Avian brood parasites exploit parental care of their hosts. In most cases parasitism reduces the reproductive success of hosts and it exerts strong selection pressure on hosts for the evolution of anti-parasitism defences (Rothstein 1990; Rothstein & Robinson 1998; Davies 2000). Aggressive attacks toward parasites nearing nests, and recognition and rejection of parasitic egg in host nests, seem effective defences against parasitism (Rothstein 1975, 1990; Davies & Brooke 1988, 1989a, b; Moksnes & Røskaft 1989; Moksnes 1992). Whereas aggressive behaviour may be a defence against nest predators and thus might not be a direct response to parasitism, recognition and rejection of parasitic egg in host nests, seem effective defences against parasitism (Rothstein 1975, 1990; Davies & Brooke 1988, 1989a, b; Moksnes & Røskaft 1989; Moksnes 1992). Whereas aggressive behaviour may be a defence against nest predators and thus might not be a direct response to parasitism, recognition and rejection of parasitic eggs is certainly an adaptation that has evolved in response to brood parasitism. Unsuitable hosts, unable to rear parasitic nestlings, in general show no such behaviour, furthermore various suitable hosts with no apparent history of being parasitized have been shown only to rarely recognise or reject eggs even when they look unlike their own (Davies & Brooke 1989a, b; Soler & Møller 1990).

Anti-parasitism adaptations by hosts, in turn, should act as a selection pressure for the evolution of counter-adaptive strategies by parasites to beat host defences. It is not surprising therefore that the females of some parasites behave in a cryptic manner when parasitizing and laying eggs that mimic those of hosts (Brooke & Davies 1988; Moksnes et al. 1990). Close egg mimicry is presumed to be a direct response to host defences allowing them to discriminate and reject dissimilar eggs.

In parasitic interactions, by definition, a conflict of interest between parasites and their hosts is inevitable and it has been suggested that this conflict leads to a co-evolutionary arms race in which parasites evolve to exploit their hosts in more effective ways while those same hosts evolve strategies to mitigate the impact of parasitism (Dawkins & Krebs 1979). In other words, each side evolves adaptive behavioural traits to maximize their fitness, however these traits are in conflict. This simplistic description of the co-evolutionary arms race is both appealing and persuasive, however, the consequences of the arms race are not obvious, as we shall see later.

In this paper, I focus on the co-evolutionary inter-
action between an obligate specialist brood parasite, the Common Cuckoo *Cuculus canorus* and its hosts in a closed system, and discuss the consequences of the co-evolutionary arms race from a theoretical viewpoint. The argument pursued here may be applicable to any specialist parasite. Firstly, I discuss evolution as a process of fitness maximization, using the concept of adaptive landscape and then extend it to co-evolution. Secondly, I consider the theoretical aspects of the co-evolutionary arms race as it relates to egg appearance, and suggest possible consequences of the arms race. Finally, I express the importance of theoretical research in connection with field studies and stress the need for further study in order to better understand co-evolution between avian brood parasites and their hosts.

**FITNESS MAXIMIZATION OF PARASITES AND HOSTS**

Natural selection is a process by which the mean fitness of a population is increased generation by generation (Roughgarden 1996). The evolutionary process can be viewed in terms of an “adaptive landscape” depicting fitness plotted against a continuous set of possible strategies (Futuyma 1998). The mean fitness of a population always increases in the process and evolution is envisioned as the process of climbing up the adaptive landscape surface towards a peak of maximum fitness. Let us now consider and focus on the level of discrimination and rejection of non-mimetic parasitic eggs, *r*, as a host defence strategy (0 < *r* < 1). Without defence *r* = 0; hosts always accept parasitism and hosts can only reproduce when not parasitized. As hosts show higher levels of defence they are able to reduce the reproductive damage caused by parasitism more effectively and the mean fitness in general increases as *r* increases. As a result we have an adaptive landscape of hosts plotted against strategy *r* (see Fig. 1).

If the host’s defence entails a small cost, such as recognition and rejection error, i.e., hosts reject their own eggs mistaking them for the eggs of parasites, or if they accidentally damage their own eggs while attempting to reject a parasitic egg, then mean fitness should peak at *r* = *r*#. This is because at the perfect defence point *r* = 1, no parasites can reproduce and there is no risk of parasitism, thus there is no merit in discriminating and rejecting parasitism given the cost involved. In this case the host population will finally settle down to the peak *r* = *r*# where it exhibits imperfect defence against parasitism (Takasu et al. 1993).

If, however, the host’s defence entails no cost, then the adaptive landscape is an increasing function of *r*, but will level off as *r* approaches 1 for the following reason. As the host evolves higher levels of defence, it becomes more difficult for parasites to reproduce successfully (parasitism is rejected more frequently) and the parasite population declines. This leads to a reduced risk for hosts being parasitized and the selection force driving the host defence *r* decelerates as *r* increases. The population density of parasites finally declines to zero when hosts have acquired a certain defence level and the host population does not necessarily establish perfect defence (*r* = 1) even when there is no cost for defence (Takasu et al. 1993).

Host defences evolve on the surface of the adaptive landscape (see Fig. 1). It should be noted, however, that the evolution of parasites like egg mimicry is at this moment frozen while hosts evolve a higher level of defence. This is not necessarily true in actual parasite-host interactions in general. Immediately after the host population begins to defend itself against non-mimetic parasitic eggs (*r* > 0), selection for parasites to overcome their host’s defences, e.g., better egg mimicry, should begin in the parasite population. It should be noted also that evolution of egg mimicry by parasites affects the shape of the hosts’ adaptive landscape. As egg mimicry improves, host defences become less effective and the cost of rejection due to increased recognition error (as shown in Fig. 1) might increase. The evolution of host defences on the host’s adaptive landscape is closely correlated with the evolution of egg mimicry by parasites.

How then does egg mimicry by parasites evolve?

![Fig. 1. Host fitness plotted against host strategy; defence level *r*. As hosts show higher defence levels their fitness increases but levels off. If host defences entail costs the fitness landscape shows a peak. The degree of egg mimicry by parasites affects the shape of the fitness landscape.](image-url)
To see this graphically we need to draw the landscape of the parasite’s fitness against the parasite strategy. The evolution of egg mimicry is viewed as the movement of the parasite population climbing up the landscape. When the parasite’s strategy is egg mimicry $m$, ($m=0$ represents very poor mimicry and $m=1$ represents a perfect match with the host’s eggs) (see Fig. 2), the landscape is generally an increasing function of $m$ because better mimicry will make parasitism more successful. The adaptive landscape of the parasite, however, depends on the host’s strategy $r$. If a host shows no defence $r=0$, the degree of egg mimicry does not matter at all for parasite reproduction. As $r$ increases, the slope becomes steeper and it pays for parasites to more closely mimic their host’s eggs.

The co-evolutionary arms race between parasites and hosts is a process wherein each side seeks a fitness maximum on the landscape surface but the landscapes correlate with each other. Where the evolution of a host’s defence and that of a parasite’s counter-defence can be separated, i.e., they occur in different time scales, we reach a conventional view of the arms race between parasites and hosts (Davies & Brooke 1988, 1989a, b; but see Lovászi & Moskát 2004). Recently, however, a new line of research has been attracting attention, i.e., the possibility that hosts may change their egg appearance in order to overcome egg mimicry by parasites. Øien et al. (1995), Soler and Möller (1996), and Stokke et al. (1999) have shown that inter- and intra-clutch variation of host egg appearance correlate with the rejection rate and they have suggested that hosts may evolve to reduce intra-clutch variation in egg appearance and to increase inter-clutch variation, thereby making it easier for hosts to recognize parasitism but difficult for parasites to mimic eggs (Stokke et al. 2002; but see Karcza et al. 2003).

Takasu (1998) modelled the evolution of egg mimicry by parasites together with that of host rejection behaviour. The degree of egg mimicry $m$ was defined as the probability that a rejecter host individual accepts a parasitic egg in the nest. As Stokke et al. (2002) have shown it is logically possible that hosts can make it easier to detect parasitism by laying eggs that are less similar to mimetic parasitic eggs (see Fig. 3). In this scenario, parasites evolve better egg mimicry to increase $m$ while hosts change their egg appearance so that they are not mimicked to reduce $m$.

Takasu (2003) modelled this co-evolutionary change of egg appearance of parasites and hosts in more details, assuming a hypothetical situation in which parasites evolved to make their eggs increasingly similar to those of their hosts, but that hosts escalate further only with regards to chick appearance, in which chick discrimination and mimicry might evolve (Langmore et al. 2003).

The detailed consequences of the arms race, however, are not so simple, as we shall see. Due to the inter-dependency of the adaptive landscapes of hosts and parasites, the consequence of the arms race varies depending on detailed assumptions set up in the process; as we see in the next section.

**CO- EVOLUTIONARY CHANGE OF EGG APPEARANCE—POSSIBLE SCENARIOS**

We have discussed the co-evolutionary arms race between parasites and their hosts on the adaptive landscapes where hosts evolve the ability to discriminate between parasitic eggs and their own and to reject parasitism, while parasites evolve sophisticated egg mimicry in order to counter host defences. Many field studies have shown that many cuckoo-host interactions fit well with this arms race scenario (Rothstein 1975, 1990; Davies & Brooke 1988, 1989a, b; but see Lovászi & Moskát 2004). Recently, however, a new line of research has been attracting attention, i.e., the possibility that hosts may change their egg appearance in order to overcome egg mimicry by parasites. Øien et al. (1995), Soler and Möller (1996), and Stokke et al. (1999) have shown that inter- and intra-clutch variation of host egg appearance correlate with the rejection rate and they have suggested that hosts may evolve to reduce intra-clutch variation in egg appearance and to increase inter-clutch variation, thereby making it easier for hosts to recognize parasitism but difficult for parasites to mimic eggs (Stokke et al. 2002; but see Karcza et al. 2003).

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Takasu (2003) modelled this co-evolutionary change of egg appearance of parasites and hosts in more details, assuming a hypothetical situation in which parasites evolved to make their eggs increasingly similar to those of their hosts, but that hosts
made their eggs more dissimilar to those of parasites. Critical assumptions set up in the model were: (1) all host individuals are potentially egg-rejecters but that they may accept parasitic eggs depending on the degree of egg mimicry, i.e., how well a parasitic egg resembles the host’s eggs (Victoria 1972; Brooke & Davies 1988; Higuchi 1989, 1998; Moksnes et al. 1993), and (2) egg appearance is a trait with bound and individuals showing the trait in its extreme form have lower fitness. The result of the model analysis was counter-intuitive but might have possible implications for the arms race with respect to egg appearance. It was shown that if egg appearance is asexually inherited, i.e., daughters lay eggs similar in appearance to those of their mothers; then parasites and hosts finally exhibit a stable, discrete, polymorphism with respect to egg appearance. Discrete egg types coexist both in the host and parasite population and perfect mimicry is not necessarily achieved (Fig. 4). Female birds have a set of sex chromosomes ZW, and it has been suggested that egg appearance is inherited by daughters, with the genes coding for egg appearance being on the heterosexual chromosome W (Brooke & Davies 1988; Collias 1993; Gibbs et al. 1996, 2000; Marchetti et al. 1998; Davies 2000; Gosler et al. 2000). Asexual inheritance of egg appearance means that there are independent female lines with specific egg types in any given population because mating does not affect egg appearance. This makes possible the disruption of the distribution of host egg appearance when the parasite population evolves better egg mimicry, which in turn results in a disrupted distribution of parasite egg appearance (Fig. 4).

Clearly, the evolution of egg mimicry by parasites alters the adaptive landscape of hosts and this results in discrete polymorphism in egg appearance (Takasu 2003). In asexual inheritance the shape of the distribution of egg appearance is free to change (each line with a specific egg type behaves independently) and it is difficult to draw the adaptive landscapes of hosts and parasites because they depend not only on the value of the strategy (egg appearance) but also on the
shape of the distributions. The average fitness of a population, however, should increase as time passes by changing the distribution form and as both parasites and hosts co-evolve finally toward the discrete polymorphic state where their fitnesses are maximized.

Previous empirical studies have suggested that egg appearance is asexually inherited (e.g., Goler et al. 2000), but we do not actually know if this rule can be applied to the cuckoo and its hosts in general. Takasu (in prep.) analyzed the co-evolutionary change of egg appearance when it is sexually inherited by offspring. The genetic control of egg appearance in birds is not well known in general. For some species both male and female contribute to a daughter’s egg appearance (Collias 1993). With the assumption that a large number of genes on autosomal chromosomes additively contribute to express offspring egg appearance, we can assume that an offspring’s egg appearance is distributed around the mid-value of the two parents’ egg appearances with a certain degree of variance created by recombination and mutation. The model analysis showed that there are two qualitatively different consequences in the arms race: (1) When the variance of parasite egg appearance is larger enough than that of host, parasites successfully establish perfect mimicry and the system comes to rest at a stable state; otherwise, (2) hosts can successfully undermine egg mimicry by altering the appearance of their eggs and the system continues to show endless co-evolutionary oscillation. Sexual inheritance, in contrast, maintains a uni-modal distribution of egg appearance and prevents disruption of the distribution. Finally, either one of the two possibilities is realized depending on the within-population variances of egg appearance in host and parasite populations (Fig. 5).

In the first case above, a broader width of the parasite’s distribution of egg appearance acts as a stabilizing force to keep the distribution of hosts fixed at a point. Both the fitness of parasites and hosts are locally maximized and they rest at this stable state (see Fig. 6). In the second case, a broader width of the host’s distribution makes it possible to undermine perfect egg mimicry by parasites, and hosts can always evade parasites. The fitness of hosts is minimized when that of parasites is maximized, and a stable state is never achieved.

As these model analyses show, the consequences of the arms race concerning egg appearance vary depending on specific assumptions, especially on the mode of inheritance (asexual or sexual) of egg appearance.

**DISCUSSION**

In this paper, my aim has been to examine how the co-evolutionary arms race between parasites and their hosts proceeds in terms of the adaptive landscape and I have shown various possible consequences of the arms race concerning egg appearance. As model analyses have shown, the trajectory of the arms race varies depending on the specific assumptions inherent in the models. Contra-intuitively, discrete polymorphism can occur as a stable state and thus parasites may not achieve perfect egg mimicry when host egg appearance is asexually inherited. Furthermore, and beyond expectation, was the perpetual oscillation when egg appearance is sexually inherited. These are
the results of mathematical analyses and thus the logical consequences of the assumptions used in the models.

In the real world there is, as yet, little evidence that hosts can counter egg mimicry by changing the appearance of their eggs. In order to test this idea we need to quantify the egg appearance of both hosts and parasites in the field and see if polymorphism does exist or trace how egg appearance changes over time or differs among populations breeding in different geographical ranges. In areas where host populations have suffered parasitism for a long time, the profiles of host eggs may differ from those of populations in areas lacking parasitism, or alternatively, the profiles of parasite eggs may differ from population to population depending on the history of parasitism. Until recently, ornithologists and evolutionary biologists have focussed primarily on studying the ability of hosts to recognize and reject dissimilar eggs, as a defence against parasitism. Furthermore, the extent of egg mimicry has been considered to evolve only within the parasite population. Here I suggest the importance of testing the idea that hosts may nullify egg mimicry by altering the appearance of their eggs, as model analyses have shown. Stokke et al. (2002) demonstrated that parasitic pressure could act as a selective force leading to change in the host’s egg appearance. Further empirical study on egg appearance, both of hosts and of parasites, is needed.

Egg appearance is a trait composed of many factors, including background colour, and shape and colour of spots, and quantitative measurement is not an easy task. Human visual assessment may provide a rough means of measuring and quantifying such variation (Stokke et al. 1999, 2002; Honza et al. 2001; Karcza et al. 2003), but more objective methods are required. The relative reflectance of an egg’s surface and the pattern of the reflectance curve plotted against wavelength might be objective measures of egg appearance (Cuthill et al. 1999; Cherry & Bennett 2001; Moskát et al. 2002; Langmore et al. 2003; Aviles & Møller 2004) or image characterization may also be informative (Soler et al. 2000). As yet we have little evidence explaining how egg appearance is inherited by offspring (Collias 1993), however, as model analyses has shown, the mode of inheritance could critically affect the consequence of the arms race concerning egg appearance. Further study of egg appearance, focusing on quantitative measurement and genetic control, is needed.
By means of mathematical modeling it is possible to elucidate very clearly, which consequences result from which assumptions. Verbal arguments alone would not be able to derive or suggest the possibility of discrete polymorphism or the perpetual oscillation of egg appearance of parasites and their hosts. Apart from the validity of the assumptions, mathematical modeling is certainly a very powerful tool for the exploration of the logical consequences resulting from basic assumptions. Of course, the assumptions used in such models must be based on sound biological reasoning and their validity should be tested by empirical study. I stress here the importance of mathematical modeling as a tool for providing possible testable ideas derived from specified assumptions that are unambiguously expressed in mathematical terms.

I speculate that by studying the egg appearance of hosts and parasites in various areas with various histories of parasitism we might be able to observe co-evolution in action. With feedback from new findings demonstrated by empirical study, theoretical study will be able to provide new ideas and suggest possibilities that can be tested in further empirical study. Empirical and theoretical studies should operate in close parallel and as a result we will be able better to understand co-evolutionary interactions between avian brood parasites and their hosts in general. Following the struggle concerning egg appearance the arms race may proceed to a new stage wherein hosts discriminate odd-looking chicks while parasites counter by mimicking chicks (Davies & Brooke 1989b; Langmore et al. 2003) and the arms race may continue endlessly. Or the arms race may be trapped into a locally stable state in which both parasites and hosts enjoy local fitness maxima.

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