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EVOLUTION OF BROOD PARASITISM IN ALTRICIAL BIRDS

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Among the 8600 living species of birds there are about 75 brood parasites which make no nest, laying their eggs in the nests of other birds. Here we wish to examine the behavior patterns and environmental circumstances which may have led to the development of this form of parasitism. This will involve comparisons with the adaptations of nonparasitic relatives of modern brood parasites. Thus, we are attempting to evaluate not only why modern brood parasites may have developed their unusual habits but also why certain close relatives have not.

Brood parasitism has evolved independently a number of times in birds. Best known are the cuckoos, with a complex of Old World species (and three less specialized New World species) highly specialized in the parasitic habit (Friedmann, 1933, 1948). Also, all the African honey guides (Indicatoridae) whose breeding biology is known are brood parasites (Friedmann, 1955). Among passerines brood parasitism has evolved independently in African weaver birds (Ploceidae) and in several species of blackbirds (Icteridae). The only obligate parasite in precocial species is the South American Black-headed Duck (*Heteronetta atricapilla*), but the North American Redhead (*Aythya americana*) has populations at various stages of parasitism, from completely independent to complete brood parasitism (Weller, 1959). The independent evolution of brood parasitism in these diverse phyletic lines is clear. But brood parasitism has not necessarily evolved only once in each group. The polyphyletic origin of such a specialized habit within a group might seem quite improbable, but the conditions which might lead to the development of such a habit suggest that this is a possibility.

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EXISTING HYPOTHESES OF BROOD PARASITISM

Progressive degeneration of nesting instincts.—Although brood parasitism has long been of interest to ornithologists and some of the more common brood parasites are quite well known, existing theories are not adequate to explain the evolution of this reproductive pattern. Those suggestions that have been made all involve, in one way or another, the “degenerative breakdown” of the normal breeding behavior of birds. A frequent suggestion has been that the development of brood parasitism has

resulted from a degeneration of nest-building activities. For example, it has been suggested that the fragile, open nest of the Yellow-billed Cuckoo (*Coccyzus americanus*), a nonparasitic American species, is a hint of a trend toward brood parasitism (Herrick, 1910; Miller, 1946). Other suggestions have involved the breakdown of egg-laying and incubation behavior. Irregular patterns of incubation combined with the discovery of an interrupted egg-laying pattern in the parasitic European Cuckoos (*Cuculus canorus*) led to the suggestion that the degeneration of the nesting instincts of American cuckoos may in part be a trend toward parasitism (Herrick, 1910; Miller, 1946; Makatsch, 1955; Weller, 1959).

Failure to synchronize nest building and egg laying.—Herrick (*op. cit.*) suggested that the European Cuckoo has degenerated to parasitism through a continued failure to synchronize nest building with egg laying. Eggs were ready to lay before there was a nest to receive them. Thus the need arose to place eggs somewhere other than in the appropriate nest. More recently, Friedmann (1960) has expanded this argument, suggesting that reproductive failures, as a species phenomenon, led to parasitism. He summarizes (p. 37): "endocrine imbalance or change, may have brought about the loss of broodiness and ushered in the parasitic mode of reproduction."

To take a specific example, Friedmann (1929:343-356) argued that the several sorts of brood parasitism exhibited by cowbirds of the genera *Agelaioides* and *Molothrus* represent stages through which the more "highly evolved" parasites have passed. Thus, the Bay-winged Cowbird (*Agelaioides badius*), which occasionally makes its own nest but normally uses the nests of other birds, incubates and rears its own young. The Screaming Cowbird (*Molothrus rufo-axillaris*) parasitizes only the Bay-winged Cowbird, but both the Shiny Cowbird (*M. bonariensis*) and the Brown-headed Cowbird (*M. ater*) parasitize most of the small passerines found within their geographic ranges. Friedmann erected a phylogenetic sequence for these birds, to which he still subscribes (1963:vii), on the following assumptions: (a) A group evolved where most species occur today. This puts the evolution of the cowbirds in South America. (b) More "primitive" species occupy the ancestral home, the more recently evolving species for the most part being confined to more peripheral areas. By this criterion *A. badius* and *M. rufo-axillaris* should be phylogenetically the oldest and *M. ater* the youngest. (c) Simpler courtship displays and vocalizations are more primitive than complex displays and vocalizations. *A. badius* would then be the most primitive species, *M. ater* the most advanced, with *M. rufo-axillaris* and *M. bonariensis* being intermediate. (d) Black or blackish-blue is a "climax" type of color while grays, whites and browns are more "primitive." By this criterion *A. badius* is again the most primitive and *M. bonariensis* and *M. ater* the most advanced.

Since these lines of evidence all supported the contention that *A. badius* is most primitive, Friedmann (*op. cit.*) suggested the following hypothesis to explain the evolution of brood parasitism in this group. The Bay-winged Cowbird is strictly monogamous and the most strongly territorial of the cowbirds, but, unlike most birds which first establish their territories and then choose a nest site, these cowbirds first find a nest, if necessary evicting the rightful owners, and then extend the territory around the nest. As a result the territory is of secondary importance and the "instinct" to defend it is correspondingly lessened, initiating a trend of reduced territorial defense in the males. Also, the female Bay-winged Cowbird is reported to be very shy and nervous while incubating, and without the protection of the male she might be unable to care for the eggs and young properly. Since territorial behavior appears to be weaker in the more highly evolved cowbirds, Friedmann (*op. cit.*) postulated

that a continuing reduction of territorial protection impaired reproductive success and invited parasitism.

Screaming Cowbirds sometimes establish territories for considerable periods in the spring and then desert them without having bred. Friedmann suggests that this also indicates that the reduced territorial instincts of the males are often too weak to hold the territory until the female is ready to lay. This lack of attunement between territorial instincts of the males and egg-laying behavior of the females led to the evolution of brood parasitism.

Most of these assumptions are no longer tenable. In mammals, where the fossil record is more adequate, it is now well known that the assumption that a group evolved in the region where most extant species occur is as likely to be wrong as right. Similarly, the assumption that certain species of a genus are more primitive than others or can be derived from one another must also be rejected. The complexity of displays and vocalizations is influenced by many factors and may become more simple or more complex in the course of evolution. The same applies to the degree of sexual dimorphism in plumage. Thus, any attempt to infer a phylogenetic series among extant species of cowbirds is probably misleading.

In any case this theory shares certain fundamental features with all the other views seriously considered by ornithologists. First, social parasitism is viewed, either implicitly or explicitly, as degenerative, despite the fact that some brood parasite species are very successful. Second, populations are viewed as evolving as a group toward brood parasitism as a result of the progressive deterioration of their normal responses. Such orthogenetic views are incompatible with current knowledge of the mode of operation of natural selection in sexually reproducing species. Undoubtedly marked changes in reproductive behavior have accompanied the evolution of brood parasitism. But such behavioral changes cannot have been the selective force initiating and orienting evolutionary change. One cannot postulate the development of endocrine imbalances, faulty incubation behavior, or incomplete nest-building responses simultaneously in all members of a population of birds. Rather such malfunctions appear sporadically and are obviously disadvantageous in most species. What we must explain is how such endocrine imbalances reduce territorial behavior and how faulty incubation behavior and incomplete nest-building responses result in the production of more surviving offspring, when they do occur, so that the genes responsible for the behavioral changes spread and eventually dominate the entire population (Selander and Kuich, 1963). To this basic problem current theories suggest no answers. Moreover, some of the behavior patterns of nonparasitic species that have been cited as examples of incipient degeneration toward parasitism may be highly adaptive to their owners. For example, the nests made by a population of Yellow-billed Cuckoos in Arizona are probably quite adaptive, or at least can be as easily explained by adaptive as maladaptive factors. The open nest structure may permit a view of approaching predators from below. Also for cuckoos as well as numerous other predaceous birds which feed their young with sizable prey items, the time required to make and treat each kill may put a premium upon extending the period of maximum nestling energy demands. Therefore, interrupted laying in this species appears to have adaptive significance (Hamilton, 1965).

HYPOTHESIS FOR THE DEVELOPMENT OF BROOD PARASITISM

Our purpose here is to present another theory for the evolution of brood parasitism, compatible with current concepts of natural selection. Basically this involves a defini-

tion of the ecological conditions which may confer a selective advantage upon individuals with parasitic tendencies. We make the assumption that brood parasitism is derived from nonparasitic ancestors. Baker (1942:100) has suggested an alternative: that parasitic cuckoos were derived from reptiles and do not have nonparasitic ancestors. This suggestion ignores the phyletic position of cuckoos among birds and seems especially improbable. This analysis would not have been possible without the great volume of data patiently gathered during the past 35 years by Friedmann (1929, 1948, 1955, 1960, 1963, 1964).

It is useful to treat altricial and precocial species separately. Among altricial species it is necessary for the host species to care for the nestlings until they are capable of feeding themselves, whereas with precocial species parental care during development may be a considerably lesser task, the young contributing to their own maintenance almost as soon as they are hatched. Usually the parent of precocial species provides some protection against predators and helps in finding food, but the influence of the addition of more offspring upon the effectiveness with which a female bird can carry out these responsibilities is much less well known than for altricial species. This makes it difficult to evaluate the fate of eggs of precocial birds placed in the nests of other precocial species. The subsequent discussion is intended to apply only to species with altricial offspring.

In "The Origin of Species," Darwin (1872) discussed the possible evolution of brood parasitism in European Cuckoos. After first citing an instance of an American cuckoo (sp. ?) successfully reared by a Blue Jay (*Cyanocitta cristata*), he suggested (p. 198) that the proliferation of such a habit could have led to the development of brood parasitism in the European Cuckoo.

"If the old bird profited by this occasional habit through being enabled to migrate earlier or through any other cause; or if the young were made more vigorous by advantage being taken of the mistaken instinct of another species than when reared by their own mother, encumbered as she could hardly fail to be by having eggs and young of different ages at the same time; then the old birds or the fostered young would gain an advantage. And analogy would lead us to believe, that the young thus reared would be apt to follow by inheritance the occasional and aberrant habit of their mother, and in their turn would be apt to lay their eggs in other birds' nests, and thus be more successful in rearing their young. By a continued process of this nature, I believe that the strange instinct of our cuckoo has been generated."

That brood parasitism is indeed an adaptive process is our contention here. A part of Darwin's arguments just cited shares the difficulty of resorting to degenerate characteristics of nonparasitic ancestors, however. We will demonstrate later that according to current evidence not available to Darwin there are preferable explanations of an adaptive nature for these characteristics. Nevertheless, Darwin in this section seized the nucleus of a method of explanation, that is, adaptiveness, which has frequently been missing in subsequent discussions of the possible circumstances surrounding the origin of brood parasitism.

The initiation of brood parasitism.—A fruitful approach to the study of the evolution of behavior is to seek precursors of some trait in the behavior of related species. Such an analysis of brood parasitism suggests several possibilities. First, nest destruction during the egg-laying period is encountered by all species of birds. A female confronted with this situation would have to deposit subsequent eggs somewhere. Since another completed nest with eggs would provide the best orienting stimulus for egg laying, it is reasonable to assume that, insofar as possible, some females whose nests had been destroyed might attempt to lay additional eggs in the

nests of other nearby birds. Deposition in other nests of the same species is likely, especially in colonial species. However, some eggs might also be laid in the nests of other species since, especially in highly territorial species, the egg-laden female will be more likely to be familiar with the nests of other species rather than those of her own species. In some circumstances this would probably be more likely since the female would have difficulty gaining access to nests of her own species in other territories.

If this category of accidents is to be favored by selection, it is necessary that there be some genetic predilection for the active seeking of nests of the same and/or alien species as opposed to casual dumping of the eggs. Nest destruction immediately triggers a behavioral change which results in a reinitiation of the nesting cycle in most species of birds. Individuals which placed eggs in the nests of other birds might be expected to attempt a second nesting, and it is reasonable to assume that such individuals might leave more offspring than those individuals lacking a tendency to seek out nests. The effect of this selection is to make female birds more receptive to the releasing stimuli from nests they have not built themselves, thus setting the stage for the second possibility, namely that in which the initial parasitism results simply from the releasing stimuli of foreign nests being strong enough to trigger egg-laying behavior even though the rightful nest is intact. Under these circumstances brood parasitism would be favored if accident prone individuals produced more surviving offspring per parent than parents which had had no such accident.

An additional possibility is that occasional lack of synchronization between nest building and egg laying may result in the production of an egg before a nest is complete enough to receive it. Again we may expect that in such a circumstance the completed nests of other individuals, especially those showing eggs, will orient at least a part of the eggs so produced into foster homes. This is the circumstance favored by Herrick (1910) as a starting point for the development of brood parasitism. The difference between his and our interpretation is that Herrick suggested that this was likely to have been a characteristic of all members of the incipient brood parasitic population. We suggest that such a circumstance, if it were one of the situations which initially led to brood parasitism, represented the extreme variation of a normal nonparasitic population.

Our task, therefore, is to identify possible circumstances in which ecological conditions would favor the occurrence of and promote reinforcement of either of the two behavior traits just mentioned. Once selection is operating to promote the spread of parasitism, it will also operate to enhance its effectiveness, and the development of specialized parasitic adaptations can be anticipated. As the spread of selection-reinforced parasitism proceeds, the population balance will become increasingly weighed in favor of parasitism and the trend may be accelerated. Swamping of the nonparasitic portion of the population would then result, terminating in its elimination. Intermediate stages are therefore probably of relatively short duration and should not be expected to be common in nature.

The ecological requirements for the initiation of successful brood parasitism may be quite stringent. The preconditions we have just suggested are probably universal among birds, but brood parasitism is comparatively rare. Also, there are many obstacles standing in the path of successful parasitism. Host nests must be found at precisely the right time since an egg deposited during incubation would hatch after those of the host species, if at all, and the young would be at a strong competitive disadvantage. The eggs must be accepted for incubation and the young accepted

as objects to be fed. The food delivered to the young by the host species must be suitable for normal growth and development. Eggs of insectivorous species deposited in nests of species with markedly different diets would have little chance of success. It is noteworthy that there is no known case of a Brown-headed Cowbird successfully fledging from nests of American Robins (*Turdus migratorius*), Cedar Waxwings (*Bombycilla cedrorum*), or Goldfinches, *Spinus tristis* (Young, 1963; see also Friedmann, 1963:40). Finally, when independent, the foster young must desert the company of the species with which it was raised and associate with members of its own species. Otherwise these individuals, no matter how successful they were in fledging, would be genetically useless. Taken together these factors suggest that eggs dumped in the nests of the same species would be expected to have the greatest success. But this would be countered by the strong territorial behavior of most small birds which would make access to the nest more difficult.

Assuming that our general hypothesis is correct, we can now proceed to suggest those adaptations of hosts and parasites and those aspects of the ecological environment that would favor the spread of accidentally dumped eggs.

Characteristics of avian breeding biology preadapting the system to brood parasitism.—It is possible to identify certain features of the basic breeding biology of birds which permitted the evolution of brood parasitism. First, there is a phase of incubation of the egg outside of the body without which there would be no chance for a foreign genotype to intervene. Second, there has apparently been no prior selection in favor of fine discrimination in egg recognition in most birds. This is presumably due to the fact that under normal conditions eggs remain stationary in the proper nest unless they are destroyed by predators. Thus, there has never been any prior selection to enhance such discriminatory ability. Moreover, in species which do not have a history of being afflicted by brood parasites, oversized eggs are not necessarily rejected; indeed, they often seem to be preferred. The Oystercatcher (*Haematopus haematopus*), for example, will attempt to incubate an enormously oversized artificial egg, ignoring its own nearby (Tinbergen, 1948). The Redpoll (*Carduelis flammea*), a sparrow-sized bird, will attempt to incubate a hen's egg or even a tennis ball, so big relative to the size of the bird that it cannot even balance on it (Poulsen, 1953). The Ringed Plover (*Charadrius hiaticula*) prefers a more distinctively marked egg to its own cryptically colored one (Koehler and Zagarus, 1937), and finally a nest with more eggs than the normal complement may be selected in preference to the actual clutch (Tinbergen, *op. cit.*). Thus, in the situation which must have obtained at the time of incipient brood parasitism, unusual characteristics of parasite eggs relative to prospective hosts would not necessarily have been selected against; they may have been preferred.

Such artificial stimuli, exceeding the usual upper dimensional limits or other characteristics of stimuli, have been termed supernormal stimuli (Tinbergen, 1951) if responsiveness or preference for such abnormal objects exceeds that for normal ones. Thus, confronted with the choice of a stimulus object which is of the normal order of magnitude encountered in nature and one which has been experimentally enlarged upon, an organism may prefer the magnified object. The adaptive significance of this phenomenon seems to be that in nature selection against further enlargement upon the stimulus results for reasons other than its stimulus value. Yet the stimulus filtering process operates to be maximally sensitive to the largest features of the stimulus. In the absence of selection influencing the characteristics of the stimulus object, which is, of course, an experimental artifact, it is possible to pre-

sent a stimulus which, while not maximally adaptive in nature, is nevertheless more motivating than any feature of the normal range of variation of normal stimulus objects.

There has apparently been no prior selection for individual recognition of nestlings in most altricial birds, presumably for the same reason. In any clutch of nestlings the most actively begging individuals are most likely to be fed. The rate of transportation of food to nestlings is known to be influenced by the begging rate—the more active the begging the more trips per unit time. Therefore, if a sizable foster nestling is introduced, it may act as a supernormal stimulus, eliciting maximum effort from the foster parents, even to the exclusion of their own nestlings. The concept of the supernormal stimulus is again useful. There is, in the nonparasitic situation, no adaptive advantage which would enhance selection favoring the development of an upper limit of responsiveness to begging.

Preadaptations of the brood parasite.—Success of eggs laid in the nests of other species could be expected to be improved if the parasite initially had an incubation period somewhat shorter than that of the host. Its eggs would then hatch sooner than those of the host and the larger young would be at a competitive advantage within the brood. Moreover, eggs deposited during the early stages of incubation would still have a chance of hatching successfully. With good foraging conditions, the young might survive even though it was the last to hatch. Second, survival would be improved if the young of the parasite were broadly adapted to a diversity of foods and able to develop on whatever food might be delivered to them in foster nests. Since most small birds feed their young on insects, this may not be a very significant factor. Third, if the initial cause of parasitism is merely accidental laying, more eggs will be laid if the parasite is an indeterminate layer, that is, it lays eggs until a certain clutch size is reached, since its own clutch would then be complete rather than reduced.

Accidental laying of eggs in foreign nests is perhaps more likely in species in which nests are built by the males. In these species the females are accustomed to laying in nests they did not build themselves and the mere sight of empty nests should be highly stimulating.

Preadaptations of the host species.—For several reasons, brood parasitism is more likely to evolve if the potential parasite is less common than the potential host. A rare species, when making a mistake in laying, is more likely to lay in the nests of other species than in nests of its own species. The reverse is true in the case of more common species. Selection for the development of anti-parasitism devices is likely to be less stringent in common species parasitized by rare forms. A smaller proportion of the host species will be affected under such circumstances, permitting by comparison slower adaptation in the host to the effects of the parasite.

If the host species is indeterminate in its laying characteristics and the egg of the parasite is deposited during incubation, the host would be expected, at least part of the time, to reduce its own clutch by the number of parasitic eggs added. This would mean that the parasite would not enter into intrabrood competition for food as an added member but merely as a substitute member in the normal clutch. In altricial birds clutch size is adapted to the number of young the parents can successfully feed (Lack, 1954). Therefore, the probability of survival of the parasitic nestling should be enhanced.

If the host is a colonial species whose breeding season is properly timed with respect to that of the evolving parasite, the location of nests suitable for deposition

should be easiest, and, since territorial behavior tends to be weaker in colonial species, access to the nests may be more readily obtained than in territorial species.

The role of the ecological situation.—The ecological situation will influence the adaptation of both the host and parasite making the evolution of brood parasitism more likely in some habitats than others. Thus, in the tropics where nest predation is more intense, a higher proportion of individuals should be confronted with the problem of a place to deposit eggs. Short incubation periods will be found in regions where there is strong selective pressure for rapid fledging, such as arid and semiarid areas where food is sporadically available for short periods of time. Broad adaptations to a variety of foods would be expected in species that were somewhat opportunistic in their foraging behavior. This would be true of omnivores in general and of species with major morphological adaptations as adults for the exploitation of specific foods which are, however, not suitable as food for nestlings. Such species would be required to shift to alternative foods for the purpose of raising young and might be expected to be opportunistic in their foraging at that time, not being well adapted to the food they must obtain.

Indeterminate laying is also characteristic of species whose food supply is somewhat unpredictable as it often is in arid and semiarid regions. Also species exploiting variable and unpredictable food supplies often have extended egg-laying periods with incubation beginning with the first egg (Lack, 1954:40). This gives a potential parasite more time to deposit additional eggs.

Coloniality among altricial birds is most commonly encountered in areas where (a) feeding areas are widespread but nesting areas are restricted to smaller areas and/or (b) the temporal and spatial distribution of the food is so unpredictable that defense of feeding areas is not energetically profitable (Brown, 1964; MacArthur, Lewontin, and Orians, MS). These conditions are commonly met in savannas for species with tree-nesting requirements and, in general, in the ecological instability characteristic of regions with erratic rainfall. Moreover, these are also the conditions which are likely to favor strong synchrony in the breeding seasons of the birds, thus enhancing the ability of the parasite to find suitable nests in which to lay.

Not all of these preconditions are likely to be necessary to evolve brood parasitism in any given case, and it is therefore profitable to examine the major groups of brood parasites individually to determine which, if any, of these characteristics they seem to possess.

Preadaptations of cuckoos to brood parasitism.—The Old World cuckoos of the Subfamily Cuculinae of the Family Cuculidae are all brood parasites. Several excellent experimental, behavioral, and comparative studies of these species have been made (Chance, 1922, 1940; Stuart Baker, 1942; Rensch, 1924, 1925; Jourdain, 1925; Makatsch, 1937, 1955; Friedmann, 1964). These studies are, however, of a remarkably adapted system, with highly evolved adaptations and counteradaptations. We wish here to begin by reviewing those characteristics of nonparasitic cuckoos which may have preadapted the group to turn to parasitism. Nonparasitic cuckoos, like their parasitic relatives, are generally solitary birds that establish large territories and take a diversity of quite large food items. They are generally large birds; only certain of the parasitic species are reduced to a dimension comparable to their smaller hosts. The diets of the nonparasitic species are somewhat unusual, including predilections for lizards and snakes, including venomous species. The nonparasitic North American species of *Coccyzus* are noted for their capacity to handle hairy and toxic

lepidopterous larvae, items largely ignored by other insectivorous species which deal with smooth caterpillars of similar dimensions.

There are several accounts of the discovery of eggs of the nonparasitic North American species in the nests of other species of birds (Herrick, 1910; Bent, 1940). However, there is no conclusive evidence that this occurs more frequently than in other species of birds. These stray eggs seem most likely to be explained by accidental laying in the nests of other birds.

The basic features of the breeding biology of the North American species of *Coccyzus* suggest certain preadaptations to the parasitic habit which may also have been characteristic of the Old World species at the time they began to evolve as parasites. Their nestlings are adapted to receiving a comparatively coarse diet, consisting of hairy caterpillars, beetles, all kinds of orthopterans, and perhaps even berries. In crossing species lines this comparatively omnivorous ability would be a particularly suitable basis for the development of parasitism. Alternatively, it may be that many of the Eurasian cuckoos exploited similar unusual foods as adults but were forced to shift to alternate items when feeding nestlings. If the adults were less efficient in finding these alternate foods, survival of young in foster nests might even have been better than in young raised by their parents.

Parasitism in the cuckoos is obviously highly adapted and it is therefore difficult to postulate the breeding biology of the cuckoos at the time of the initiation of parasitism, the probable initial hosts, or the probable ecological situations. Many of the Asian and African species of cuckoos are relatively host specific (Friedmann, 1948; Ali, 1931; Stuart Baker, 1942). Related to this host specificity is a degree of egg mimicry which represents a specialization from which it would be hard to adapt to a broader spectrum of hosts. The requisite synchrony could have pertained either in temperate latitudes where the temperature cycle and its dependent events synchronize breeding or in tropical regions with highly seasonal rains. Parasitic cuckoos today are found in both these areas but may not have evolved in both.

The short incubation period of the nonparasitic cuckoos is another important preadaptation. Both the Yellow-billed (Hamilton, 1965) and Black-billed cuckoos (Spencer, 1943; Hamilton, *op. cit.*) have 10- or 11-day incubation periods, among the shortest recorded for birds, and it is quite possible that the parasitic mode has resulted in no additional shortening of incubation periods among cuckoos. The adaptive significance of this extremely short incubation period is apparently to facilitate rapid initiation of utilization of a temporarily relatively unpredictable food resource (Hamilton, *op. cit.*).

Since cuckoos today, both parasitic and nonparasitic, are in general larger than the host species they parasitize, the eggs of the nonparasitic ancestral stock of parasitic cuckoos were probably larger than the eggs of the host species. This might have posed problems for egg acceptance, but in the beginning the supernormal stimulus process was probably operative for both eggs and nestlings.

Too much evolution has intervened and too much change has taken place in the sensory responses of both parasite and host for us to be able to reconstruct more completely the conditions as they probably occurred at the time parasitism began. However, the recent spread of the Brown-headed Cowbird into many regions of North America in which it did not formerly occur provides the opportunity to study the evolution of the responses of new host species (for example, see Mayfield, 1960). Indeed, Mayfield (1964) has suggested that those species now providing the most vulnerable hosts for the cowbird have only recently been parasitized by this species.

This is a confirmation of the extent to which mutual evolution has resulted from the parasite-host interaction in regions where there has been a long history of interaction between the two. When parasites are introduced to new hosts the delicate balance which both members of the relationship have achieved as a result of prolonged interaction will not be a part of the interaction. The new parasite is more likely to induce excessive mortality, and, where normal hosts are also available, unusual hosts may be eliminated altogether.

Finally, the basic demeanor of cuckoos may have been a valuable preadaptation to brood parasitism. The Yellow-billed and Black-billed cuckoos as well as many other species of cuckoos are solitary feeders, hunting much like hawks, with long periods of motionless waiting for sizable prey items to reveal themselves (Hamilton, 1965). Thus, the cuckoo's way of making a living is to study the environment. This contrasts with the frequent post changes of smaller insectivorous species which may move from perch to perch almost constantly, searching for small prey items at close range. The same vigilance pattern is apparently used by the highly specialized parasitic *Cuculus canorus* in its search for potential host nests (Chance, 1922). The basic rhythm of movement, measured in minutes rather than seconds in the case of nonparasitic cuckoos, would allow a sufficient interval of watchfulness insuring timely detection of an adequate number of potential nests.

Preadaptations of honey guides to brood parasitism.—The honey guides are woodpecker-like birds capable of digesting wax as adults and some of which guide mammals to sources of honey stored in trees by social insects (Friedmann, 1955, 1960). Of the 11 species, five are known to be brood parasites, two others are suspected of being so, and the breeding biology of the other four is completely unknown. For the most part they parasitize related groups of hole-nesting species, and, from their picine affinities, it seems likely that the independently nesting stock from which they were derived was also hole nesting.

Competition for nest sites is common among hole-nesting species, particularly among those that do not excavate nest cavities. Under these circumstances accidental placement of eggs in the holes of other species should be particularly common. Moreover, eggs left behind by the birds evicted from the hole may be incubated by the victors, possibly giving selective advantage to individuals less tenacious in defense of their nesting hole. Both eggs and young of hole-nesting species are less readily visible so that there should be less likelihood of rejection than in open nests. Also, hole-nesting species usually have larger clutches and slower nestling development (Lack, 1954:41), giving the potential parasite a longer time span during which deposited eggs might be successful.

Preadaptation of blackbirds to brood parasitism.—Cowbirds, as their names imply, are adapted as adults to feeding among herds of large mammals, capturing insects flushed by the movements of the mammals. Over most of North America today the Brown-headed Cowbird moves into the wooded habitats where most of its hosts nest only for short periods of time. The recent spread of this species into previously uninhabited regions is perhaps related to the spread of domestic animals which provide suitable foraging conditions for the adult birds (Mayfield, 1964). Clearly, the distribution of the Brown-headed Cowbird was not formerly limited by the range of suitable host species but by conditions required by the adults. Initially, nesting success in the ancestors of Brown-headed Cowbirds may have been dependent upon the presence of sufficient large mammals near the nests since the species is apparently poorly adapted for obtaining food under other conditions. No

precise data are available, but cowbirds probably obtain advantages comparable to those gained by Cattle Egrets (*Bubulcus ibis*) associated with cattle (Heatwole, 1965).

It is likely that a species dependent upon big game animals for foraging would have accelerated incubation periods and nestling growth since the movement of the herds of mammals would result in suitable foraging being of precariously short and unpredictable duration. The adverse effects of this situation on reproductive success may have been considerable, giving further advantage to eggs deposited in the nests of other species. Cowbirds have probably always been grassland and savanna species so that close relatives with colonial, synchronous breeding were probably readily available to be parasitized. Even today most cowbirds parasitize other icterids, some of which are colonial.

In any event the incubation period of the Brown-headed Cowbird is not today appreciably shorter than incubation periods of its nonparasitic blackbird relatives. As with the cuckoos this characteristic is probably a preadaptation rather than an adaptation (Miller, 1946).

Preadaptations of weaver birds to brood parasitism.—The parasitic weaver birds are all tropical birds of savanna or savanna-like habitats (Friedmann, 1960). They subsist primarily on small grass seeds and are believed to have evolved in tropical savannas. Moreover, they all parasitize primarily other species of weaver birds (Nicolai, 1964), many of them colonial. In this circumstance it is easy to visualize the routes to parasitism. Since these birds parasitize within the group to which they belong, the general nutritive adaptations of the group would of itself be a preadaptation enhancing the success of accidental parasitism. Also, many of the parasitized nests are domed, with small entrance holes, so that the advantages suggested for hole nesters are applicable.

Other features of the breeding biology of the weaver birds may have increased the probability of egg deposition in foreign nests. In most nonparasitic weavers the nests are partly or completely built by the males so that females normally lay their eggs in nests they have not built. Many of the estrildines often take over old nests of other species and one species, the Brown Twin-spot (*Clytospiza monteiri*), never builds its own nest. Since female weavers ancestral to the present parasitic forms probably laid their eggs in nests constructed either by their mates or by some other species, the stimulus of an empty nest, or even one with eggs, may have been strong enough to trigger egg laying. Such individuals subsequently would have been expected to hatch and raise a brood of their own, but the increased reproductive output of these individuals could have quickly led to the evolution of brood parasitism. Since the breeding season is synchronized and confined to a short period of food abundance which follows the rainy periods, trees may have considerable numbers of birds of several species nesting in close proximity at the same time. Thus, accidental placement of eggs should be more likely to occur than under any other circumstances and the probability of correct timing should be maximized.

The colonial weaver birds are therefore adapted to breed as rapidly as possible when conditions become suitable. On the other hand, the conspicuousness of their large colonies in the trees of the savanna has led to the evolution of very elaborate nests, in large part in response to predators (Collias and Collias, 1963; Crook, 1963). These elaborate nests require a longer construction time and an inevitable delay in initiation of breeding. All brood parasites naturally are able to save some time, but the savings when the nest is elaborate and the food supply of short duration may

have been of particular importance in the case of the weaver birds. Some of the icterids also build elaborate tree nests in savannas and the same considerations may apply to them also.

THE MODIFICATION OF BROOD PARASITISM BY SELECTION

Once social parasitism begins to spread, penetrating the parasite population to a greater extent than was the case on an accidental basis, modifications of both parasite and host will follow. If the brood parasite is successful at all, it will spread rapidly and eliminate the nonparasitic population. The host, on the other hand, cannot counter except by slower evolutionary processes. Larger clutches should evolve rapidly among parasites since clutch size need no longer be limited by the number of offspring the parents can feed as is the case with nonparasitic altricial species. Little is known about the clutch sizes of parasites. However, there is good evidence that both the European Cuckoo and the Brown-headed Cowbird lay more eggs than species which raise their own young (Chance, 1940; Friedmann, 1929; Walkinshaw, 1949; Payne, 1965). In the case of the European Cuckoo, Payne (1965) has suggested that the available evidence is equivocal; it is possible that the large numbers of cuckoo eggs presumably laid by a single female may be a response to persistent robbing by the observer. Brown-headed Cowbirds apparently do not increase their clutch size but lay more clutches than their nonparasitic relatives (Payne, 1965). Various behavioral changes should also evolve. Among them are failure to respond to hormonal stimulation in the production of brood patches and broodiness (Selander and Kuich, 1963; Robinson and Warner, 1964), change in the stimuli releasing egg-laying behavior, change in the species composition of hosts, eggs mimicry, precision in egg deposition, and others.

There remains the problem of subsequent eggs. If the parasite initially had a clutch of normal size, as we have postulated, it should have been relatively easy to place a second egg. The shift to parasitism, however, must include the successful placement of additional eggs. As the parasite develops a larger clutch size, the placing of the subsequent eggs should become progressively difficult. The searching area of a female must be large enough to permit her to find enough nests at the right stage of development. If there are differences in timing of nesting of different host species, this may be a difficult problem. Specialization on a specific host species with relatively synchronous nesting should make this easier, and many social parasites do parasitize a single species or only a few species. However, if the host species are territorial, specialization can be achieved only at the expense of enormous searching areas for the female parasite. Under this circumstance the best strategy for a female parasite may be to time her ovulation to the events of a specific host nest and then to make do with whatever she can find for the remainder of her eggs. That this may be the strategy used by both the European Cuckoo and the Brown-headed Cowbird is suggested by an analysis of the distribution of eggs in the nests of host species (Preston, 1948; Mayfield, 1965).

In the nonparasitic American cuckoos the incubation period is 10 or 11 days, but in the parasitic European Cuckoo it is 14 days. Once a certain perfection in parasitism has developed, including the adaptive searching process, we may anticipate adjustments in incubation periods to match the corresponding duration in the host. If there is a nest eviction behavior such as we find in the European Cuckoo, close timing to coincide with rather than anticipate the host incubation period may be especially advantageous. If the breeding season of the foster parent is closely adapted

to environmental circumstances such as available food supplies, a three-day differential could be sufficiently inappropriate to elicit a selective pressure to induce a change in the length of incubation of the parasite to match the host. It is also possible that the endocrine changes which must accompany the abrupt transition from incubation to nestling care may be partly controlled by endogenous timing mechanisms. In this case, a maximum response to the nestling would be elicited only when the incubation schedule of the parasitic nestling matched that of the foster parent. While the limited number of experiments by Emlen (1941) showed acceptance of young Tricolored Blackbirds (*Agelaius tricolor*) as early as the completion of laying, this acceptance was statistical. Any frequency of desertion might, therefore, induce evolved changes which would more fully match the timing of the parasite to that of the host.

Once parasitism has evolved, it may be possible for parasitic species to spread into areas where parasitism could never have initially evolved. Thus, in any attempt to construct a theory of social parasitism it is necessary to distinguish clearly between the conditions necessary for the habit to become established initially and the conditions permitting successful exploitation once the specialization has been perfected.

Counterselection by host species.—Evolutionary changes are also to be expected in the species parasitized, including aggressive responses toward the female parasite, sharpening of discrimination of differences between eggs, and increases in the rate of desertion, building false bottoms to nests, and egg ejection. This in turn would favor convergence in egg color and shape toward the characteristics of the host (Baker, 1942).

It is as interesting to consider the counter parasitism mechanisms which have not developed as it is to study those which have developed. Young Brown-headed Cowbirds and European Cuckoos, as they reach their maximum dimension, dwarf their foster parents. Consider the ludicrous sight of a tiny Garden Warbler (*Sylvia communis*) standing atop a cuckoo to reach the mouth of the gaping parasite. Why does not the Garden Warbler take the adaptive measure of abandoning the nestling prematurely, especially when to the human observer, it is so clearly identifiable? The answer again appears to lie in the basic behavioral organization of the parent-nestling adaptation of birds. The adaptive complex of the parent-young relationship places a premium on stimulation of the parent by the young. There is no adaptive limit to this process and the supernormal stimulus presented by the cuckoo nestling is favored.

There has probably not been, in the evolutionary history of birds, any selective premium on species distinctiveness in the begging response. All altricial birds have essentially the same overwhelming demand in the nestling phase—to obtain a maximum energy transfer from parent to young in a minimum time. When a foster young is inserted into this system, it overwhelms the foster parents with stimulatory cues. Nor is there any opportunity for counterselection. To respond to any selective pressure of this sort would weaken the species responsiveness to all nestlings at far greater loss than occasional damage from parasitism.

Thus counterselections which have been favored relating to rejection of the parasite operate at an early phase. The foster egg may be recognized and rejected, a false bottom placed in the nest and the introduced egg buried, or the nest abandoned. For these responses there is a logical antecedent. Abandonment of nests is a frequent occurrence, often related to disturbance by predator or man. Its adaptive significance is clear: once discovered by a predator the nest stands marginal chance

of success. A greater potential advantage is to be gained by a fresh start elsewhere. It is easy to see how this process might be extended to brood parasites and their eggs, but, once the egg has hatched, an entirely new set of behavioral releasers appears and there is no precedent for abandoning the brood in the normal behavioral repertoire.

The remarkably precise and adaptive egg mimicry of cuckoos is of special interest with respect to evolved brood parasitism countermeasures. Among the Asian cuckoos in particular, mimicry of the host's egg has reached extremes of specialization, with certain species restricted to a small number of host species which their eggs closely mimic (Southern, 1954; Ali, 1931; Stuart Baker, 1942). The actual selective value of this premium can be determined only by evaluating the frequency of parasitism of each host species, a measurement which is difficult to ascertain accurately. But that such an ability has been a factor in shaping adaptation by the host is clear from Stuart Baker's (1942) measurements of desertions in the case of normal foster parents (8 per cent of 1042 cases) versus unusual foster parents (24 per cent of 298 cases). Unusual foster parents are under less rigorous selective pressure from parasites. In the case of the foster parents this is reflected in the lesser discriminatory ability (Rensch, 1924); in parasites by lack of convergent adaptation of egg color.

Matching the eggs of the host has led to a further evolutionary consequence in the case of cuckoos. Within certain species, for example *Cuculus canorus*, individual cuckoos are often host specific, laying in the nest of a single species or restricted group of species. Intensive study of the laying behavior of a single female (Chance, 1922) during three seasons indicated that 58 of her 61 eggs went into nests of the Meadow Pipit (*Anthus pratensis*). Each such specialization has been termed a gens. Other gentes in the same area may mimic and lay in the nests of other species. In the Khaska Hills, Assam district, for example, six gentes occur, separated mainly by habitat (and, therefore, according to host species), but this difference is far from complete (Stuart Baker, 1942). In Finland, three gentes occur with little geographic overlap (Wasenius, 1936). This circumstance of geographic isolation may have led to the development of gentes. Selective pressures induced by host desertion would then promote genetic differentiation in areas of geographic separation. So far, however, there is no direct evidence concerning the genetic status of gentes. As Southern (1954) has pointed out, reproductive isolation is probably not complete in these cases, and with relatively plastic host populations such a condition might be favored simply because of the frequent disappearance of local populations of certain host species, an event which would result in the concomitant loss of an obligate parasite. Nevertheless the strong selection pressures which favor the development of gentes probably also have led to the remarkable ramification of obligate parasitic species of cuckoos in Asia and Africa (Friedmann, 1948), each species specialized to a small group of host species. It must be emphasized that the gentes are intraspecific morphs of unknown genetic origin and characteristics.

Rensch (1924) experimented with the ability of birds to discriminate between colored eggs which were of the same species and those which were identical in shape and size but different in color. The results clearly demonstrate the role of parasitism in modifying the discriminatory abilities of species usually hosting cuckoos. Regularly parasitized species such as the Garden Warbler and Red-backed Shrike (*Lanius collurio*) remove the alien egg. Other species, not cuckolded, such as the European Blackbird (*Turdus merula*), Barn Swallow (*Hirundo rustica*), and European Linnet (*Carduelis cannabina*), do not discriminate against the odd egg. In the parasitized species which reject the alien egg, the species' own eggs as such are not recognized;

rather the odd egg is identified, and if a clutch of inappropriate eggs is substituted and a single egg from the individual's own clutch is included, this is the egg that is rejected (Rensch, 1925). Thus, neither parasitized nor nonparasitized species recognize their own eggs, and the developed ability to reject eggs is based upon detection of the nonconforming nature of alien eggs.

No experiments have tested the ability of foster parents versus nonfoster parents to discriminate size of eggs. The conformity of parasitic cuckoo eggs to a size considerably smaller than that of nonparasitic cuckoos of the same size does, however, suggest the development of a considerable discriminating ability. Actually the parasitic eggs, while drastically reduced in size, are, nevertheless, significantly larger than those of the host, except in some of the more perfectly adapted cases. Presumably this difference represents a balance between the decreasing discriminatory capacity of the hosts, and the selective advantage of a larger egg, but no data are available on this point.

The habit of removing an egg from the nest of the prospective host at the time of laying is characteristic of weaver birds and cuckoos. The female European Cuckoo holds the egg in its bill while laying (Chance, 1922). This eliminates the possibility that the cuckoo might err and remove one of her own eggs, since but one egg per nest is laid, and the cuckoo is required only to remember what nests she has utilized. Two cuckoo eggs are seldom found in the same host nest, and when they do occur are probably the result of two female cuckoos laying in the same nest. This category of errors is normally prevented by the territorial social system of cuckoos, parasitic or not. The advantage of the removal of an egg would not seem to be tied to the numerical characteristics of the adaptive nature of clutch size since the young cuckoo resolves the competitive aspects of nest life at birth by promptly evicting its nest mates. Rather we suggest that this may relate to satisfying the foster parent that no change has taken place, perhaps through stimuli to the brood patch, a possible reception area mediating the numerical features of egg laying (Stresemann, 1927-1934). The visual stimuli from the clutch probably do not play a significant role in a bird's appreciation of the size of the clutch (Koehler, 1940). If correct, this suggestion indicates further the extent to which the behavioral evolution of the parasitic cuckoos is influenced by the sensory system of their hosts.

Lack (1954:42-43) has argued that egg removal by the adult Great Spotted Cuckoo (*Clamator glandarius*) has its adaptive basis in reducing nestling competition. The nestling Great Spotted Cuckoo does not eject its nest mates. While this may indeed be advantageous, the comparative argument applied by Lack has no merit since the adult European Cuckoo also robs one egg before laying, even though there will be no subsequent nestling competition. Rather one may argue that such a behavior pattern (robbing one egg) may have been a preadaptation to parasitizing the species which the Great Spotted Cuckoo parasitizes.

Some hosts of parasitic cuckoos respond to the local intrusion of the adult female parasite by mobbing her (Curio, 1963). How elaborate these responses are is uncertain. Nor do we know the extent to which these responses may be more than a response to the intrusion of an unfamiliar bird into the nest area (Schleidt, 1961). An additional problem, so far uninvestigated, is the development of plumages of adult cuckoos relative to the host. Females of some species of cuckoos have very cryptic color patterns, which may represent an adaptation to avoiding mobbing responses or may facilitate undetected observation of potential host behavior. The silhouette of many cuckoos resembles that of a falcon, and adaptive mimicry may

be involved. The interesting implications of this general problem can be elucidated best by comparative studies of the behavior of host and parasite, a large task.

The fact that parasites are for the most part larger than their hosts may represent a preadaptation to countering this response, since parasitizing cuckoos often forge ahead with their task to the accompaniment of vigorous mobbing.

The peculiar gape markings of the parasitic weaver birds and some of their hosts has been a subject of much discussion and controversy. Neunzig (1929) and Southern (1954) suggest that this is a highly adaptive mimicry enabling the parasites to compete with their nestmates. But Hoesch (1939), Chapin (1954), and Friedmann (1960) have argued that these fantastic structures are evidence of common descent, too unique to be considered mimetic. The matter has recently been clarified by Nicolai (1964) in studies of the behavior, especially song, of various weavers. He has discovered that each parasitic nestling learns and uses the entire vocal repertoire of its host. But in addition, it retains aggressive notes which are like the same calls of the Euplectinae, a subfamily of the Ploceidae. In other characteristics such as the seasonal alteration of plumage types, plumage characteristics, and courtship the Viduinae and Euplectinae are similar and differ from the Estrildidae. If this evidence be deemed conclusive, then, since the Euplectinae lack the mouth markings typical of the other two groups, this characteristic must be mimetic. Friedmann's (1960) opposite conclusion, based upon an incorrect determination of the relationship of the Estrildidae and Viduinae, is thus invalidated.

A further consideration of the evolution of mouth markings with respect to parasitic adaptation is now in order. This is a development which is only characteristic of parasite nestlings which must share the nest with nestlings of the host species. Thus Lorenz (1935) has pointed out that in those cuckoo species whose nestlings evict their nestmates there is no evidence of matching of mouthpart coloration. In other species such as the Great Spotted Cuckoo which shares the nest with the nestlings of the host there is evidence of mimicry. This evidence seems to us to provide a link in interpreting the evidence concerning the weaver birds. In the deep nests of the weavers incipient parasite nestlings had no opportunity to eject nestmates or eggs. Probably the mouth markings of the hosts were considerably less dramatic, and the development of similar rudiments by the parasitic nestlings increased their probability of survival in a nest with competitors. The extreme development of these structures, which today exceed those of all other birds, is perhaps the result of selective pressure induced by parasitism, for the relative survival of both parasite and host would be enhanced by each carrying more effective stimuli to direct parental feeding than the other. This possible interspecific competition would be enhanced by the superposition of the additional nestling upon the normal nestling brood. The possibility that these markings may have developed hand in hand in both parasite and host, each driving the other to new extremes, seems to have been missed by previous authors. Yet the evidence, both of subfamilial relationship (Nicolai, *op. cit.*) and of the absolute uniqueness of this extreme adaptation, strongly suggests this possibility.

Nicolai (1964) has concluded that imprinting has been extremely important in the evolutionary history of the parasitic weaver birds, restricting each parasite species to a single estrildine host. This, he argues, has led to parallel racial and species differentiation and host specificity between the parasitic Viduinae and the host Estrildinae. Since the entire vocal repertoire of the host seems to be learned and the courtship calls of both host and parasite male are therefore identical, the matter

of species recognition among the Viduinae becomes a matter of special interest. Perhaps the elaborate courtship dances and remarkable plumage characteristics of the parasitic Viduinae are an adaptation to visual insurance of host specific mating.

These conclusions are far from agreeing with Friedmann's (1960) conclusion that host specificity is not characteristic of the Viduinae and that in certain areas viduines occur and maintain themselves where the usual host does not occur. These differences can best be resolved by field studies which evaluate population densities of potential hosts and parasites and the relative proportion of parasitism directed to each host species.

DISCUSSION

By postulating a general accidental origin of brood parasitism dependent only upon genetically controlled tendencies to deposit eggs in the nests of other species, possibly, although not necessarily, as a result of nest destruction or accidental placement of eggs during the egg-laying period, we have been able to suggest conditions which might be expected to favor the further spread of such tendencies. A review of avian brood parasites has indicated that in general they possess features which might be expected to have helped maximize the success of dumped eggs. From this survey we are led to a number of conclusions.

(1) Success should be greatest for eggs placed in other nests of the parasite species, and the releasing value of these nests should be such as to promote the habit of laying eggs in them.

(2) Similarly, at their early stages of brood parasitism, many parasites may have parasitized primarily other closely related species. This tendency is still manifest in many brood parasites whose hosts belong to closely related genera.

(3) The potential parasite should be relatively rare with respect to the potential host with the result that parasitism is most likely to evolve in species with unusual foraging ecologies that result in their comparative rarity. Moreover, this unusual adult foraging ecology is likely to pose problems at the time of breeding, particularly if the food of the adults is unsuitable for nestlings. It is interesting that most of the social parasites have unusual diets or foraging behavior, such as following big game, eating wax and hairy caterpillars, and utilizing very small grass seeds.

(4) Parasitism is most likely to evolve in regions where the breeding effort of many species is highly synchronized and where colonial close relatives are available to be parasitized. This should help maximize success of dumped eggs since the problem of synchronized timing should be minimized and access to host nests may be easiest. These conditions are likely to obtain either in temperate latitudes or in tropical regions with strongly seasonal rainfall. Today most social parasites are found in tropical and subtropical regions with seasonal rainfall. It is always dangerous to infer too much about evolutionary histories from present-day distributions, but it seems likely, considering the conditions and groups involved in brood parasitism, that tropical savannas were a major scene for the evolution of brood parasitism.

(5) Species in which females normally lay in nests built by their mates are more likely to possess response mechanisms easily triggered by the sight of empty nests and should be more likely to place eggs accidentally in nests of other species. In fact Davis (1942) has suggested that there have been two avenues of evolution to brood parasitism, one via accidental laying and the other via use of old nests or actual stealing of them. In part, however, this merely pushes back the problem one step farther. Why should a species take over nests of other species in the first place?

The fact that species closely related to brood parasites often exhibit this behavior could indicate a causal relation or merely that both behaviors are the result of an undetermined common cause. For example, if the males build the nests, both the evolution of accidental egg deposition and nest usurpation may be more easily accomplished, both achieving savings in time and energy and both initiated by the response patterns of the nonparasitic females. Alternatively, nest stealers may even have had a parasitic ancestry.

These conditions need not all be satisfied for brood parasitism to emerge in any species or group. Each contributing factor will operate independently for each population, and each characteristic will have a selective value relative to the environmental ecology of the potential parasite and the feeding ecology, behavior, and numerical status of the potential host. There is no evidence which can, at the present time, permit us to quantify the selective value of these contributing factors. What we can say is that once the sum of these characteristics reaches the level at which that part of the population which is genetically parasitic comes to the point of rearing more offspring than that which does not, selection will operate to reinforce the habit; it will spread throughout the potential parasite population, and the nonparasitic segment of the population will be eliminated. At incipient stages it is to be expected that various demes will represent all conditions from completely parasitic to nonparasitic, with the environmental conditions placing different selective values on each contributing trait and condition.

Direct experimental verification of this type of evolutionary hypothesis is impossible, but we can suggest further research which would help to provide insights into the validity of the hypothesis we have advanced here. For example, the basis for species recognition in altricial birds is critically in need of investigation. Unfortunately nearly all of the efforts on this interesting problem have been carried out with precocial species. Most notable of these are the extensive experimental studies of Schutz (1965) with many species of ducks. He exposed ducklings to conspecific and heterospecific partners, both ducklings and mature individuals. The sexual imprinting descriptively reported by Lorenz (1935) was confirmed. There is, however, under equal choice conditions, a tendency toward species-specific imprinting. Most interesting to our discussion here, sexual imprinting in ducks does not have the brief critical period for its establishment typical of the following reaction. Instead the critical period in ducks can be measured in weeks. Now it would be most interesting to know how the timing and threshold for sexual imprinting differs between brood parasites and their nonparasitic relatives if it is indeed a characteristic of them.

Recently preliminary experiments with the altricial Ring Dove (*Streptopelia risoria*) have been carried out by Klinghammer and Hess (1964), but in their tests they used humans as the imprinting objects. The responses of doves reared by individuals of other bird species are still unknown and cannot be surmised from the behavior of birds in a human-bird choice situation. Since the successful evolution of brood parasitism would seem to require innate species recognition, it is important to know how widespread innate species recognition is among altricial birds.

Since we have suggested that the feeding ecologies of brood parasites may have been of critical importance in aiding the evolution of this mode of reproduction, it is important to know more about the food and foraging of the American nonparasitic cuckoos and particularly of the parasitic Eurasian ones whose ecologies are largely unknown. Also studies of the breeding biology of nonparasitic species normally asso-

ciated with moving herds of large mammals would be helpful in elucidating the problems encountered in this way of life.

To date little experimental work has been done on the behavior of female birds whose nests have been destroyed during the period of egg laying. A combined field and laboratory study of this aspect of avian behavior could be most profitable.

In general our knowledge of avian digestive physiology is limited to a few commercially important species and virtually nothing has been done with the ontogeny of digestive abilities. Since many species of birds are fed entirely different foods as nestlings than those they eat as adults and since we have suggested that this may have been a factor influencing the evolution of brood parasitism, studies of the development of digestive abilities in the young of brood parasites in comparison to non-parasitic species would be useful. For example, at what age does the young honey guide acquire the ability to digest wax? Is a young honey guide as efficient at digesting insects as young woodpeckers and barbets? What adaptations enable young cuckoos to digest caterpillars avoided by most other birds?

Studies of this sort may provide insights which will necessitate either the rejection or substantial revision of the view we have advanced, but for the present we suggest that our hypotheses provide a reasonable interpretation of known facts consistent with current knowledge of natural selection, and that they are sufficiently broad to allow for the range of circumstances under which independent evolution of brood parasitism in different groups might have taken place.

SUMMARY

Brood parasitism has evolved a number of times among birds. Existing theories to explain the evolution of this mode of reproduction, while differing in detail, all invoke progressive "deterioration" of normal reproductive instincts. However, all changes in reproductive behavior will occur sporadically among individuals of a population and the major problem is to explain how these changes, when they do occur, result in their possessors producing more living offspring than more typical individuals. To this problem, current theories provide no answers. An alternative hypothesis, based upon genetically controlled tendencies to deposit eggs in the nests of other species, possibly, although not necessarily as a result of nest destruction, accidental placement of eggs, or lack of synchronization of nest building and egg laying is advanced. This theory is consistent with current understanding of natural selection and leads to the identification of those ecological and behavioral factors most likely to promote such behavior and give it selective advantage. The existence of a phase of incubation of the egg outside the body of the adult provides the opportunity for the intervention of the foreign genotype. The highly evolved response mechanisms of birds with respect to eggs and young preclude some potentially adaptive rejection behaviors on the part of potential and actual hosts.

Success of accidentally placed eggs should be improved if the incipient parasite has short incubation periods, is adapted to a wide variety of foods, and is indeterminate in its laying pattern. If the host species is more common than the parasite, is also an indeterminate layer, and is colonial, brood parasitism is likely to be favored from this direction. These properties of host and parasite are perhaps most likely to be met in tropical savannas and temperate latitudes. Not all of these preadaptations need be characteristic of each host and parasite species, but a survey of the groups of brood parasites indicates that each possesses several of them.

Once brood parasitism becomes established, it should spread rapidly through the

population, and further modifications of both host and parasite are to be expected and are known to occur. These involve adaptations of egg (color and size mimicry), changes of incubation periods, and the development of special behavior patterns by nestlings. Direct confirmation of evolutionary hypotheses such as this one is impossible, but several lines of research are suggested which should throw further light on the modes of origin of this breeding system.

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