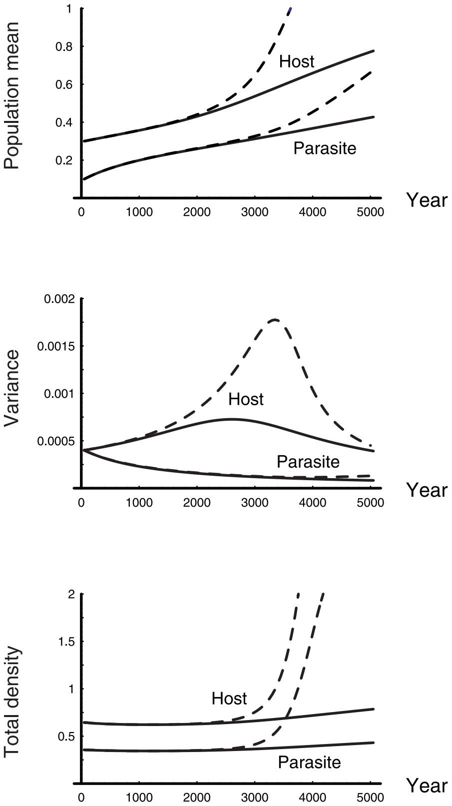

Fig. 2. Corresponding temporal change of the population means and variances of egg appearance, and the total densities of the parasite and host populations calculated from the full dynamics (solid lines). The normal approximation dynamics is shown by dashed lines.

As the distance between the means, $d = m_H - m_P$, increases up to the threshold d_C given in the previous sub-section, the monomorphic equilibrium density H^* approaches the stable equilibrium density of the hosts in the absence of parasites, $k(f + s_H - 1)$, and the first term in the bracket becomes negligible to make Δd negative. This shows that the further the population mean of the parasite egg appearance is from that of the host, the faster the parasites chase the hosts. This is due to the in-built inequality that all parasites are at the mercy of the host to accept or reject, and that not all hosts are parasitized. We also see from (12) that the sensitivity γ and the distance d scale the rates of the co-evolutionary change of the population means of egg appearance and that a smaller parasite survival rate facilitates the change in the parasite's mean egg appearance.

In this sub-section, I have shown that the normal distribution approximation precisely reflects the early transient stage of the full dynamics if initial distributions are given proportional to normal. In this case, we can evaluate the rates of the co-evolutionary change in mean egg appearance using ecological parameters. The approximated dynamics eventually fails to apply because the distributions can no longer be assumed to be normal as time passes. Note again that the full dynamics (1) and (2) does not require the normality of distributions. Without assuming the normality, however, it would not be possible to derive the approximated dynamics. Extensive numerical analyses, however, show that qualitatively the same transient behaviours are obtained starting from a broad set of initial unimodal distributions; a conventional view of an arms race – 'parasites chasing their hosts escaping from the parasites' – holds again as long as the initial distributions $P_0(x)$ and $H_0(x)$ are unimodal.

Equilibrium distributions of egg appearance

Even when unimodal distributions are used as initial distributions, their unimodality is eventually lost and complex behaviour arises. Figure 3 illustrates the full dynamics after the normal approximation fails to apply. Some host traits behind the parasite distribution emerge. This 'jumping emergence' is essentially the same as in Doebeli (1997), where the classical Nicholson-Bailey host–parasitoid model was extended to cover quantitative traits. Jumping is always possible for any initial distribution, the support of which is equal to the trait space – that is, $\forall P_0(x)$, $H_0(x) > 0$ for $\forall x \in [-L/2, L/2]$ (the normal distribution satisfies this condition). If all traits are available initially in a population, they never disappear within a finite time, although some of them might go extinct as time goes to infinity. Thus, as the population mean of the parasite egg appearance shifts rightward, host traits near the opposite side of the trait space can reproduce more successfully and begin to increase. In response, parasite traits near the newly emerged host traits begin to increase and the parasite's population mean is pulled back leftward.

As time passes further, $P(x)$ is distributed around the midpoint of the trait space ($x = 0.5$ in Fig. 3) and $H(x)$ is distributed at both the edges of the trait space ($x = 0$ and $x = 1$). Numerical calculation shows that $P(x)$ and $H(x)$ converge to a stable equilibrium where the parasite population is monomorphic at $x = 0.5$, but the host exhibits dimorphism with two discrete traits at $x = 0$ and $x = 1$.

It can be shown that non-trivial equilibrium of the full dynamics (1) and (2), if any, is given as a combination of the delta functions (point distributions) – that is, only discrete traits are allowed to survive in an equilibrium state. It is, however, extremely difficult to predict stable equilibrium (the positions of the discrete traits and their equilibrium

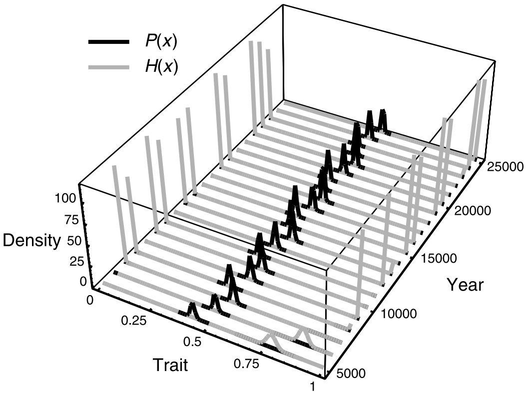

Fig. 3. Temporal change of $P(x)$ and $H(x)$ after 5000 years calculated from the full dynamics. Parameters and initial distributions are the same as in Fig. 1. Both the parasite and host populations begin to show spike-like distributions, but have not yet reached stable equilibrium.

densities) for general parameter values. Extensive numerical analyses have shown that (1) the initial distributions $P_0(x)$, $H_0(x)$ do not affect which discrete traits survive, as long as their supports coincide with the trait space ($P_0(x)$, $H_0(x) > 0$ for $\forall x \in [-L/2, L/2]$), and (2) the sensitivity of host discrimination γ is key for determining the numbers and the positions of the discrete traits. Figure 4 shows the full dynamics for a larger γ, in which three discrete traits survive both in the parasite and host populations. Although the dynamics does not reach equilibrium and shows a chaotic-like oscillation after 10,000 iterations, the discrete traits have been fixed in the trait space.

The dependence of the surviving discrete traits on γ is illustrated in Fig. 5. As γ is increased, the discrete traits bifurcate to give rise to new ones and greater numbers survive both in the parasite and host populations; both exhibit polymorphism of egg appearance. The interval between these discrete traits is roughly proportional to the width of the acceptance function w.

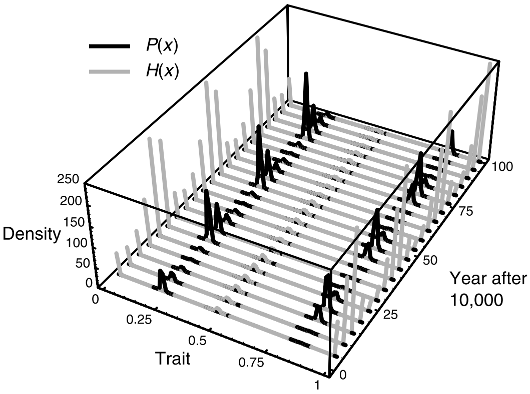

Fig. 4. Temporal change of $P(x)$ and $H(x)$ after 10,000 years calculated from the full dynamics for a larger host sensitivity $\gamma = 9$. Parameters and initial distributions are the same as in Fig. 1 except γ.

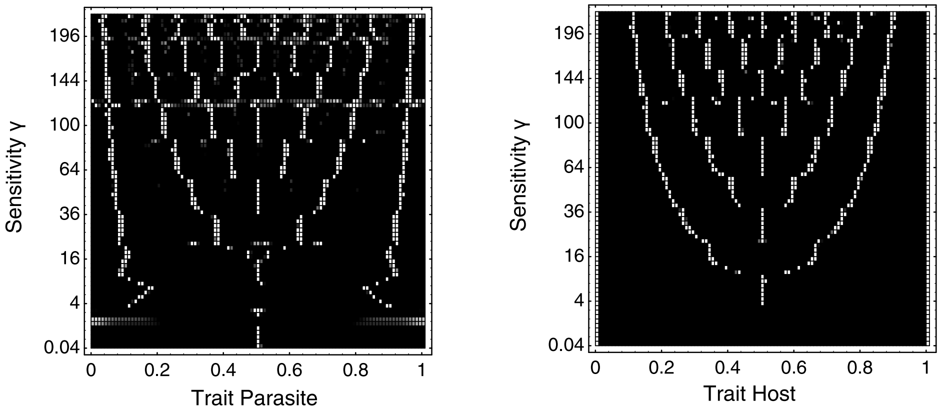

Fig. 5. Dependency of the surviving traits on the sensitivity γ. Density plots of $P(x)$ and $H(x)$ calculated from the full dynamics, averaged over 10,000 years after 1 million iterations, are shown for the host sensitivities $\gamma = 0.2^2 = 0.04$, $0.4^2 = 0.16$, $0.6^2 = 0.36$, . . . , $15^2 = 225$. High density is shown in white.

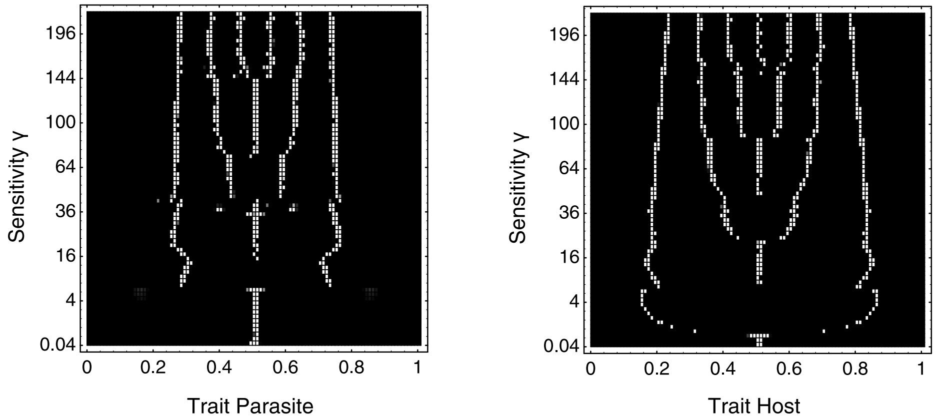

Fig. 6. Dependence of the surviving traits on the sensitivity γ when a particular egg type is preferred in the host population in the absence of parasitism, $k(x) = k_{\max}N(m, \sigma^2)$. $k_{\max} = 100$, $m = 0.5$, $\sigma = 0.2$. Density plots of $P(x)$ and $H(x)$ calculated from the full dynamics, averaged over 10,000 years after 1 million iterations, are shown for the same range of the host sensitivity γ. High density is shown in white.

So far, I have assumed that ecological parameters are independent of egg appearance – that is, they are neutral in the absence of parasitism. Without parasitic interaction, however, a certain type of egg appearance might be preferred for some reason, such as anti-predator camouflage. This effect can easily be embedded in the model by assuming that the parameter k corresponding to the carrying capacity of the host population is a function of x with a maximum at some appearance. The drawback is that this makes the normal distribution approximation derived above virtually impossible. However, numerical analyses have provided qualitatively the same results as shown in Fig. 6. Again, only discrete traits survive both in the parasite and host populations. The innate preference confers an advantage to a particular egg type, so that only one discrete trait survives in the host population when the sensitivity γ is small.

The discreteness of the equilibrium distributions remains qualitatively the same even if we introduce mutation (e.g. females of one egg type produce a few offspring of slightly different types). With such a mutation, the distributions after a long run again have several peaks, each corresponding to the position of the discrete trait in the absence of mutation (the sharpness of the peaks depends on the mutation rate). Thus I conclude that the discreteness (polymorphism) observed in this model is robust, not an artifact of the model framework.

DISCUSSION

Co-evolution of egg appearance as a quantitative trait

In the model presented here, co-evolution of egg appearance is viewed in terms of the dynamics of density distributions along a continuous spectrum. As shown in the analyses, we observe a conventional view of the arms race as 'parasites chasing their hosts escaping from the parasites' in the early stage of the dynamics provided that the initial distributions

$P_0(x)$ and $H_0(x)$ are unimodal. If $P_0(x)$ and $H_0(x)$ are given proportional to normal, we can evaluate the rate of co-evolutionary change of total densities, population means and variances of egg appearance using ecological parameters by an approximated dynamics.

Technically, the normal distribution approximation developed here appears to correspond to the quantitative genetic recursion (QGR) in Taper and Case's notation (Taper and Case, 1992), although the present model ignores genetic structure. Quantitative genetic recursion describes the temporal changes of total density, population mean and variance assuming that the distribution of a phenotypic trait is always kept normal. Taper and Case's (1992) discussion is based on a classical Lotka-Volterra competition model, but as they note, it could be applied to general host–parasite or prey–predator interactions. Most theoretical studies of quantitative traits follow the conventional schemes of quantitative genetics that also assume the normality of the trait distribution (Lande, 1980). However, the normality of distribution is not always guaranteed, as egg appearance is probably inherited by a daughter from her mother (Gibbs *et al.*, 2000; Gosler *et al.*, 2000). It would be interesting to investigate the link between the present model and QGR or conventional quantitative genetics models.

Theoretical viewpoints aside, we have few data to estimate the temporal change of egg appearance of avian brood parasites and their hosts. Also, little evidence is available showing that egg patterns have been changing co-evolutionarily. However, recent field studies have shown the possibility that parasitic interactions affect egg appearance of hosts (Øien *et al.*, 1995; Soler and Møller, 1996; Stokke *et al.*, 1999). Nakamura (1990) reported that the Common Cuckoo had started parasitizing a new host, Azure-winged Magpie *Cyanopica cyana*, in central Japan in the previous two decades. The magpie population suffered severe parasitism so that multiple parasitism was commonly observed. But it began to show a rapid increase in egg discrimination (Nakamura *et al.*, 1998). This should impose strong selective pressure for a co-evolutionary change in egg appearance of both the magpie and the cuckoo populations. Long-term monitoring and quantitative evaluation of egg appearance is needed.

Discreteness of surviving traits

The model analyses have shown that the distributions $P(x)$ and $H(x)$ are eventually reduced to point distributions; discrete traits are winnowed both in the parasite and host populations despite the initial continuous distributions. Although the model exhibits a chaotic-like behaviour that depends on parameter values, it does not take much time for the surviving discrete traits to be fixed in the trait space. It is surprising that the arms race for egg appearance settles down to such a state of polymorphism. It would appear that the discreteness is a general consequence of the arms race for a quantitative trait, where matching differences in the trait is of primary importance as in avian brood parasitism. On the other hand, in cases where a graded difference is of primary importance, escalation of the trait is possible and the system might exhibit cyclic behaviour if the exaggerated trait entails a cost (Sasaki and Godfray, 1999).

Brown and Vincent (1987, 1992) developed a game theoretic approach to model the co-evolution of predator–prey communities. In light of the evolutionarily stable strategy (ESS), they formulated an analytical procedure to calculate ESS assemblages of multiple predator and prey species, where communities of one prey and one predator, two preys and one predator, two preys and two predators, and so on, are realized depending on the predator's niche width. The width of the acceptance probability function in this model appears to correspond to that of the predator in their models. Although I could find no analytical procedure to predict the numbers and the positions of stable equilibrium discrete traits in this model, there seems to be an important link with the models of Brown and Vincent. A critical difference is that they assumed the dynamics always led to a stable equilibrium and did not consider explicit population dynamics. The game theoretic approach by Brown and Vincent, however, might be helpful in deriving a stable equilibrium state for this model. On the other hand, Kisdi (1999) studied the branching of a quantitative trait under asymmetric competition. The branching process of the equilibrium discrete traits, as shown in Figs 5 and 6, might be analysed following this approach.

The discreteness of phenotypic distributions, as shown in the present model, has been demonstrated in other contexts. Sasaki and Ellner (1995) analysed the evolutionarily stable phenotype distribution in a population under a randomly fluctuating environment. They showed that distinct phenotypic classes rather than continuous ones could be realized as an ESS and that more distinct traits survived as the degree of environmental fluctuation was increased, as in Figs 5 and 6. In a rough comparison, the fluctuating environment in their model would correspond to the host population as a background to support parasites in the present model. The discreteness also occurs if we read the continuous phenotypic spectrum as space in which individuals interact. Sasaki (1997) analysed a model in which individuals compete with neighbours in a continuous space and the effect of the competition is described by an integral kernel as in the present model. Sasaki showed that a highly clumped (discrete) distribution could occur due to the competition with neighbours. The present results, together with these previous ones, suggest that the discreteness along a continuous spectrum could occur in a wide range of contexts.

In the real world, it is unclear whether distinct egg types exist (polymorphism) in sympatric parasite and host populations. It is clear that various egg types exist in a parasite population; the Common Cuckoo lays eggs of a wide variety of types (Higuchi and Sato, 1984; Davies and Brooke, 1998; Higuchi, 1998; Nakamura *et al.*, 1998) and the Red-chested Cuckoo, *Cuculus solitarius*, in southern Africa lays eggs of at least three different types, none of which matches those of the most commonly used host (Cherry *et al.*, 1998; S.M. Kuiper, personal communication). However, it is unclear whether such variations exist within a host population. The lack of polymorphism of host egg appearance might be attributed to: (1) a particular egg type being favoured in the host population because of factors other than parasitism, such as camouflage against predation; or (2) the range of possible appearances is much narrower in the host population than in the parasite population (both the parasite and host populations share the same trait space in this model) because selection operates more harshly on the parasites due to the in-built inequality of parasitic interactions, so that the parasites have evolved various egg types but the hosts have yet to do so. Few data are available to test the idea that the arms race for egg appearance results in polymorphism. A comparative study focusing on quantitative evaluation of egg appearance is needed.

How to model co-evolution

The concept of a co-evolutionary arms race is widely accepted (Dawkins and Krebs, 1979). The process could be modelled in various ways. Monomorphic dynamics would be the simplest, in which the (co)evolutionary change of a particular ecological feature, such as the attack rate by a predator or the degree of egg mimicry, is reduced to the change in a parameter under focus (Abrams and Matsuda, 1997; Takasu, 1998b). Or we may model it more realistically based on the assumption that phenotypic distributions are normal and co-evolutionary change of the means and variances is analysed (Slatkin, 1980; Taper and Case, 1985, 1992; Frank, 1993, 1994; Saloniemi, 1993; Dieckmann *et al.*, 1995). In either case, we look at co-evolution focusing on parameters that characterize the target populations, such as population means and variances.

The assumption of monomorphic or normality of phenotypic traits, however, is not always justified, as in the case of egg appearance in avian brood parasitism. Indeed, we need to describe and analyse the temporal change of the 'distribution' of such traits. This type of modelling is possible using integro-difference or integro-differential equations, an approach that has recently been gaining support as a useful theoretical tool to model (co)evolution (Doebeli, 1996a,b, 1997; Sasaki and Godfray, 1999; Doebeli and Dieckmann, 2000). I suggest calling this approach 'ideal free evolution'. By 'ideal free', I mean that (1) all possible traits are made available in the target populations along a continuous spectrum and (2) each trait reproduces asexually. The first point is not what occurs in nature; all evolution is mutation-limited. As shown in the model analysis, however, surviving discrete traits are independent of the initial distributions if all traits are provided initially. The second point might also not be realistic. It ignores genetics but brings a merit of tractability to the model. Most ESS models focus only on phenotypic traits and ignore the detailed genetic background only to seek a solution in terms of optimization, but they succeed in providing insightful results. The 'ideal free evolution' approach appears to warrant further study.

This approach could be applied to general evolutionary topics that involve (co)evolutionary change in quantitative traits, such as predator–prey interactions, competition, symbiosis and community dynamics. I believe that avian brood parasitism is an excellent system to study co-evolutionary processes using both empirical and theoretical approaches. Further study will enrich our understanding of co-evolutionary processes in general.

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APPENDIX

Derivation of the normal distribution approximation

Given the population densities producing egg type x, $P(x)$ and $H(x)$, the population means of the parasite and host populations, m_P and m_H, respectively, are given as follows:

$$m_\mathrm{P} = \frac{\int xP(x)\mathrm{d}x}{\int P(x)\mathrm{d}x} \qquad m_\mathrm{H} = \frac{\int xH(x)\mathrm{d}x}{\int H(x)\mathrm{d}x}$$

And the variances, σ_P^2 and σ_H^2, are given as follows:

$$\sigma_\mathrm{P}^2 = \frac{\int x^2P(x)\mathrm{d}x}{\int P(x)\mathrm{d}x} - m_\mathrm{P}^2 \qquad \sigma_\mathrm{H}^2 = \frac{\int x^2H(x)\mathrm{d}x}{\int H(x)\mathrm{d}x} - m_\mathrm{H}^2$$

In the normal distribution approximation, the total densities, P' and H', the population means, m'_P and m'_H, and the variances, σ'^2_P and σ'^2_H, in the following year are given using the following calculus:

$$\int_{-\infty}^{\infty} \exp[-(ax^2+bx+c)]\mathrm{d}x = \sqrt{\frac{\pi}{a}}\exp\left[\frac{b^2}{4a}-c\right]$$

$$\int_{-\infty}^{\infty} x\exp[-(ax^2+bx+c)]\mathrm{d}x = \frac{-b}{2a}\sqrt{\frac{\pi}{a}}\exp\left[\frac{b^2}{4a}-c\right]$$

$$\int_{-\infty}^{\infty} x^2\exp[-(ax^2+bx+c)]\mathrm{d}x = \frac{2a+b^2}{4a^2}\sqrt{\frac{\pi}{a}}\exp\left[\frac{b^2}{4a}-c\right]$$

where a, b and c are real constants ($a > 0$).

The variance of parasite egg appearance in the following year, σ'^2_P, is given using the following calculus:

$$E[x^2] = \frac{\int x^2P'(x)\mathrm{d}x}{\int P'(x)\mathrm{d}x} = \frac{s_\mathrm{P}P\{1+2\gamma(\sigma_\mathrm{P}^2+\sigma_\mathrm{H}^2)\}^2 + (1-\mathrm{e}^{-P})H(1+2\gamma\sigma_\mathrm{H}^2)^2 + 2\gamma\sigma_\mathrm{H}^2(1+2\gamma d^2+2\gamma\sigma_\mathrm{H}^2)C}{\{1+2\gamma(\sigma_\mathrm{P}^2+\sigma_\mathrm{H}^2)\}^2\,\{s_\mathrm{P}P+(1-\mathrm{e}^{-P})HC\}}$$

as a function of P, H, $d = m_\mathrm{H} - m_\mathrm{P}$, σ_P^2 and σ_H^2, where

$$C = \frac{1}{\sqrt{1+2\gamma(\sigma_\mathrm{P}^2+\sigma_\mathrm{H}^2)}}\exp\left[\frac{-\gamma d^2}{1+2\gamma(\sigma_\mathrm{P}^2+\sigma_\mathrm{H}^2)}\right]$$

In the same way, we can derive the variance of the host, σ'^2_H, using

$$E[x^2] = \frac{\int x^2H'(x)\mathrm{d}x}{\int H'(x)\mathrm{d}x} =$$

$$\frac{(f+s_\mathrm{H})(d^2+\sigma_\mathrm{H}^2)\{1+2\gamma(\sigma_\mathrm{P}^2+\sigma_\mathrm{H}^2)\}^2 - f(1-\mathrm{e}^{-P})(1+2\gamma\sigma_\mathrm{P}^2)\{d^2(1+2\gamma\sigma_\mathrm{P}^2)+\sigma_\mathrm{H}^2\{1+2\gamma(\sigma_\mathrm{P}^2+\sigma_\mathrm{H}^2)\}\}C}{\{1+2\gamma(\sigma_\mathrm{P}^2+\sigma_\mathrm{H}^2)\}^2\{f+s_\mathrm{H}-f(1-\mathrm{e}^{-P})C\}}$$

Change in population means when the variances are small

If the variances, σ_P^2 and σ_H^2, are small enough, the change in the population means per year, Δm_P and Δm_H, can be Taylor expanded to give the following series:

$$\Delta m_P = \frac{2(1 - e^{-P})He^{-\gamma d^2}}{s_P P + (1 - e^{-P})He^{-\gamma d^2}} \gamma d \, \sigma_P^2 + O(\sigma_P^4, \sigma_H^4)$$

$$\Delta m_H = \frac{2f(1 - e^{-P})e^{-\gamma d^2}}{f + s_H - f(1 - e^{-P})e^{-\gamma d^2}} \gamma d \, \sigma_H^2 + O(\sigma_P^4, \sigma_H^4)$$

Substituting the internal equilibrium of the monomorphic dynamics (4) and (5) into these equations gives (12).