

Successes and Failures in Avian Egg and Nestling Recognition With Comments on the Utility of Optimality Reasoning¹

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SYNOPSIS. Interactions between parasitic birds and their hosts provide some of the best examples of recognition that has obvious and strong adaptive value. But these interactions also involve numerous failures of recognition that result in enormous losses in fitness. The failures are more significant than the successes because they are exceptions to basic evolutionary theory which predicts that organisms behave optimally. The egg recognition behavior of North American passerines separates species into two discrete groups. In "rejecter" species nearly all individuals are intolerant of nonmimetic parasitic eggs. In "accepters" nearly all individuals tolerate such eggs. Rejecters possess a true recognition of their own eggs, apparently learning this in an imprinting-like process. No adaptive explanation accounts for the lack of rejection in accepter species. Many of these species are victimized heavily by parasitic cowbirds and have eggs divergent from those of the cowbird. They readily accept clutches containing only cowbird eggs. But accepters do show egg recognition in some contexts. They abandon clutches whose total volume of eggs falls below a critical value; they eject and visually discriminate among eggs that are broken, thus showing that they are capable of the critical behaviors needed to reject parasitic eggs. Since most accepters occur in taxa that also contain rejecters, I propose that stochastic processes are largely responsible for their nonoptimal behavior. Even though many birds reject parasitic eggs, all or nearly all accept nonmimetic parasitic nestlings, a situation for which there is no reasonable optimality explanation. Although these recognition studies demonstrate the value of optimality reasoning because they are based on clearly defined predictions arising from the expectation of adaptiveness, they also demonstrate some general problems inherent in optimization models. It is argued here that while optimality reasoning is the best and most all-inclusive paradigm in biology, its value will be enhanced if its limitations are recognized. When warranted, conclusions of non-optimality should be stressed and optimality itself should be tested and not employed only as an assumption used to formulate hypotheses.

INTRODUCTION

Unless it is directed solely at elucidating proximate physiological mechanisms, any study dealing with recognition, or virtually any biological phenomenon, is likely to touch upon the concept of adaptiveness. Although the notion of adaptiveness pervades all of the biological sciences, it is a concept that is usually difficult to apply in a rigorous fashion. While intuitively appealing, adaptive or optimality hypotheses are often difficult to test because they tend to consider a trait in isolation from the rest of the organism. Further, many adaptive explanations depend upon subtle processes that an organism may not be capable of carrying out and usually the degree of putative adaptive advantage cannot be quan-

tified and hence may be so slight as to be unimportant.

However, some systems allow relatively straightforward studies of adaptiveness. They involve strong selective pressures that are easily identified, present various options among which some are clearly superior and depend upon behavioral or other processes that are undoubtedly feasible for the organisms in question. Some systems of brood parasitism present such features. In this type of life history, one species—the host—cares for the offspring of another—the parasite. Typically, this is done at great cost to the host's own reproduction so some sort of recognition and antiparasite action should occur under the expectations of optimality. Some hosts show acute discrimination but, remarkably, others show little or no recognition even though parasitic and host offspring have obvious differences.

A lack of recognition can be understood

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somewhat in socially parasitic insects. In these systems many hosts and parasites show obvious morphological differences that we can easily perceive visually; but the hosts communicate largely via olfactory and tactile means and the parasites have essentially broken the hosts' communicatory code by developing similar or identical signals (Hölldobler, 1971). In the case of avian brood parasitism though, the hosts interact with their young largely via vision (and to a lesser extent, audition), yet major differences often exist between parasites and hosts even in the visual communicatory channel. In this paper, I deal with the types of recognition or lack thereof that birds show towards eggs and present some comments on nestling recognition. I have three objectives: 1) to review recent work on recognition, mostly of eggs, that relates largely to host defenses against parasitic birds; 2) to add new data to this literature; 3) to discuss the failures of recognition and what these imply about the reliability of formulating hypotheses based on the assumption that organisms perform in an optimal fashion.

The word "optimal" is not being used here to convey the notion of absolute perfection but to convey the idea that organisms come as close to perfection as one could reasonably expect given the particular constraints on their evolution. The value of optimality reasoning, which Gould and Lewontin (1979) call the "adaptationist program," is controversial. Critics such as Gould and Lewontin argue that the paradigm is nearly tautological whereas others (Maynard Smith, 1978) strongly endorse it. My position is somewhat intermediate. The egg recognition studies I present demonstrate the valuable contribution that optimality reasoning can make to the formulation of testable hypotheses. But at the same time, these studies demonstrate that some systems seem to be far from optimal and thus that a rigid insistence on adaptive explanations is likely to be counterproductive. Furthermore, although both critics and supporters of optimality reasoning agree that adaptiveness itself cannot be tested and that the concept can be used only as an assumption that helps us to for-

mulate hypotheses, I hope to show that there are instances in which the expectation of adaptiveness can be tested directly.

THE DICHOTOMY BETWEEN ACCEPTER AND REJECTER SPECIES

To assess how hosts respond to parasitic eggs, I developed an experimental approach that simulates parasitism by the Brown-headed Cowbird (*Molothrus ater*). This species, the only parasitic bird widespread in North America, is a generalist that has been reared by at least 139 of the 216 species it is known to have parasitized (Friedmann *et al.*, 1977, p. 5). My objective in the experimental parasitizations was to ascertain the frequency with which various species reject cowbird eggs and to determine whether certain factors, such as recency of sympatry with the parasite, serve as reliable predictors of the nature of antiparasite defenses. I also wanted to determine whether an intensive study of adaptations in one coevolving system might provide insight into the evolution of adaptations in general.

An experimental approach is essential to any rigorous determination of host rejection (Rothstein, 1975a) because observing naturally parasitized nests leaves many variables uncontrolled. If, for example, hosts rapidly eject parasitic eggs then most such eggs may disappear before observers see them and the prevalence of this defense will remain unknown. In most cases, cowbirds deposit one egg per nest and remove one host egg (Friedmann, 1963) so I did likewise in my experiments. Usually I used artificial cowbird eggs cast in plaster of Paris; the properties of these eggs, as well as various controls for their artificiality, are described elsewhere (Rothstein, 1975a, b). Experimentally parasitized nests were checked periodically to determine the "hosts'" responses. Three types of events were assumed, *a priori*, to constitute rejection: ejection—all host eggs present but experimental egg missing; egg damage—due presumably to attempted ejections; nest desertion—all eggs present but birds no longer in attendance.

I added single cowbird eggs to 607 nests of 43 species. The experiments showed,

surprisingly, that in most species nearly all of the individuals accept cowbird eggs. In the remaining species nearly all the individuals reject them, nearly always by ejection (Rothstein, 1975a, 1977). Hence species were easily divided into "accepters" and "rejecters" and a frequency distribution of % rejection shows significant bimodality with most species clustered near zero or 100% rejection (Rothstein, 1975c). Numerous experiments on additional species have strengthened this acceptor-rejecter dichotomy (Rothstein, unpublished). Species with intermediate rejection rates may be rare because rejection usually has such a high adaptive value that it rapidly approaches fixation after its initial appearance. Models that quantify the selective value of rejection support the interpretation of rapid fixation (Rothstein, 1975c).

The perplexing aspect of the rejecter-accepter dichotomy is that no factor likely to be important to the evolution of host defenses serves as an overall predictor of each species' status (although some factors may apply for a restricted subset of species). The rejecters, for example, have had long histories of sympatry with the cowbird but so have nearly all of the accepters. With only a few exceptions, accepters and rejecters have eggs that diverge strongly from those of the cowbird. If some feature of a species' biology increases the likelihood that it will evolve rejection, then rejecters and accepters should sort out along taxonomic lines, but no such trend exists. Four of seven passerine families with two or more species tested experimentally contain both rejecters and accepters (Rothstein, 1975a) as do at least two genera (*Icterus* and *Toxostoma*) in unrelated families (Rothstein, unpublished data). Other factors in addition to sympatry, egg appearance and taxonomy similarly fail to separate accepters and rejecters.

The one generalization that does seem to hold is that species not subjected to brood parasitism rarely if ever show rejection because egg recognition has no adaptive value in the absence of parasitism (except in special circumstances, *e.g.*, Tschantz, 1959). Few parasitic birds victimize nonpasserines and such nonpasserine groups as the An-

seriformes, Columbiformes, Ciconiiformes, Procellariiformes and Charadriiformes have been the subject of numerous studies that failed to demonstrate strongly expressed rejection behavior (Allen and Mangels, 1940; Poulsen, 1953; Tinbergen, 1960; Beer, 1961; Bartholomew and Howell, 1964). But many North American accepters are subjected to intense parasitism that results in manifest losses in fitness. The best explanation for the acceptor status of such species and for the acceptor-rejecter dichotomy is one that is unfortunately essentially untestable. I suggest that stochastic processes are major factors determining each species' status. Some species have had the appearance of suitable mutations or recombinations that code for rejection and that selection could act upon. These have evolved into rejecters. Other species have remained accepters because suitable genetic variants have not yet appeared. Later, I discuss the consequences of this explanation which admits that accepters are far from an optimal state. Below, I also discuss, but reject, alternative optimality explanations that assume it is adaptive for accepters to tolerate cowbird eggs. Besides their different responses to single foreign eggs, accepters and rejecters show other differences in their egg recognition behavior. These differences, as well as some similarities, are presented in the next two sections.

THE EGG RECOGNITION BEHAVIOR OF REJECTER SPECIES

Do rejecters really practice egg recognition?

Data showing the nearly total intolerance rejecters express towards cowbird eggs are fairly conclusive, *e.g.*, artificial or real cowbird eggs were rejected at 50 of 53 Gray Catbird (*Dumetella carolinensis*) nests and at each of 33 Eastern Kingbird (*Tyrannus tyrannus*) nests. But such results do not necessarily demonstrate recognition. Parasitic eggs may differ from host eggs in two ways, their appearance—coloration and size—and by the fact that they are outnumbered by the more numerous host eggs, *i.e.*, they are discordant. Rejecters could reject either by recognizing their eggs or those of the

parasite, mechanisms I call "true egg recognition" or TER, or by acting against any egg that is in the minority. The latter mechanism involves no recognition and is termed "rejection via discordancy" or RVD.

Experiments Rensch (1925) conducted on European passerines have long been interpreted as demonstrating RVD and it has been assumed that birds do not know their own eggs. However, numerous experiments on North American passerines showed TER. I experimented upon Gray Catbirds and American Robins (*Turdus migratorius*) by replacing all or all but one of their eggs with artificial cowbird eggs or the real eggs of another species, thereby creating situations in which foreign eggs were the majority type. The birds ejected only the foreign eggs and left their own egg, if present, at each of 17 catbird nests and at 15 of 21 robin nests. The six remaining robin nests gave no evidence for either TER or RVD (Rothstein, 1975b). Comparable experiments at one or two nests of four other rejecter species also demonstrated TER (Rothstein, 1975b, 1977) as did Victoria's (1972) data on a species of African weaverbird. Lastly, a re-analysis of Rensch's data demonstrated TER in nearly all of his experiments that yielded clear results (Rothstein, 1975b).

The generalization that rejecters practice TER and do indeed know their own eggs is strengthened by new data on an additional rejecter, the Loggerhead Shrike (*Lanius ludovicianus*). This species is an especially good choice for experiments designed to distinguish between TER and RVD because its unusually large clutch of five to seven eggs allows situations in which the bird's own egg can be made highly discordant but in which clutch size remains constant. I added real Red-winged Blackbird (*Agelaius phoeniceus*) or Tricolored Blackbird (*A. tricolor*) eggs to 21 shrike nests to test between TER and RVD. Blackbird eggs are similar in size to shrike eggs (red-wings average 25 × 18 mm, tricolors 28 × 20 mm, shrikes 24 × 19 mm [Harrison, 1978]) but are colored very differently (see below). At 11 nests, I replaced all but one shrike egg with an equal number of blackbird eggs (Experiments 1 and 2, Ta-

ble 1). The four to six blackbird eggs were ejected and the single shrike egg remained in the nest in nine cases. At one nest the shrikes removed even their own egg (perhaps after accidentally breaking it, as it was the last egg to be ejected); at the last nest the shrikes accepted the blackbird eggs, eventually fledging at least one redwing! The remaining experiment involved a manipulation not done previously on any species. Blackbird eggs equal in number to a shrike's own eggs were added and no eggs were removed, resulting in oversized clutches of 10 to 14 eggs with no minority element. The shrikes ejected every blackbird egg at eight of nine nests and accepted all the eggs at only one (Experiment 3, Table 1). I watched the shrikes at some nests and discovered that their recognition was usually expressed almost instantly. At one nest in Experiment 3, all five blackbird eggs were ejected within 5 min and dropped at points 5–11 m from the nest.

Comparable experiments at two Scrub Jay (*Aphelocoma coerulescens*) nests also demonstrated TER. At one nest I replaced all but one of four jay eggs with artificial eggs close in size to the jay eggs but colored differently (egg type II, Fig. 1, Rothstein 1975b). At the second nest all but one of four jay eggs were replaced with real blackbird eggs. In both cases the jays ejected all the foreign eggs within 1½ hr and left their own egg in the nest. Thus these new data on shrikes and jays, along with those previously cited, leave little doubt as to the prevalence of TER. It remains to be seen whether any species routinely practices RVD.

Besides demonstrating TER, the data in Table 1 show that rejection is not limited to parasitic eggs. Shrikes nearly always ejected blackbird eggs, yet these have a blue ground color and elongated blackish marks and are very much unlike both shrike and cowbird eggs which have whitish or gray ground colors with brown or gray spots. Other data (Table IV in Rothstein, 1975b, unpublished) also show that rejection is not specific to parasitic eggs, so the egg recognition of rejecters must involve a behavioral process in which the birds recognize their own eggs and reject all eggs that di-

TABLE 1. Responses of Loggerhead Shrikes to large scale manipulations of their clutches.^a

Experiment	Clutch sizes	No. of nests	No. of nests showing true egg recognition	Results
1. All but one shrike egg replaced with blackbird eggs.	5-7	8	7	Shrikes at one nest accepted 5 blackbird eggs along with one of their own. ^b All blackbird eggs ejected from the seven remaining nests. The single shrike egg remained in each of these nests but all were deserted.
2. All but one shrike egg replaced with blackbird eggs. Shrike eggs returned to nest (after ejection of blackbird eggs) within 2½ hr after being removed.	6-7	3	2	All blackbird eggs ejected; the single shrike egg was also ejected from one nest (no. 75-23). Shrikes accepted the return of their eggs at two nests (one of which was 75-23) but deserted the third nest.
3. Blackbird eggs equal in number to shrike eggs added. No eggs removed.	5-7	9	8	Shrikes at one nest accepted 5 blackbird eggs along with 5 of their own. ^c All blackbird eggs ejected from the eight remaining nests and all shrikes continued to incubate their clutches.
4. All but one shrike egg removed. No eggs added.	5-6	5	— ^d	All nests deserted by the next nest check, which was from one to four days after clutch reduction.

^a Experiments were conducted 20-30 km north of Pozo, San Luis Obispo Co., California from 1974 to 1976.

^b Two of the blackbird eggs hatched after about 6 and 9 days and at least one redwing fledged.

^c Incubation of all 10 eggs proceeded for 6 days at which time I removed the blackbird eggs.

^d Experiment did not deal with the question of true egg recognition *versus* rejection via discordancy.

verge to a certain degree. Experiments on two species indicated that rejecters learn this recognition via an imprinting-like process when the birds breed for the first time (Rothstein, 1974, 1978). Other experiments show that there is no key parameter that rejecters use to discriminate between eggs. American Robins respond to ground color, markings and egg size (Rothstein, 1983).

Responses to partial clutch reduction

The TER experiments show a significant aspect of egg recognition that is largely unrelated to brood parasitism. Nearly all passerines desert their nest and lay eggs in a new one if all their eggs are removed. Optimality reasoning suggests that birds might also desert if they lose only some of their eggs, *i.e.*, if they experience partial clutch reduction or PCR, because the costs of building a new nest and laying a full sized

replacement clutch might be outweighed by the potential benefits of such a clutch. Birds that ejected foreign eggs and were left with only one of their own eggs in the TER experiments in this and previous studies (Rothstein, 1975*b*, 1977) always deserted their nests, due, as I will show, to PCR. These desertions are curious since it would have been more efficient for the birds to dispense with the ejections if they were going to abandon their nests. Either the ejections themselves were a disturbing factor that elicited desertion or two independent behaviors occurred in succession: 1) First the foreign eggs elicited ejection; 2) Then the fact that the clutch was severely reduced (but not totally so) elicited desertion, *i.e.*, a response to PCR. The shrike experiments on TER were designed to test between these alternatives and thus to determine experimentally if there is a response to PCR.

Experiments 1 and 3 (Table 1) provide a relevant comparison. In the latter, shrikes ejected five to seven blackbird eggs but still had their full clutch remaining. In Experiment 1 they ejected four to six blackbird eggs and were then left with only one shrike egg. Considering only nests at which the blackbird eggs were ejected, all seven of the Experiment 1 nests, but none of eight Experiment 3 nests were deserted, a significant contrast ($P \leq 0.001$ for 7–0 vs. 0–8, Fisher exact test, Siegel, 1956). Clearly, desertion in Experiment 1 was due to PCR and not to the ejections. This is suggested further by Experiment 2 in which I returned the shrikes' eggs after they ejected blackbird eggs. Desertion occurred at only one of three nests. Similarly, I returned the jay eggs after the foreign eggs were ejected in the two Scrub Jay experiments on TER cited above. In both of these cases the jays did not abandon their nests. Lastly, as a direct test for a response to PCR, I reduced five shrike clutches to one egg (Experiment 4, Table 1) eliciting desertion in every case. Thus in addition to recognizing individual eggs on the basis of their appearance, rejecter species are responsive to reductions in their overall clutch size.

Optimality and the compartmentalized nature of behavior

The experiments showing TER and a response to PCR demonstrate a fundamental aspect of animal behavior, the compartmentalized nature of most behavioral patterns. It is clear that rejecter species in my experiments responded independently to the presence of foreign eggs and to PCR, otherwise they would not have ejected eggs before abandoning their nests. In general animals do not respond to all aspects of a situation, as humans generally do, but rather they respond in a somewhat independent fashion to a limited number of stimuli. This point is of course not new. It was proposed by Whitman (1899) in his particulate theory of behavior and is central to Lorenz's (1937) concept of sign stimuli. This is not to say that animals are incapable of complicated behaviors. They may even have something akin to self awareness (Griffin, 1976) but we should al-

ways realize the limitations of animal behavior. Animals may respond to all of the factors going into the cost-benefit considerations of an optimality model but they are almost certain to do so in a relatively uncoordinated way that evinces a lack of understanding of the entire situation. The result may well be a response that is not as optimal as humans would predict.

THE EGG RECOGNITION BEHAVIOR OF ACCEPTER SPECIES

Alternatives to the nonoptimality explanation

My assertion that acceptor species are not behaving adaptively should be challenged, as is true of any nonoptimality explanation, because such challenges may lead to new data and insights. A species might fail to reject because it is protected by alternative defenses that make it unlikely that parasitism will occur. Some birds defend their nests against adult parasites but even among these species, many nests are parasitized (Robertson and Norman, 1977), so the alternative defense does not negate the high potential adaptive value of egg rejection. Another alternative explanation is that accepters fail to reject because parasitism is beneficial. Smith (1968) described a probable example of such a situation but the system is atypical (Payne, 1977) and even in it the parasitism is often demonstrably harmful. The "parasitism is good" hypothesis can be rejected as a general explanation for the behavior of acceptor species. North American ornithologists have a long tradition of careful nesting studies. Much to the chagrin of many investigators, the cowbird has played a significant role in many dozens of these studies, nearly all of which have demonstrated lowered reproductive output due to cowbird parasitism (Friedmann, 1963).

A modification of the "parasitism is good" hypothesis might be that host young that survive in the presence of parasites experience an elevation in quality that compensates for their reduced chances of survival. But there is no evidence for such a hypothetical occurrence. Indeed in many acceptor species the odds of any host nestling surviving parasitism are so small that such

survivors would literally have to be super-birds to compensate for their decreased chances of fledging, *e.g.*, only six host young fledged from 19 naturally parasitized Eastern Phoebe (*Sayornis phoebe*) nests that would have produced about 66 phoebes had the birds rejected (Rothstein, 1975c). Further, for many hosts improved quality of young reared with parasites is an untenable hypothesis because the parasitic nestlings routinely kill all of the host young by pecking them, as in some honeyguides and probably the Striped Cuckoo (*Tapera naevia*) or by pushing them from the nest, as in the Common Cuckoo (*Cuculus canorus*) (Payne, 1977; Morton and Farabaugh, 1979).

Although the “parasitism is good” hypothesis can be rejected, an alternative optimality explanation called the “rejection is worse than acceptance” hypothesis is worth considering. Accepters may behave as they do because even though parasitism is deleterious, the costs of rejecting it are worse. Zahavi (1979) speculated that a potential cost of rejection is inflicted by the parasite, which might return to parasitized nests and destroy all of the host’s offspring if its own egg or nestling is missing. There is no evidence that any parasite has this behavior. If the cowbird routinely “punished” reluctant hosts as Zahavi speculates, the fact would probably have been discovered long ago, since many investigators remove cowbird eggs from nests they are studying (*e.g.*, Knapton, 1978).

It is more likely that any costs of rejection that exist are inherent in the rejection process itself. Rejection by ejection is virtually costfree in most cases but a possible cost is mistaken ejection of the host’s own eggs if parasitic and host eggs are similar. However, most accepters have eggs that are highly divergent from cowbird eggs (Rothstein, 1975a) as is true of some hosts of the Common Cuckoo that usually accept non-mimetic eggs (Lack, 1963). Another potential cost of ejection is accidental damage to the host’s own eggs if the bird’s bill shape or size does not enable it to easily manipulate parasitic eggs. One rejecter species, the Cedar Waxwing (*Bombycilla cedrorum*), frequently damages its own eggs while re-

moving cowbird eggs (Rothstein, 1976) and has developed an apparent response to this cost. Among rejecters, only the waxwing shows a shift from mostly rejection if a cowbird egg appears early in the nesting cycle to mostly acceptance late in the cycle when a cowbird egg is unlikely to receive enough incubation to hatch. The bill shapes and sizes of nearly all accepter species suggest that their ejection capabilities are equal to or greater than those of the waxwing (Rothstein, 1975a). Thus they too should try to eject, but they do not seem to.

Acceptance or ejection with a probability of risk are not the only options. A bird can simply desert a parasitized nest and start all over again; nest desertion is common among naturally parasitized nests, although there is little evidence as to the specific stimuli that elicit desertion (Rothstein, 1975a). Nest desertion always incurs a cost since the birds must build a new nest and lay more eggs and these costs could be worse than parasitism. Of course an optimal and reasonable strategy for a host that cannot easily eject is to attempt to eject and to then desert if the ejection process causes the loss of too many of the bird’s own eggs. The Cedar Waxwing seems to do this but there is no evidence that accepter species follow this strategy.

The “rejection is worse than acceptance” hypothesis is undoubtedly false for hosts that lose all of their young due to parasitism, *e.g.*, the hosts of the honeyguides and cuckoos cited above and many of the smaller hosts of the cowbird. I suggest that the hypothesis is false for most other species as well, based simply on the ejection capabilities of hosts and how they are known to respond, *i.e.*, the lack of “attempt to eject then desert” strategies. Besides evidence based on inference, these hypotheses can fortunately be subjected to direct experimental tests. First, there is variation in the sizes of cowbird eggs and if ejection incurs a cost then a bird should be more likely to eject small cowbird eggs since these can be manipulated with relative ease. To test this expectation, I parasitized four accepter species with undersized cowbird eggs smaller than the birds’ own eggs. There were no significant differences between the

rejection rates of these undersized eggs and those of standard cowbird eggs (Rothstein, 1975a).

Secondly, the cost of parasitism varies, since a third of naturally parasitized nests receive two or more cowbird eggs (Friedmann, 1963, p. 12) and this is more detrimental than one cowbird egg. If accepters tolerate single cowbird eggs because the costs of rejection are greater than those of parasitism they should be more likely to reject, especially by nest desertion, as the intensity of parasitism increases. Such a conditional response has been described in some empirical studies of cowbird parasitism but the observations are open to various biases (Rothstein, 1975a, in preparation). To experimentally test for a conditional response, I parasitized two accepter species by replacing one host egg with one cowbird egg on each of two consecutive days. I found no evidence for a conditional response. Rejection occurred at three (3.3%) of 92 Red-winged Blackbird nests that received one cowbird egg and at one (6.7%) of 15 that received two. In the Eastern Phoebe there was rejection at three (6.0%) of 50 one-egg nests and at two (5.0%) of 40 two-egg nests.

Under optimality reasoning, accepters are more likely to show a conditional response if left with a clutch containing only cowbird eggs or cowbird eggs and only one egg of their own, situations that occur naturally. To test this expectation, I replaced all but one host egg with artificial cowbird eggs at some nests (Experiments 1 and 5, Table 2) and at others I replaced all of the host's eggs with artificial cowbird eggs (Experiments 2 and 4) or with the strongly nonmimetic real eggs of another species (Experiment 3). Experiments on one accepter, the Chipping Sparrow (*Spizella passerina*), employed undersized artificial cowbird eggs (17.3×13.6 mm) as well as standard ones because the latter are so much larger than sparrow eggs (21.1×16.3 mm vs. 18×13 mm [Harrison, 1978]) that a tendency to reject them might be outweighed by their possible stimulus value as supernormal stimuli (Tinbergen, 1960). These large scale clutch manipulations were accepted at 33 of 34

nests of two accepter species (Table 2) whose eggs contrasted strongly with the introduced eggs in both ground color and maculation (see Harrison, 1978). Experiments on other accepters produced similar results (Rothstein, in preparation). Clearly no optimality explanation can account for acceptance of clutches containing only foreign eggs. At the very least, birds accepting clutches containing none of their own eggs can be assumed to lack a conditional response to the common occurrence of multiple parasitism.

Thus, if species tolerate one nonmimetic egg—*i.e.*, are accepters—they accept clutches consisting solely of such eggs and thus exhibit little or no egg recognition. One complication enters into this generalization. Accepters are responsive to the overall egg volume in their nest. This is mediated through a response to PCR (next section).

Responses to partial clutch reduction

A response to PCR is apparently universal among both accepters and rejecters. Extensive experiments on Eastern Phoebes and Common Grackles (*Quiscalus quiscula*) and limited data on other accepters (Rothstein, in preparation) demonstrate the response and show that the likelihood of desertion is significantly correlated with the degree of PCR, as expected under optimality reasoning. Among grackles, for example, desertion occurred at only two of 23 nests that were reduced from four to three eggs but at each of five nests reduced from four eggs to one ($P < 0.01$).

Responses to PCR could be mediated via either "egg counting" or "volume assessment" mechanisms. In the former, desertion occurs when the clutch is reduced to some critical number of eggs. In the latter, the combined volume of eggs is the critical value. Egg number and volume are, of course, highly correlated, but not perfectly so. Experiments on grackles and phoebes indicate that accepters do not count eggs but instead employ the volume assessment mechanism (Rothstein, in preparation). Volume assessment produces the seemingly paradoxical finding that phoebes are less likely to desert if their four to six egg clutch

TABLE 2. Responses of accepter species to large scale manipulations of their clutches.^a

Species	Experiment	Rejections	Acceptances	Total nests	Results
Red-winged Blackbird	1. All but one egg replaced with standard artificial cowbird eggs (clutch size = 4)	0	5	5	All birds accepted the clutches for at least 6 days after which experiment was terminated or the remaining redwing egg hatched.
	2. All eggs replaced with standard artificial cowbird eggs (clutch size = 3 or 4)	0	7	7	All birds accepted the clutches for at least 6 to 17 days. ^b
	3. All eggs replaced with real Loggerhead Shrike eggs (clutch size = 3 to 5)	1	6	7	Birds at one nest ejected the eggs (or a predator removed them). The clutches were accepted at the six remaining nests for at least 7 to 19 days. ^b
Chipping Sparrow	2. All eggs replaced with standard artificial cowbird eggs (clutch size = 3 or 4)	0	5	5	All birds accepted the clutches for at least 6 to 13 days. ^b
	4. All eggs replaced with undersized artificial cowbird eggs (clutch size = 2 to 4)	0	7	7	All birds accepted the clutches for at least 7 to 18 days. ^b
	5. All but one egg replaced with undersized artificial cowbird eggs (clutch size = 4)	0	3	3	All birds accepted the clutches for at least 5 days after which experiment was terminated or the remaining sparrow egg hatched.

^a Red-winged Blackbird experiments 1 and 2 were conducted in New Haven Co., Conn. in 1969 and 1970. Experiment 3 was done in San Luis Obispo and Santa Barbara Cos., California in 1976. Chipping Sparrow experiments were done in Cheboygan and Emmet Cos., Michigan in 1969.

^b In a few cases I terminated experiments after 6 days but normally the period over which the birds incubated the foreign eggs lasted at least until the time their own eggs were scheduled to hatch. After this time the birds began to desert their nests but a few incubated for close to twice the normal incubation period.

is reduced to two cowbird eggs than to two of their own eggs. This occurs because cowbird eggs, being larger than phoebe eggs, represent a greater proportion of the original clutch volume before PCR. Although he was concerned with other questions, Holcomb's (1970) data support volume assessment. He found that Red-winged Blackbirds are more likely to desert if their eggs are replaced with an equal number of undersized egg models than if the models are the size of redwing eggs.

The PCR experiments and other data

(Table 2) summarized above allow the following generalization concerning the egg recognition of accepters: These species are unresponsive to egg coloration in all contexts, and are unresponsive to the sizes of individual eggs but respond indirectly to egg size through its effect on total clutch volume. Whether rejecter species respond to PCR via volume assessment is unknown and will be difficult to determine because the size of individual eggs is a factor eliciting rejection in these species (Rothstein, 1983).

Responses to broken eggs

Besides responsiveness to the combined volume of their clutch—*i.e.*, to PCR—accepters respond to one other aspect of their eggs. They remove eggs with surface irregularities that indicate the egg is broken. Damaged eggs endanger the entire clutch because they may leak their contents, which upon drying “glue” the remaining eggs to the nest lining or to one another making it difficult for the bird to turn its eggs. On the other hand, unless they have only a hairline fracture, damaged eggs have little reproductive value because they rarely hatch. Clearly birds should, under optimality reasoning, remove broken eggs. Early experiments on egg recognition, mostly in nonpasserines, indicated that birds will incubate odd shaped eggs that have rounded edges, but not those with sharp edges (Noble and Lehrman, 1940; Poulsen, 1953; Tinbergen, 1960). A reasonable interpretation is that the latter are rejected because they mimic broken eggs and some investigators (McClure, 1945; Poulsen, 1953) who deliberately broke eggs found that such eggs are ejected. But quantitative information on responses to broken eggs is largely lacking, especially for passerines.

To determine how passerines respond to broken eggs, R. Kemal and I (Kemal, 1979; Kemal and Rothstein, in preparation) conducted two series of experiments on Red-winged Blackbirds. In one series a small piece of white chicken eggshell was glued at a 45° angle to one redwing egg in a clutch. This broken egg simulation was rejected within one day at 52 (81.3%) of 64 nests which were tested after one to nine days of incubation, thereby demonstrating a strong response. Using optimality reasoning, we predicted that the response would weaken after 10 or 11 days of incubation when redwing eggs hatch, otherwise the birds might eject their own emerging offspring. This was confirmed as rejection occurred at only two (28.6%) of seven nests tested on the tenth day of incubation and not tested previously ($P \leq 0.025$ for 52–12 *vs.* 2–5).

Responses to broken eggs were also tested by replacing a redwing's entire clutch

with an equal number of artificial cowbird eggs, one or two of which simulated a broken egg. There were three major types of simulations: 1) piece of shell spotted like the rest of the cowbird egg and glued at a 45° angle; 2) piece of spotted shell glued flat; 3) piece of white shell glued flat. Of these, type 1 simulated the greatest degree of damage; it was ejected and the birds continued to incubate the remaining cowbird eggs at 12 of 14 nests. Type 2, which was a weaker tactile stimulus, was ejected in only 3 of 20 cases. Type 3, which was an equally weak tactile stimulus but a strong visual stimulus because the white shell contrasted with the rest of the egg, was ejected in 9 of 18 cases. The comparison between types 2 and 3 is significant ($P \leq 0.025$ for 3–17 *vs.* 9–9) and demonstrates that in at least some contexts, accepter species exercise visual discrimination based on egg coloration.

Broken egg experiments using artificial cowbird eggs at 25 nests of 5 other accepter species suggest that a response is nearly universal but that at least one species, the Barn Swallow (*Hirundo rustica*) does not eject broken eggs (Kemal, 1979). Direct experiments have not been done on rejecters but they too seem to remove broken eggs. Numerous Cedar Waxwing and Northern Oriole eggs disappeared from experimental nests after the birds broke them while trying to eject cowbird eggs I had placed in their nests (Rothstein, 1976, 1977). The two Scrub Jay experiments on TER (cited above) are relevant here. I accidentally broke an egg while I returned the jay eggs to each nest after the birds had ejected foreign eggs. In both cases the broken egg disappeared. Thus although more data are needed, it seems likely that as with PCR, recognition of broken eggs is universal or nearly so among accepter and rejecter species.

The evolutionary significance of responses to PCR and broken eggs

In contrast to brood parasitism, birds respond in a relatively optimal fashion to PCR and broken eggs. Nearly all passerines seem to respond to the latter situations, whereas many show no response to parasitic eggs.

As I have argued, the acceptance of parasitic eggs is best interpreted as a case of nonoptimality. Interpreting as nonoptimal the lack of a trait that would infer significant adaptive value, is meaningful only if it is reasonable to expect the evolution of the trait. One way to determine whether a hypothetical adaptation is reasonable is to determine whether comparable species possess the trait. On this basis, rejection is clearly reasonable because acceptor and rejecter species occur in the same family and even genus.

A still more powerful way to assess the reasonableness of a trait is to somehow cause a species that lacks the trait to express it or a similar trait. The experiments on PCR and broken eggs come close to doing this. Despite their lack of responsiveness to egg coloration and to the size of individual eggs, accepters are responsive to certain features of their clutch. They respond to information concerning the combined volume of their clutch and they eject broken eggs. If accepters can eject broken eggs they almost certainly can do the same with parasitic eggs. The broken egg experiments are especially significant since they showed that an accepter species exercises visual discrimination of eggs in some contexts. Surely if a redwing is capable of visually detecting that a spotted egg has a small piece of immaculate shell on it, it has the ability to discriminate between its own eggs and the highly divergent ones of the cowbird. I return here to the notion of compartmentalized units of behavior. Accepters possess behaviors such as visual discrimination of egg features and ejection that are needed to reject parasitic eggs. But they express these behaviors only in contexts unrelated to parasitism, which is counter to what optimality reasoning predicts.

THE ACCEPTANCE OF PARASITIC NESTLINGS

In contrast to egg rejection, there are no clear cases of outright rejection of nestlings. The only major exception may occur in the parasitic viduine finches which mimic the complicated mouth patterns of their estrildine hosts (Nicolai, 1964; Payne, 1973) but even here there is a need for experi-

mental studies (Payne, 1977). The nestlings of some other parasitic birds are at least crude mimics of host nestlings (Lack, 1968; Payne, 1977) but this may be due to selective pressures other than those of host rejection (Rothstein, 1975a). Even if some hosts will be shown conclusively to reject nestlings, this behavior is at best rare. Hosts that feed nonmimetic nestlings obviously behave nonadaptively in a situation in which their sensory abilities are adequate for an adaptive response. The point is shown most dramatically by hosts of the Common Cuckoo. Limited egg recognition experiments suggest that many of these species reject nonmimetic eggs (Rensch, 1924; Ali, 1931; Dement'ev *et al.*, 1966, p. 497) only to be parasitized successfully by mimetic cuckoo eggs that hatch nestlings that bear little resemblance to the host's own young. Although several adaptive explanations predict that nestling rejection should be less prevalent than egg rejection (Rothstein, in preparation) none account for the total or nearly total lack of the former. The absence of nestling rejection can, I suggest, only be regarded as an example of nonoptimality.

DISCUSSION

In his excellent review of optimality reasoning, Maynard Smith (1978) stresses that the approach is valuable because it enables researchers to construct predictive models that help identify selective pressures and that can elucidate the ways in which real or hypothetical traits work. Optimality reasoning is thus a way of organizing what we think we know about a system into a model that can test this knowledge and associated assumptions and use them to generate additional knowledge. In this regard, optimality reasoning has served me well, as it has nearly all biologists. Although it often failed to generate the correct predictions concerning egg recognition, optimality prompted numerous questions that resulted in new findings. No other paradigm could have been as useful, as there would have been little basis on which to make clear-cut predictions if I had not expected behavior to be adaptive.

Despite its heuristic value, the optimality

approach presents serious difficulties. Maynard Smith (1978) states that we should use the assumption of optimality to guide research but should not attempt to test this assumption. Unfortunately, there are good reasons to believe that natural selection occasionally fails to produce even a near optimal solution and that some traits are not adaptive (Gould and Lewontin, 1979), a point Maynard Smith acknowledges. This then creates a fundamental problem. Predictions arising from the optimality paradigm are almost never borne out perfectly. In my studies, some predictions were not borne out at all. When a model's predictions are not verified the model needs to be rejected or modified. But what should be modified? If Maynard Smith's suggestion is followed, we should modify ideas concerning presumed selective pressures and question "facts" that were thought to be valid. Perhaps, though, all of these aspects are correct and an optimality model reflects both valid facts and a complete understanding of how a system works but fails to produce verifiable predictions because the system is not in fact optimal. There is no sure way out of this dilemma. At the very least the problem should make us reluctant to use consistency with adaptive explanations as a criterion for accepting weak results.

Host defenses against parasitic birds involve a system in which we fail to see potential adaptations that require little in the way of recognition skills and that impinge little, if at all, on the rest of the animal's behavior and structure. If optimality predictions are not borne out in a system such as this, then how reliable are they in more complicated systems that involve behaviors requiring recognition of subtle cues or the balancing of complicated cost-benefit considerations? Published studies that emphasize optimality nearly always produce results consistent with natural selection but as Gould (1980) has suggested, this may to some extent occur because the data and available interpretations are so involved that it is possible to weave an adaptive story out of almost any results. The danger is that such explanations may be accepted despite their *post hoc* nature because most

biologists are uncomfortable with phenomena that have no adaptive explanation.

Biology has derived enormous benefits from the adaptationist program, but the paradigm will serve even better if we are aware of its pitfalls. Applications of the paradigm should require the same rigorous standards for evidence that exist in other fields and investigators need to especially avoid the acceptance of weak optimality results simply because of the intuitive appeal of adaptive explanations. Others (Curio, 1973; Lewontin, 1978; Maynard Smith, 1978; Gould and Lewontin, 1979; Gould, 1980) have reviewed the problems and values of the optimality approach and I will not do so here; but I do offer two suggestions.

Test all reasonable optimality hypotheses and if these fail conclude, tentatively at least, that a system is not optimal.

Most of the alternatives to adaptiveness (Gould and Lewontin, 1979) do not generate testable predictions whereas optimality reasoning nearly always does so. Thus knowledge is most likely to be increased by first asking questions based on optimality. Also, since most traits are probably adaptive, one is likely to produce support for some hypothesis most quickly if all optimality explanations are exhausted before considering nonoptimality. But if all reasonable optimality hypotheses are tested and the system still seems to be far from optimal, as is true for the host defenses of many birds, a tentative conclusion of nonoptimality should be endorsed. I stress tentative because nonoptimality is a lack of adaptiveness and it is impossible to prove that something does not exist.

Nonoptimality conclusions that are well founded have several values. First, they are more heuristic than their alternative—adaptive conclusions that depend on weak evidence. The latter tend to stifle further inquiry because many investigators will be satisfied that an explanation consistent with adaptiveness is at least available. By contrast, a conclusion of nonoptimality is likely to serve as a stronger stimulus for the development of new hypotheses, some of

which may produce adaptive explanations that can be supported strongly.

Secondly, we need to know the relative importance of the various processes that can be responsible for nonadaptiveness. Probably all evolutionary biologists would agree that at least some of the processes Gould and Lewontin (1979) discuss are real; but possible examples of these processes will be overlooked if there is a stress only on results that conform to adaptiveness. Lastly, anything that casts doubt on the all-inclusive nature of an established principle is likely to be productive. When a paradigm is in its infancy it may be worthwhile to disregard inconsistencies lest they retard the development of clearly stated principles. But the adaptationist program does not need this kind of protection. It is now generally well understood, due largely to G. C. Williams (1966), and its usefulness has been demonstrated innumerable times. What is needed now is a better understanding of its limitations.

Whenever possible optimality itself should be tested.

Both supporters (Maynard Smith, 1978) and critics (Gould and Lewontin, 1979; Gould, 1980) of optimality reasoning agree that one cannot test a system to determine if it is optimal. To do so requires complete knowledge of the selective pressures involved and of the phenotypic constraints upon potential adaptations and it is argued that we can never be certain that we know all of these important aspects of a system. This view is overly restrictive. Throughout science we can never be certain that all important facts are known but there are points at which we proceed with work based on the assumption that important factors are known. Host defenses against parasitic birds are, I believe, such a system. The considerations are sufficiently simple and the natural history facts sufficiently well-known that it is clear what is adaptive. Thus in this system and perhaps others, research guided by optimality reasoning is as much a test of optimality as an effort to learn more about the system.

Testing optimality itself is valuable for the same reasons as formulating conclu-

sions of nonoptimality. By getting some measure as to the frequency with which optimality is approached we will be able to apply the adaptationist program more successfully. Testing the central tenet of the adaptationist program will increase its scientific merit because we may be able to show that optimality can be falsified.

Systems used to test optimality must have clearly defined questions. If large numbers of such systems are studied successfully, I suspect that recognition studies will play a prominent role. Recognition questions often generate clear dichotomies that can be studied with experimental, rather than merely correlative, procedures. It may turn out that too few systems of any type are sufficiently well-known and amenable to critical tests of optimality to allow meaningful conclusions. But unless we search for suitable systems we will miss an opportunity to enhance the value of optimality reasoning.

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