Evolutionary Equilibria in Avian Brood Parasitism

An Alternative to the "Arms Race–Evolutionary Lag" Concept

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The contributions of research on avian brood parasitism to the study of coevolution have been recently demonstrated (Rothstein 1990; Davies and Brooke 1991). Numerous experimental studies have shown the existence of coevolved adaptations in parasites and hosts (reviewed in Rothstein 1990). However, whereas most of these studies conclusively demonstrate the occurrence of coevolution, the details of the mechanisms on which these coevolved systems are based are still a matter of controversy. A major query is: are such systems continuously coevolving as in an arms race or, rather, are they in an evolutionary equilibrium? Under the "arms race" view, the acceptance of parasitic eggs or nestlings, which reduces host fitness, is a result of an evolutionary lag in the development of counteradaptations by the host (Rothstein 1975a, 1982a; Dawkins and Krebs 1979; Davies and Brooke 1988, 1989b; Moksnes et al. 1990). The lag, in this case, might be due to the absence of a new genetic variant (Rothstein 1975b) or to the time it takes for such a variant to spread in the host population (Kelly 1987; Davies and Brooke 1989b). On the other hand, under the equilibrium view, acceptance is an inevitable result of an equilibrium among various selective pressures (Zahavi 1979; Rohwer and Spaw 1988; Brooker and Brooker 1990; Petit 1991; Lotem et al. 1992). The two alternate views differ in the predictions they present for the future. The evolutionary lag model predicts further evolutionary change in the system (i.e., evolution of new counteradaptations or improvements in such adaptations), whereas the evolutionary equilibrium model predicts that no evolutionary change will occur as long as the system's conditions do not change (temporal fluctuations may occur in a dynamic type of equilibrium, but not a consistent evolutionary change in one direction).

Since the 1970s, the "arms race–evolutionary lag" concept has dominated the field of avian brood parasitism to the extent that the possibility of an evolutionary equilibrium has been almost completely ruled out in the major discussions (Rothstein 1975a, 1982a, 1990; Davies and Brooke 1988, 1989b; Harvey and Partridge 1988). However, excluding a few cases in which the interaction between the parasite and the host is known to have begun within recent decades (Cruz et al. 1985; Nakamura 1990; Soler 1990; but see Zuniga and Redondo 1992), there is no conclusive evidence for an evolutionary lag other than the absence of more convincing explanations (Rothstein 1982a, 1990; Davies and Brooke 1989b). Thus, the main question in this debate is whether all the possibilities for the existence of an evolutionary equilibrium have been considered and properly tested. In this chapter we argue that the role of equilibrium in the coevolution of parasitic birds and their hosts has been underestimated.

We limit most of our discussion to egg rejection, which seems to be of primary importance. Although it is not the only defense

mechanism used by hosts, it is the most common, the best studied and probably the most effective one (reviewed in Rothstein 1990). Egg rejection protects the host young from competition with the parasite nestling or from being ejected by them (in the case of some cuckoo species). As it occurs early in the breeding cycle, egg rejection is also more likely to save time required for renesting if nest desertion or egg burial is involved. Because of its effectiveness, egg rejection might have a higher selective advantage and is expected to evolve faster than other defenses such as nestling rejection (Dawkins and Krebs 1979; Davies and Brook 1988). Hence, as long as it is believed that the absence of egg rejection is due to a lag in evolution, the lack of nestling rejection or any other defense mechanisms simply results from the same lag. On the other hand, if the absence of egg rejection is found to represent an evolutionary equilibrium, further investigation of the absence of other defenses is especially relevant (see McLean and Maloney, this vol.).

We will now review the possible costs and benefits of egg rejection, present them in a combined model, and suggest some possible ways in which an equilbrium might be expressed in a host population. We then discuss available data on avian brood parasitism in relation to the equilibrium hypothesis.

COSTS AND BENEFITS OF EGG REJECTION: A COMBINED MODEL

Because parasitism has been shown to reduce host fitness (Payne 1977; May and Robinson 1985), rejecting the parasitic egg is expected to be advantageous. Egg rejection, however, might also incur several possible costs (Rothstein 1976; Zahavi 1979; Davies and Brooke 1988) that reduce the selective advantage of rejection and result in a slower evolutionary rate and a longer evolutionary lag (Davies and Brooke 1989b). If the sum of all costs of egg rejection exceeds the benefit, then accepting the parasitic egg would be adaptive and could be explained as an evolutionary equilibrium. Davies and Brooke (1989b) presented a model for acceptance as an evolutionary equilibrium based on a single rejection cost (the cost of recognition errors). Other theoretical models (May and Robinson 1985; Takasu et al. 1993) assumed the existence of a general cost factor, but did not investigate its biologic components and the interaction between them. To understand better the combined quantitative effect of all the costs and benefits of egg rejection, we describe the rejection costs and benefits suggested in the literature, and propose a combined cost–benefit model.

The model

The model, illustrated in fig. 12.1, compares two pure strategies — an accepter and a rejecter. Each arrow in the scheme represents the probability of a certain event (i.e., the probability of being parasitized, of correctly identifying the parasitic egg, etc.). The payoff at the end of each course of events represents the reproductive success of the host under the specific circumstances. The overall payoff of each strategy is the sum of all the payoffs, each multiplied by its probability of occurrence.

The payoff to an accepter

The payoff of an accepter when not parasitized is the average reproductive success of an unparasitized nest and is designated as X. When an accepter is parasitized, it pays the parasitism cost "PC" and thus its payoff is $X - PC$. The value of PC usually varies between zero and X (Payne 1977), but could also be negative, if being parasitized is advantageous (Smith 1968), or greater than X, if parasitism reduces also the host's future reproductive success.

The payoff to a rejecter — costs when parasitized

Several costs can reduce the benefit of rejection in parasitized nests:

1. Parasite laying damage (PLD): If a parasitized rejecter ejects the parasitic egg without any rejection cost, its payoff is still reduced by PLD, the damage already caused by the parasite during the laying period (i.e., by removal, pecking, or accidental breakage of host eggs; Payne 1977; Wyllie 1981; Soler 1990). PLD is actually part of PC (parasitism cost).

2. Ejection cost (EC): The ejection of the parasitic egg itself might be accompanied by an accidental breakage of host eggs, which reduces the payoff (Rothstein 1976, 1977; Davies and Brook 1988; Rohwer and Spaw 1988; Rohwer et al. 1989; Moksnes et al. 1991).

3. Desertion cost (DC): Deserting a parasitized nest, which is a different strategy than egg ejection, may incur a desertion cost
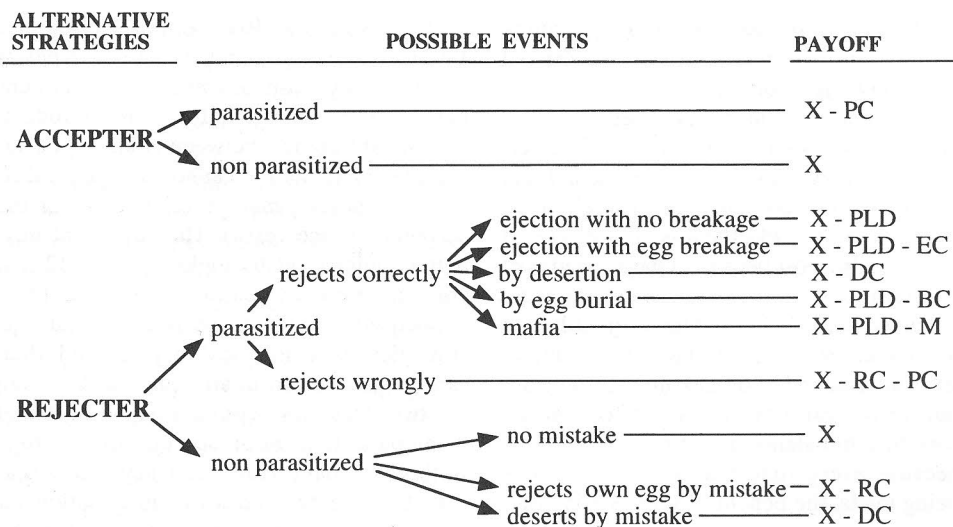
Figure 12.1 A combined cost–benefit model of egg rejection. The model compares two alternative strategies, an ACCEPTER and a REJECTER. Each arrow in the scheme represents the probability of a certain event (i.e., the probability of being parasitized, of correctly identifying the parasitic egg, etc.). The payoff at the end of each course of events represents the reproductive success of the host under the specific circumstances (see detailed explanations in the text). The overall payoff of each strategy is the sum of all the payoffs, each multiplied by its probability of occurring. REJECTS CORRECTLY: rejects the parasite egg. REJECTS WRONGLY: rejects own egg instead of the parasite egg. X: the average reproductive success of an unparasitized host assuming no rejection cost. PC: parasitism cost, the reduction in host reproductive success due to parasitism. PLD: parasite laying damage, the damage already caused by the parasite during the laying period by removal, pecking or breakage of host eggs (PLD is part of PC). EC: ejection cost, egg loss due to accidental breakage of host eggs when ejecting the parasite eggs. DC: desertion cost, the reduction in host reproductive success due to loss of time and energy, smaller clutch size and lower fledgling survival in the renest, or even inability to renest. BC: burial cost. The reduction in host reproductive success due to the loss of time, energy and of a preferred breeding date, when burying a parasitic egg with nest materials. MAFIA: the probability that the parasite revisits the parasitized nest and preys upon the host eggs or nestlings if the parasite egg has been removed. M: the reduction in brood size due to such "mafia" predation by the parasite. RC: recognition cost, egg loss due to mistaken ejections of host's own eggs.

resulting from loss of time and energy, smaller clutch size and lower fledgling survival in the renest, or even inability to renest (Zahavi 1979; Rower and Spaw 1988; Davies and Brook 1989b; Petit 1991; Moksnes et al. 1993).

4. Burial cost (BC): As in desertion, burial of a parasitic egg with nest materials may also incur a cost due to the loss of time, energy, and of a preferred breeding date (Clark and Robertson 1981; Davies and Brooke 1988).

5. There is a probability, which we term the "mafia" effect, that the parasite revisits the parasitized nest and preys upon the host eggs or nestlings if the parasitic egg has been removed (Zahavi 1979; Soler et al. 1995). The payoff in this case is reduced by M, the number of host young lost due to predation by the parasite. In a more general form, this arrow in the scheme can be modified to account for any kind of effect (including positive) on the success of a parasitized nest resulting from the parasitism event. For example, parasitized nests from which the parasitic egg has been ejected could have a higher success rate than nonparasitized nests because the parasite does not prey upon nests it has parasitized but only upon other host nests (Davies and Brooke 1988; Arcese et al. 1996).

6. Recognition cost (RC): When egg mimicry by a parasite is well developed, a parasitized host may eject or bury one of its own eggs instead of the parasitic egg (Davies and Brooke 1988). In such a case ("rejects wrongly" in fig. 12.1) it loses the egg and also has to pay the cost of parasitism (PC). In cases where X = PC, the loss of an egg (RC) is not really a cost because a parasitized host that fails to reject the parasitic egg raises no young (Rothstein 1990). However, although in these cases the loss of the egg is meaningless, the probability of making such recognition errors can have a great effect on the cost–benefit balance of egg rejection. This is because every time that such an error is being made, the benefit of rejection is lost.

The payoff of a rejecter — costs when not parasitized

It has been suggested that recognition errors can also be made by rejecters when not parasitized (Zahavi 1979; Rothstein 1982b; May and Robinson 1985; Davies and Brooke 1988; Marchetti 1992). This may lead to rejection (by ejection or by egg burial) of one or more of the host's own eggs and thus to a recognition cost (RC), or to desertion of an unparasitized nest which incurs the cost of desertion (DC: see above).

Comments and conclusions related to the model

The distinction between costs when parasitized and costs when not parasitized

The relative importance of costs when parasitized and costs when not parasitized is influenced by the cost of parasitism (PC). In systems where hosts lose all their young if parasitized (X = PC), it is unlikely that rejection costs when parasitized alone could outweigh the benefit of rejection (Rothstein 1990). However, if there are costs when not parasitized, an equilibrium might occur even when parasitized hosts lose all their young (Zahavi 1979; May and Robinson 1985; Rothstein 1990; Lotem et al. 1995).

The distinction between costs when parasitized and costs when not parasitized is especially important when the effect of parasitism frequency is discussed. If costs when not parasitized are involved, the parasitism frequency has an important effect on whether rejection is eventually better than acceptance or vice versa (May and Robinson

1985; Davies and Brooke 1989b; Lotem et al. 1992). On the other hand, if costs when parasitized are the only costs involved, the frequency of parasitism can affect only the magnitude of the existing difference between a rejecter's and an accepter's payoffs, but cannot change the direction of selection (i.e., make a rejecter better than an accepter or vice versa). This argument might be better understood by looking at fig. 12.1: in the absence of costs when not parasitized, the "non-parasitized" segments of rejecter and accepter strategies have identical payoffs and therefore can be removed from an equation that compares the two strategies (assuming equal probability of being parasitized as an accepter or as a rejecter). In this case, parasitism frequency becomes a coefficient of the two sides of the equation and, as such, it affects only the magnitude of the absolute difference between the two sides but not the direction of the difference.

The combined effect and its implications

The rejection payoff is a consequence of the combined effect of several factors. Therefore, rejection rates may not be clearly correlated with a single factor. This may explain why some predictions of the equilibrium hypothesis, tested with a single factor, have been rejected. For example, Davies and Brooke (1989b) expected that rejection rates should be lower among common cuckoo hosts with small bills. Such birds suffer a higher ejection cost (egg breakage) and/or rely on nest desertion which may be a more expensive rejection method. The overall rejection cost, however, might not be higher among such birds. The cost of desertion could be compensated for by a lower probability of suffering other costs. For example, small hosts may lay small eggs relative to the cuckoo eggs (see Davies and Brooke 1989a, fig. 1) and therefore might be less likely to make recognition errors. In addition, desertion cost might be relatively low when parasitism cost is especially high. For small hosts, rearing a cuckoo may be especially expensive and is more likely to result in a loss of future reproductive potential. According to this reasoning, rejection rates should not necessarily be lower among small hosts.

The cost of misimprinting — an additional possible cost

If egg recognition is attained by an imprinting-like process (Rothstein 1974, 1978; Lotem et al. 1992,

1995), an additional possible cost, which was not included in the model, should be considered. A naive breeder that is parasitized during the learning period may learn to recognize the parasitic egg as one of its own (Rothstein 1974). This cost, which we termed the "misimprinting cost," may increase the probability of accepting such parasitic eggs for the host's entire lifetime, and thus reduce the potential benefit of the rejecter strategy. The cost of misimprinting can be reduced if hosts have an innate preference to be imprinted on egg types that are similar to their own (see Lotem et al. 1995). On the other hand, the cost of misimprinting can be very high if the host learns to recognize only parasitic eggs and consequently rejects all of its own eggs. This situation is unlikely to occur in natural conditions because usually both egg types are present in a parasitized nest. Such a misimprinting cost, however, may be a major constraint on nestling recognition, where the probability of having only the parasitic nestling in the nest is relatively high (Lotem 1993). The cost of misimprinting can greatly complicate the model illustrated in fig. 12.1. It may prevent first-time breeders from rejecting, and imposes a severe long-term cost on rejecters that were parasitized during their first breeding. In such circumstances learned recognition may become maladaptive (see Lotem 1993 for a specific model treating this case; also McLean and Maloney, this vol.).

POSSIBLE TYPES OF EQUILIBRIUM

An evolutionary equilibrium resulting from the cost–benefit balance described above may be expressed in a host population in several ways.

An accepter host species

A "rejecter mutant" would not spread in the host population when the overall payoff of an accepter is, on average, greater than that of a rejecter, resulting in an accepter host species.

Intermediate rejection rate

In many parasite–host systems, both rejections and acceptances are exhibited within the host population (Smith 1968; Rothstein 1976; Clark and Robertson 1981; Cruz et al. 1985; Mason and Rothstein 1986; Davies and Brooke 1989a; Higuchi 1989; Soler and Møller 1990; Moksnes et al. 1990; Petit 1991; Lotem et al. 1992; Fraga, this vol.). Although most workers agree that some of

the cases (e.g., Smith 1968; Rothstein 1976; Clark and Robertson 1981) are likely to represent an evolutionary equilibrium, evolutionary lag is still a common explanation for most other cases. Under the arms race–evolutionary lag concept, the coexistence of rejections and acceptances represents a dimorphic population in which rejection has not yet reached fixation (Kelly 1987; Davies and Brooke 1989b), a monomorphic population in which rejection is not yet well developed (Davies and Brooke 1989b), or a combination of the two. Alternatively, such intermediate rejection rates may represent the following types of evolutionary equilibria:

A genotypic model

Two genotypes, rejecter and accepter, may coexist in the host population if they are equally adaptive. Coexistence can be stable as a result of a frequency-dependent mechanism in which rejecters have an advantage only when parasitism levels increase, but a high frequency of rejecters, in turn, reduces parasitism levels (May and Robinson 1985; Brooker and Brooker 1990). This mechanism can operate only in systems where there are costs when not parasitized and thus fluctuations in parasitism rate can change the direction of the selection (see above). It is also possible that such changes in selection could be maintained by annual fluctuations in other ecologic factors, such as food abundance or nest site availability, which can affect the cost and benefit balance of the two genotypes (Petit 1991). For example, in years when the host population is dense, nest sites may be limited and thus the cost of desertion might be higher. Food abundance, on the other hand, may affect the intensity of the competition between the parasite and the host nestlings and can thus affect the cost of parasitism.

Mixed strategy — a conditional response

In systems where being a rejecter is better on average than being an accepter, a conditional response may evolve if, under some circumstances rejection is more costly than acceptance. In such cases a rejecter mutant, which suppresses the rejection behavior when it results in a net cost, should spread in the host population. For example, in a case where hosts reject by nest desertion, and late in the season renesting success becomes lower than that of a parasitized nest, the mixed strategy "reject early in the season and accept at the end of

the season" should be better than rejection. While such conditional (phenotypic) behavior would be the best strategy for the host, it might also give the parasite some opportunities to be successful. More examples of conditional response will be discussed later in this chapter.

Genotypic variability in the adjustment of the conditional response

The adjustment of the conditional behavior (or, in other words, the reaction norm to parasitism) is likely to be based on some genetic rules that were favored by selection. When the system's conditions (i.e., parasitism frequency, rejection cost, etc.) fluctuate, different adjustments (reaction norms) will be favored under different conditions. For instance, if we take the example discussed above, in some years, the best rule can be "reject during May and June but accept in July," whereas in other years it woud be "reject during May but accept during June and July." If an optimal mechanism, which monitors all possible changes in the system and modifies the adjustment of the conditional rules accordingly, is impossible or too costly to develop, the suboptimal result might be a genotypic variability in the adjustment of the conditional behavior. Such genetic variability in reaction norms can be stabilized in the population as a result of changes in the direction of selection as suggested for the genotypic model (see above).

EVIDENCE FOR EQUILIBRIUM IN AVIAN BROOD PARASITISM

Measuring the costs and benefits

Measuring the costs and benefits of egg rejection, and then entering the measured values in the theoretical model (fig. 12.1), provides a critical test of the equilibrium hypothesis. There is one case in which such direct measurements clearly suggest that the acceptance of a parasitic egg under some circumstances represents an evolutionary equilibrium (Smith 1968). However, this case is an exception, because it is the only one reported in which under certain circumstances being parasitized is advantageous $(X - PC > X)$, and then, obviously, there is no value in rejection.

Among systems in which parasitism is deleterious and yet accepted by the host, there is no single study in which all costs and benefits of egg rejection have been measured and can be used for a critical test of the model. Several studies provide measurements of ejection cost due to egg breakage (Rothstein 1976*a*, 1977; Davies and Brooke 1988; Rohwer et al. 1989), of the frequenty of recognition errors in parasitized nest (Molnar 1944; Davies and Brooke 1988), and of the success rate of renests after deserting or burying a parasitized clutch (Clark and Robertson 1981; Burgham and Picman 1989). In a recent study of a cuckoo host (Lotem et al. 1995), we attempted to provide data on all rejection costs and benefits, including the cost of desertion, the "mafia" probability, and the probability of making recognition errors in parasitized and nonparasitized nests. However, as we explain below, some direct measurements might be misleading if host response is conditionally determined.

The problem of conditional behavior

In a conditional response, the host suppresses the rejection behavior when rejection is more costly than acceptance. However, the cost selecting for the conditional behavior cannot be measured because the host becomes an accepter, and avoids the cost of rejection. Ignoring this problem could lead to underestimating the relative cost of egg rejection because what will be measured is only the costs and benefits under the circumstances in which rejection is adaptive. For example, the response of great reed warbles *Acrocephalus arundinaceus* toward cuckoo eggs was found to be conditionally determined according to the host age (Lotem et al. 1992, 1995). Most rejecters were likely to be experienced breeders. In such a case, direct measurements of costs and benefits might be irrelevant; measuring the frequency of recognition errors made by adult rejecters would not indicate the cost that naive breeders might have to pay if they tried to discriminate between egg types. This problem does not exist if rejecters and accepters are two different genotypes. In this case direct measurements of rejection costs and benefits will reliably reflect the fitness of each genotype. Hence, knowing whether the two strategies in a population represent different genotypes or a conditional response is an essential prerequisite for conducting direct measurements of rejection costs and benefits.

In some cases, the problem of conditional response can be solved by experimental simulation of egg rejection. By removing the parasitic egg from a parasitized nest, one can measure the potential benefit of rejection and the "mafia" probability (see Lotem et al. 1995). For measuring

the cost of desertion, parasitized nests can be destroyed to force renesting. However, it is not possible to measure directly the cost of egg ejection (due to egg breakage), or the probability of recognition errors, when the host itself does not perform the rejection. Unfortunately, without these values the model cannot provide a conclusive test of the equilibrium hypothesis.

Can the costs outweigh the benefits?

Although measuring the costs and benefits of egg rejection has not yielded complete quantitative results, the available data can help to assess whether equilibria seem reasonable. By entering the known values into the proposed model (fig. 12.1), one can calculate the unknown values required to create an equilibrium. For example, using the model with data collected in our study of great reed warblers in central Japan, we provided a range of conditions in which the cost of recognition errors can outweigh the benefit of rejecting a cuckoo egg (Lotem et al. 1995). Because we found no evidence for a mafia effect, and no major differences between the payoffs of rejection by ejection, by nest desertion or by egg burial, we simplified the original model (fig. 12.1) as illustrated by table 12.1. The equations derived from table 12.1, and describing the overall payoffs of each strategy are: $(1 - p)X$ for accepter, and: $p(1 - e)(X - 1) + (1 - p)(1 - e)X + (1 - p)e(X - 1)$ for rejecter, where "p" is the probability of being parasitized, "X" is the clutch size (usually four or five eggs), and "e" is the frequency of recognition errors in parasitized and unparasitized nests. Based on these equations, the minimal frequency of errors required to justify acceptance (i.e., to make accepter and rejecter payoffs equal) is given by: $e = (p - pX)/(2p - pX - 1)$, and illustrated by
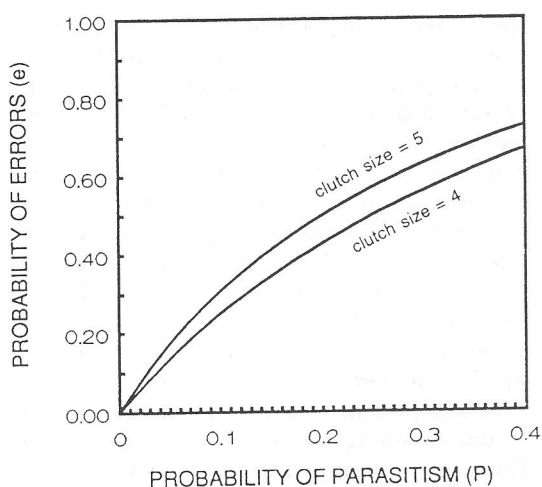

Figure 12.2 The minimal frequency of errors (e) required to justify acceptance for a given rate of parasitism (p), assuming clutch size of four and five eggs. (Based on Fig. 8 in Lotem et al. 1995.)

fig. 12.2 (see Lotem et al. 1995 for more details). The results of the model suggest that under parasitism frequency of 20%, the frequency of errors required to justify acceptance should exceed 43% (when $X = 4$) or 50% (when $X = 5$). On the other hand, if parasitism rate is around 1–5%, even an error frequency of 3–14% (when $X = 4$) or 4–18% (when $X = 5$) can make acceptance by a better strategy than rejection. Among cuckoo hosts in Europe, Britain, and Japan, local parasitism frequency can be as high as 20% or more (Wyllie 1981; Davies and Brooke 1988; Nakamura 1990; Rothstein 1990). Yet, it is likely that the regional parasitism frequency among many cuckoo hosts, and also in great reed warblers in Japan, is only around 1–6% (Moksnes

Table 12.1 The possible events and payoffs following acceptance and rejection of a common cuckoo egg by great reed warblers in Nagano, Japan

Strategy	Event	Payoff
Accepter	Parasitized	Zero
	Nonparasitized	Full clutch
Rejecter	Parasitized and rejected correctly	Full clutch − 1 egg
	Parasitized and rejected its own egg	Zero
	Nonparasitized, no error	Full clutch
	Nonparasitized and rejected its own egg	Full clutch − 1 egg

The overall payoff of each strategy is the sum of all the payoffs, each multiplied by its probability of occurrence. (See text and Lotem et al. 1995, for more details.)

and Røskaft 1987; Davies and Brooke 1989*b*; Lotem et al. 1995). If this is the case, the frequency of errors required to justify acceptance should not be very high (see fig. 12.2). In Europe, where cuckoo egg mimicry is well developed, the frequency of recognition errors in parasitized nests was measured as 15% (2/13) in reed warblers *Acrocephalus scirpaceus* (Davies and Brooke 1988), and 28% (13/46) in the great reed warbler *A. arundinaceus* (Molnar 1944). Although these data may not reflect the risk of recognition errors in nonparasitized nests, they suggest that an equilibrium in such systems is possible.

Similar calculations can be made for hosts of the brown-headed cowbird *Molothrus ater.* These may suggest that an equilibrium due to ejection or desertion costs is a reasonable hypothesis for hosts that do not lose most of their young when parasitized [e.g., song sparrow *Melospiza melodia* (Smith 1981), red-winged blackbird *Agelaius phoeniceus* (Røskaft et al. 1990), and prothonotary warbler *Protonotaria citrea* (Petit 1991)], but not for hosts that usually lose all of their young when parasitized (Rothstein 1990).

Another case in which the rejection costs might outweigh the benefits is that of the redhead duck *Aythya americana*, which parasitizes the canvasback *A. valisineria* (Sorenson, this vol.). In this case, the cost of parasitism cannot be recovered by egg ejection because host eggs are displaced from the nest during the parasite's egg laying (PC = PLD = 22.9%). Desertion of parasitized nests occurs only rarely, typically when there is a sudden reduction in the number of eggs in the nest or when the female is parasitized many times in a short period. In most cases, the cost of desertion may exceed the cost of parasitism because nest success of canvasback ducks may decline rapidly and substantially during the breeding season (Sorenson 1991).

In conclusion, the available measurements of rejection costs and benefits allow the equilibrium hypothesis to be supported or rejected only in a few cases. However, an equilibrium is as reasonable an interpretation as evolutionary lag for many of the cases in which hosts do not reject parasitic eggs.

Adaptive rules in the occurrence of rejections and acceptances within a host population

Strong support for the equilibrium hypothesis comes from several lines of evidence related to adaptive conditional rules evident from host responses. The conditional response model makes a unique prediction. Contrary to the genotypic model (either in equilibrium or during evolutionary lag), the conditional response model predicts that the occurrence of rejections and acceptances will not be random, but follows some adaptive rules (i.e., accept when rejection is too costly and reject when it is not). Evidence for a strong conditional effect would mean that the genotypic model cannot be the sole explanation for acceptance behavior. Such evidence is also likely to point out the factors selecting for the observed conditional behavior. The following are several examples in which host response was found to be conditionally determined and therefore a compromise among selective pressures.

Conditional response in relation to the time of parasitism

Yellow warblers *Dendroica petechia* are more likely to reject a cowbird egg (either by nest desertion or by egg burial) if it is laid early in the breeding season, or early during the host laying stage (Clark and Robertson 1981; Burgham and Picman 1989). These two conditional rules appear adaptive considering the changes in the cost-and-benefit balance under the different circumstances. The chances for a yellow warbler to renest successfully decrease toward the end of the breeding season (Clark and Robertson 1981), which implies a higher cost of desertion or egg burial that would make acceptance adaptive. Accepting a cowbird egg laid late in the host laying stage could be adaptive because the hatching probability of such an egg, like the cost of parasitism if it does eventually hatch, is relatively low (Rothstein 1976; Clark and Robertson 1981). When desertion or egg burial produces more costs than benefits, egg ejection might be an adaptive alternative. The lack of ejection in yellow warblers, however, might be due to high ejection costs incurred when small hosts try to use their small beak for ejecting cowbird eggs (Clark and Robertson 1981; Rohwer and Spaw 1988).

High acceptance rate during late incubation has been found recently also for a cuckoo host species. Moksnes et al. (1993) have shown that meadow pipits *Anthus pratensis* are more likely to accept cuckoo egg models introduced into their nests during late incubation. Moksnes et al. (1993) suggested that cuckoo eggs laid during late incubation are less likely to hatch, and that accepting them may be better than deserting a nest in a

habitat where the breeding season is short and renesting is almost impossible. The inability of meadow pipits in this study to reject by egg ejection is yet to be explained.

Conditional response in relation to nest site availability

The tendency of prothonotary warblers *Protonotaria citrea* to desert nests parasitized by brown-headed cowbirds was higher when more than three nest sites were available in the territory (Petit 1991). Petit suggested that this relationship between desertion and the opportunity to renest following desertion, supports the view that under certain circumstances acceptance of cowbird parasitism may be adaptive because the cost of desertion is greater than the cost of parasitism. As with yellow warblers, egg ejection might not have evolved in prothonotary warblers because of the costs incurred when a small host tries to eject a cowbird egg from a nest cavity (Petit 1991).

Conditional response in the bay-winged cowbird

The bay-winged cowbird *Molothrus badius* does not discriminate between its own eggs and the eggs of its parasite, the screaming cowbird *M. rufoaxillaris*, based on differences in their appearance (Fraga, this vol.). Fraga suggested that discrimination has not evolved mostly because of the high risk of recognition errors in the poor light conditions of the host nests. Fraga (this vol.) found that bay-winged cowbirds may reject an entire clutch or decide to incubate it, according to the clutch size. Clutch size apparently is a good indicator of the proportion of parasitic eggs in the clutch, and thus of the expected parasitism cost. Following this decision rule therefore seems adaptive, and may be the best attainable solution in the absence of egg recognition.

Age, experience, and the cost of recognition errors

Acceptance of cuckoo eggs by great reed warblers in central Japan occurs mainly among the younger breeders (Lotem et al. 1992). These findings led us to suggest that the cost of mistakenly rejecting an odd egg from unparasitized nests selects for greater tolerance toward divergent eggs in young breeders. This cost also favors a prolonged learning mechanism in which a host can learn to recognize the range of variation of its own eggs. Further experimental work (Lotem et al. 1995) indicated that a learning mechanism is indeed involved, and that intra-clutch variability in egg coloration is higher among young females (suggesting that the risk of recognition errors is especially high for them). It therefore seems that acceptance of cuckoo eggs by young breeders can be explained as a compromise between the cost of parasitism and the cost of recognition errors.

Stimulus summation and the cost of recognition errors

Whereas American robins, *Turdus migratorius*, usually accept experimental eggs that differ from their own eggs in any one of the three parameters that differ between robin and cowbird eggs, they reject eggs that differ in any two of these parameters. Rothstein (1982b) suggested that such stimulus summation prevents recognition errors due to unusually sized or colored robin eggs, ensuring that only a highly divergent egg such as that of the cowbird will be rejected. Among cuckoo hosts, where egg mimicry is well developed, a stimulus that increases rejection probability is the sight of a cuckoo near the nest (Davies and Brooke 1988; Moksnes and Røskaft 1989; Moksnes et al. 1993). Interestingly, although the sight of the cuckoo cannot be helpful in deciding which egg to eject, it usually stimulates the host to eject the right one (Davies and Brooke 1988). This implies that in some of the cases, the host has the ability to identify the cuckoo egg, but suppresses its rejection behavior in the absence of the second stimulus. The evolution of such a mechanism cannot be explained without considering a counterselection pressure that could justify acceptance. The fact that the second required stimulus is the sight of the cuckoo near the nest, suggests that this selection factor is the cost of recognition errors (i.e., ejecting own eggs) when not parasitized.

To test this hypothesis experimentally, Davies and Brooke (1988) presented reed warblers with a stuffed cuckoo (the second stimulus) but with no cuckoo egg model at the nest. If reed warblers could be fooled by a stuffed cuckoo and reject some of their own eggs, it would indicate that the risk of recognition errors is real, and suggest that the stimulus summation mechanism is an adaptation to minimize this risk. Davies and Brooke's results showed that only two out of 16 hosts mistakenly ejected or deserted their own eggs in this experiment. Yet, this value (2/16) is relatively conservative because even when in another

experiment, the two stimuli were provided (a mimetic cuckoo egg model and a stuffed cuckoo near the nest) only 47% (17/36) of the hosts exhibited rejection (Davies and Brooke 1988). Because only hosts that tend to reject mimetic eggs are faced with the risk of making mistakes, it seems more appropriate to evaluate the two cases of recognition errors in relation to these 47% of the tested birds. Accordingly, the rate of recognition errors prevented by this stimulus summation mechanism might be as high as 25% (two out of the 47% rejecters among the 16 tested birds). In any event, it seems that if hosts did not suppress their intolerance toward slightly divergent eggs, they would be likely to make recognition errors in about 10–25% of the nonparasitized nests. As was discussed in the previous section, such a rate of recognition errors may be sufficient to maintain an equilibrium. In other words, a host that detects a suspicious egg in the nest but fails to detect the cuckoo near the nest may do better by accepting the suspicious egg than by rejecting it. More such experiments with larger sample sizes could further support this view.

Comparative evidence for equilibrium

A comparative approach might be helpful in testing whether or not host responses toward parasitic eggs are adaptive. Some of the following comparative evidence is consistent with the evolutionary equilibrium view.

Rejection rates: cowbird hosts vs. cuckoo hosts

The hypothesis that the cost of recognition errors selects for some level of acceptance among common cuckoo hosts (see above) is supported by a comparison between cowbird and cuckoo systems. In contrast to cuckoo hosts, most cowbird hosts that exhibit egg rejection ("rejecter species") attain rejection rates of 90–100% (Rothstein 1975a, 1990, fig. 1). There are indications that some cowbird hosts learn to recognize their eggs from the first egg laid, and therefore even a yearling can reject (Rothstein, 1974, 1978). This may be possible because cowbird eggs usually differ greatly from the eggs of their host (Rothstein 1975a), and parasitism rates among cowbird hosts are usually higher than among cuckoo hosts (Rothstein, 1975b; Davies and Brooke 1989b). Discrimination is therefore easy and the risk of error is relatively low. Under these conditions, a prolonged learning mechanism

is not necessary, and a stimulus summation mechanism should not suppress rejection of a parasitic egg.

Differences between populations

Soler and Møller (1990) showed that magpie *Pica pica* discrimination against mimetic cuckoo eggs was most pronounced in an area of ancient sympatry, whereas nonmimetic eggs were discriminated against both in areas of recent and ancient sympatry. They suggested that this might be explained by: (i) differences in the duration of sympatry (because rejection of mimetic eggs evolves in a later stage of the evolutionary arms race); and (ii) gene flow from the area of ancient sympatry and selection against rejecting mimetic eggs in the absence of the parasite (which used to be the situation in the area of recent sympatry). The second explanation, if correct, suggests that a recognition cost selected against sensitive discrimination ability when parasitism was rare or absent. This may explain why also in the area of ancient sympatry, magpies still accept some of the mimetic cuckoo eggs (Soler 1990).

Zuniga and Redondo (1992) provided additional data on these two particular populations and argued that there is no evidence for differences in the duration of sympatry between the two. Alternatively, they suggested that the higher rejection frequency in one of the populations is associated with a higher parasitism rate and a higher cuckoo density. This new interpretation of the system is also consistent with an equilibrium scenario: rejection of mimetic eggs is more likely to entail recognition errors and is therefore justified only where parasitism rates are sufficiently high.

Egg rejection by favorite and rarely used hosts

Davies and Brooke (1989a) found that among suitable common cuckoo hosts, rarely used hosts exhibit higher rejection rates of nonmimetic eggs than current favorite hosts. They raised the possibility that suitable species that are now rarely used are former cuckoo hosts that evolved strong rejection ability, whereas the current favorite hosts are still in an earlier stage of their arms race with the cuckoo (Davies and Brooke 1989b). Similar results have been presented by Moksnes et al. (1990) who argued that this trend is actually predicted by the arms race model. However, although these findings can be explained by the arms

race model, they are also very much consistent with the idea of an evolutionary equilibrium. Hosts that are faced with relatively high rejection costs, as a result of their life history and ecologic circumstances (e.g., small bills, high desertion cost, or constraints on reducing egg variability within a clutch), are likely to accept cuckoo eggs more frequently and should therefore be favored by cuckoos. On the other hand, hosts that are able to attain higher rejection rates should be used by the cuckoo only rarely in the absence of better alternatives. An additional way to explain these findings as an evolutinary equilibrium is that, at present, rarely used hosts are secondary hosts for the cuckoo, and as such they are likely to be parasitized with nonmimetic cuckoo eggs. Under these conditions their best strategy might be to behave like some of the cowbird hosts that learn to recognize their eggs quickly from the first egg laid (see above). This strategy may allow them to attain high rejection rates of nonmimetic eggs (e.g., 80–100%) but very low rejection rates of highly mimetic eggs (e.g., 0–10%). The current favorite hosts, on the other hand, may adopt a prolonged learning strategy that causes them to exhibit lower rejection rates of nonmimetic eggs (e.g., 50–80%, because naive breeders tend to accept them) but higher rejection rates of mimetic eggs (e.g., 10–30%). This idea can be tested by comparing the response of all these host species to mimetic eggs.

CONCLUSIONS

When considering the available data on avian brood parasitism, the evolutionary equilibrium model seems to be both a reasonable option, and a concept supported by several lines of evidence. At least three species of cowbirds, two species of cuckoos, and one parasitic duck appear to have at least one host species that accepts their eggs as a result of an evolutionary equilibrium. Whereas in one of these examples rejection yields no benefit (Smith 1968), in the others acceptance may be favored by selection because of rejection costs. We believe that these cases are not exceptions, but, rather, represent a general phenomenon. The fact that rejection costs seem to favor some level of acceptance among yellow warblers and prothonotary warblers, suggests that such costs could favor complete acceptance (i.e., being an accepter species) among some other cowbird hosts. The risk of recognition errors may justify acceptance in many systems in which egg or nestling mimicry is involved. This might be true for a broad range of cuckoo hosts and for estrildid finches (Nicolai 1974). Yet, direct evidence for recognition errors in unparasitized nests is rare, and the importance of such errors is suggested mainly by indirect evidence (i.e., host conditional behavior and comparative evidence). Additional data on recognition errors are therefore needed to support further the equilibrium view.

It could be expected that a parasite might benefit from an evolutionary lag in host responses upon interacting with a new host population or with a new host species. In such a case the parasite is likely to be more successful, to increase in numbers, and to impose relatively high selection pressures on the host (Nakamura 1990; Soler and Møller 1990). An evolutionary lag is very likely to be the case in many passerine hosts recently exposed to the expanding cowbird population in North America and to the increasing intensity of parasitism (Rothstein and Robinson 1994). It is also possible that host response would not always be optimal because parasitism rates may fluctuate, ecological conditions may vary from year to year, and because young hosts may disperse into different environments. However, the fact that in several hosts some level of acceptance can be favored by selection, suggests that these hosts provide a stable niche for the parasite, and thus its existence no longer depends upon evolutionary lag.

In conclusion, we believe that the view that avian brood parasitism reflects a continuing evolutionary arms race, and that most variations between systems represent different stages on an evolutionary time scale, is oversimplified. The real picture seems to be composed of a mosaic of evolutionary stable and unstable systems. Possibly, the number of systems that have reached evolutionary equilibrium is far greater than was previously thought.

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