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HERBERT FRIEDMANN
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ACKNOWLEDGMENTS

To APPRAISE as accurately as possible the involved situations that exist in the species of *Clamator*, it was necessary to examine carefully large segments of the preserved material. Museum study skins were inspected to evaluate the nature, frequency, and distribution of the plumage phases, and the kinds and degrees of variation within these phases for possible suggestive clues as to their nature. The changes of plumages in all the included species were reviewed for possible phylogenetic hints they might reveal. And the eggs of the cuckoos and of their hosts were examined to determine the extent of adaptive similarity, or the lack of it, thus avoiding undue influence by earlier published opinions, some of which, as suspected, turned out to be casual and rather uncritical estimates, or were based on geographic segments of the total picture.

A research grant from the Frank M. Chapman Memorial Fund of the American Museum of Natural History enabled me to spend 3 productive weeks at the British Museum (Natural History) in London, where by far the largest assemblage of the pertinent material is stored, and also to spend a few days at the United States National Museum in Washington. To the custodians of these bird collections I express my thanks for their help.

By loan of actual specimens and by correspondence from cooperative curators of their respective collections, I have been able to tabulate the data on material of special interest in the museums of Bloemfontein, Bulawayo, Cape Town, Dundo, Durban, East London, Khartoum, King William's Town, Lourenço Marques, Nairobi, Pietermaritzburg, Port Elizabeth, Pretoria, and Salisbury, in Africa; of Bombay in Asia; of Basle, Berlin, Copenhagen, Genoa, Madrid, Milan, Paris, Stockholm, Turin, and Vienna, in Europe; and of Ann Arbor, Baton Rouge, Berkeley, Cambridge, Chicago, Los Angeles, New Haven, New York, Philadelphia, Pittsburgh, and Princeton, in the United States. To the officials of all these museums, who have kindly sent me data or specimens, I hereby tender my thanks. The following individuals also have helped with observational notes and egg-specimen data: Salim A. Ali, M. Courtenay-Latimer, G. Duve, R. Kreuger, D. W. Lamm, R. Liversidge, G. R. Mountfort, J. Ottow, C. R. S. Pitman, C. G. Sibley, C. J. Skead, G. Symons, V. G. L. van Someren, J. G. Williams, and J. M. Winterbottom.

My personal field experience with *Clamator*, limited to the three species that occur in Africa, continued to play a contributing role in the present as in earlier studies. Acknowledgments, therefore, for the support that made these field studies possible are due again to the National Research Council, American Philosophical Society, the Guggenheim Foundation, and the Smithsonian Institution.

INTRODUCTION

The genus *Clamator* is one of a number of genera of cuckoos which are parasitic in their mode of reproduction. The vicissitudes of its biological history which are reviewed in this paper are of interest in clarifying some concepts involved in the overall problems of evolution of habits in the puzzling family Cuculidae.

Brood parasitism in the cuckoos is not a "single-line" development, as it is in the cowbirds, the honeyguides, or the ducks, but comprises many genera, some of which have evolved specialized features, such as the evicting habit in the nestling stage. Other genera have developed elaborate egg morphism with related host-specific gentes, some have an extremely restricted range of host species, others have a broader choice of fosterers, while still others show none of these refinements in their mode of reproduction. In the weaverbirds it is known that the parasitic habit has arisen independently in two sections of the family (Friedmann, 1960). Whether it arose equally independently in different groups of genera of parasitic cuckoos is still uncertain, but it has developed in various ways in the 18 genera that are parasites in their mode of reproduction.

These genera, each with its own special features and its own peculiar problems, are of much interest to the student of adaptation and evolution. C. D. Darlington (1953, pp. 441-443) wrote of the European cuckoo, *Cuculus canorus,* that it was ". . . uniquely instructive in its relations with the environment. Exposed from hatching to an alien environment for innumerable generations, the behaviour of the cuckoo, the instincts of the cuckoo, are determined by its heredity. Its migration and all its malpractices follow the pattern of a parent it has never seen.

"Further, of all animals, the female cuckoo most resembles man in exercising a choice which fixes her offsprings' environment . . . the cuckoo species is divided into mating groups which specialize in laying eggs in the nests of birds whose eggs theirs most closely resemble. The cuckoo species, like any large human community, thus has a spurious plasticity which derives from its variability. This variability, again like that of a human community, is preserved by natural selection, that is, by the adaptive value of a whole range of genetic types. The cuckoo is thus the most significant of all birds for the theory of heredity and environment . . ."

Without detracting from Darlington's estimate of the inherent philosophical importance of the biology of *Cuculus canorus,* it may be suggested that the present account of a group of that bird's less completely specialized relatives may even enhance it by presenting informative perspectives and tangential views into our total concept of brood parasitism in this family. There is a real need for this, since, in spite of the known differences in the mode of parasitism in the various genera of parasitic cuckoos, the literature of the subject is devoted largely to that one species, which, it so happens, is the most highly evolved and specialized of all the members of its family and possesses many features not present in other parasitic cuckoos. This has resulted in an overly accented, rather one-sided emphasis in the usual presentations and discussions of the subject. It is hoped that the present study may help to correct this and to offset some of the literature on cuckoo parasitism.

At the same time, the situation present in the four species of *Clamator* is, in itself, well worthy of study as a survey of the evolutionary history of a compact and relatively isolated genus of the family, only distantly related to *Cuculus.* The genus *Clamator* generally is considered fairly primitive; however, its included species reveal much adaptive evolution and the effects of diverse and not altogether harmonious trends. Not only is it a primitive group of highly specialized species but also one that reveals to a greater degree than most that evolution may proceed at different rates in different characters and in different species even within a small genus, and that some of these trends may even be abandoned after a state of high perfection had been achieved. In these respects this study differs from most.

The majority of studies of evolution within limited groups of animals emphasize single characters or single aspects, such as external morphology, relatively minor changes in size, shape, or proportions, or adaptation of one part or one structure to changing habits. Also, the stress has been placed on characters that seem to have gone the whole way from a generalized to a highly specialized condition. This emphasis is understandable—it is most convincing to be able to reconstruct historically the path or paths followed by piecing together carefully and critically all the available data. This procedure, however, has tended to conceal, or at least to detract attention from, the fact that many organisms have evolved only "part way," and still have managed to survive and to succeed. This is, of course, generally implied or assumed in the stage elements of all more complete developments, but it is well to underscore it where, as in *Clamator,* some of the species have stopped at "part-way" stages.

The four species of the genus *Clamator* form a compact group that has been considered by Jourdain and Baker and other writers on parasitic cuckoos as one in which adaptive evolution in egg similarity to those of its usual hosts has gone as far as in any group of brood parasites. Yet, two of the four species have geographic segments (populations or races) that either never arrived at, or else appear to have "ignored" or to have "repudiated," the results of the adaptive evolution of their respective stocks, and this situation has been arrived at in very different ways in the two.

Thus, in the case of the jacobin cuckoo, *Clamator jacobinus,* we have a species which, throughout its extensive Asiatic and part of its African range, is parasitic chiefly on babbling thrushes, most of which lay bluish eggs. In Asia and in northeastern Africa the eggs of the jacobin are always similarly bluish or blue-green in color, but in most areas south of the Sahara the resident jacobins, using some of the same type of hosts, but more frequently, bulbuls and shrikes, lay only pure white eggs, which contrast strikingly in appearance with those of their victims.

Turning to the great-spotted cuckoo, *Clamator glandarius,* we find that this species lays but one type of egg throughout its range. In the Iberian peninsula and adjacent parts of northwest Africa, it is almost exclusively parasitic on magpies, with the eggs of which its own show extreme similarity. So great, indeed, is the resemblance, that it has been cited frequently as an example of "perfected" adaptive evolution, and some not uncritical collectors have had the experience of collecting sets of eggs containing both species without realizing this until later. However, in Egypt and in most of Africa south of the Sahara where there are no magpies, this cuckoo parasitizes crows of several species, and also it lays frequently in the dark, hole nests of starlings. Its eggs show little resemblance to those of these hosts.

If it could be demonstrated that the egg type of *Clamator glandarius* had evolved as an adaptation toward the use of magpies as hosts (it is the only species of *Clamator* laying speckled eggs, which egg type in cuckoos generally is considered an "advancement" from the more primitive unmarked eggs), then it would follow that the geographic spread of this cuckoo to areas where there are no magpies would appear to be a matter involving something akin to a "repudiation" of the specialization it had achieved earlier through natural selection with the magpie as the effective agent. This, if established, would open a rare opportunity to study the biology of a highly adapted species in a new environment where this adaptive excellence no longer is a special advantage, but where it is apparently no critical encumbrance with new and nonadapted hosts.

In attempting to trace the course of the evolution of a group of organisms, or of a habit and its correlated morphological characters, it is a common experience to find that the trend generally is toward a more and more perfected stage of adaptation, eventually reaching a degree of perfection beyond which it cannot, or at least does not, go. From the general to the specialized, from the "good enough to survive" to the obviously advantageously adapted, seems to be the history of case after case. What is unusual is to find a highly adapted evolutionary product apparently *departing* from the particular set of conditions which its past history appears to have been concerned in meeting more effectively, and carrying with it in its secondary path the primary adaptations no longer needed or especially advantageous to it.

On the other hand, if it should seem more likely that the great-spotted cuckoo developed its speckled-egg type south of the Sahara, and subsequently spread to Mediterranean areas, where its egg happened to "fit" so well with those of a new host, this would have to be considered as a most unusual instance of preadaptation. It should be kept in mind, however, that the known facts concerning host egg similarity, or mimicry, in parasitic cuckoos generally cannot be explained satisfactorily on the basis of any assumed preadaptations, but, on the contrary, indicate the degree to which real adaptations in egg coloration have been evolved.

The situation in the jacobin cuckoo is just the opposite. The seemingly similar success of the white-egg laying population with that of the blue-egg layers raises the problem of the efficiency as selective agents of the relatively uniformly blue-egg laying hosts.

Inasmuch as host adaptation is an important part of the biology of brood parasitism, the picture in *Clamator* commends itself for careful study and interpretation. This is attempted in the present report. Still other biological problems, similarly apparently arrested in their development as "part-way" stages in the species of *Clamator,* concern development of plumage morphisms and of migratory behavior. Thus, in two of the four species we find geographically delimited melanistic plumage phases, more restricted in range in one than in the other, but in neither has the black morph replaced, or achieved reproductive isolation from, the pale, or normal, morph. Also, all four species are migratory in parts of their total respective ranges and not in other parts. The extent of migratory movement within a single species varies from none at all to thousands of miles. Geographic segments of each, not necessarily even subspecifically distinct, differ markedly from other conspecific segments in this important trait. These are also discussed with all available evidence in the following pages.

The four species of crested cuckoos comprising the genus *Clamator* form a group of birds that still reveal much—that in other groups has been concealed—in their continued progress toward greater adaptive excellence.

PHYLOGENETIC RELATIONSHIPS

The genus *Clamator* contains four species of crested cuckoos of Africa, Asia, and parts of Mediterranean Europe (fig. 1)—*jacobinus, levaillantii, coromandus,* and *glandarius.* It forms a natural, easily recognized group, characterized by a well-developed occipital crest of elongated feathers, by a transilient mode of remigial molt, and by the nares in the form of linear ovals. It agrees with the subfamily Cuculinae in being parasitic in its breeding, but lacks the evicting behavior pattern in its young. It agrees with the Cuculinae in most other characters, but varies from that group in the direction of the Phaenicophaeinae in having only 13 cervical vertebrae (14 in the Cuculinae and in the other subfamilies of cuckoos), and in having the muscle formula "ABXYAm" (Berger, 1960). No one has proposed merging it with any other genera, and practically all of its recent investigators (Stuart Baker, Berger, Friedmann, Jourdain, Peters, the Stresemanns, etc.) have generally agreed that it is a primitive group in its particular subfamily, the Cuculinae. This is

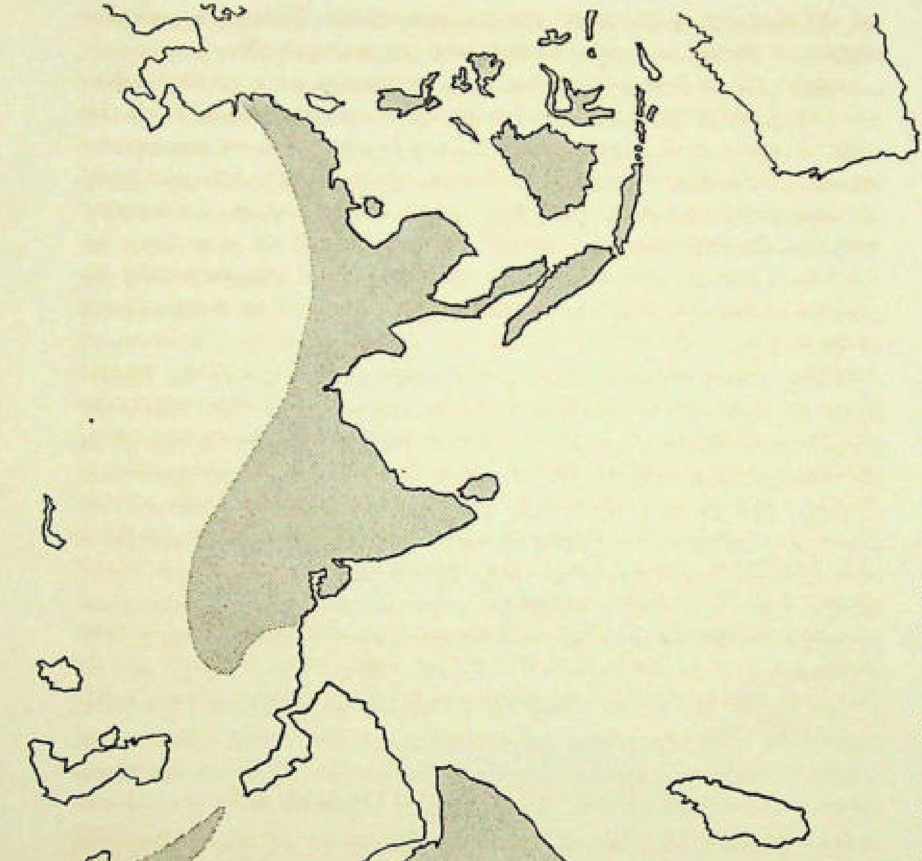

FIG. 1.—Geographic range of *Clamator*.

the subfamily that not only contains most of the genera of parasitic cuckoos (all but the two Neotropical *Tapera* and *Dromococcyx*), but also contains no cuckoos that are not parasitic, as do the other five subfamilies. In their recent study of the molting patterns of the cuckoos, the Stresemanns (1961) have pointed out also the primitive nature of *Clamator's* transilient mode of remigial molt, and have mentioned the absence of evicting behavior in its young as another evidence of primitiveness. Peters (1940) seems to have been so convinced of the primitive nature of the genus *Clamator* that he actually placed it at the very beginning of his list of all the members of the family.

While I also conclude that the crested cuckoos are to be looked upon as among the primitive, oldest sections of the subfamily Cuculinae, I doubt that this subfamily may justifiably be placed at the base of the whole family. Inasmuch as nest-building, incubation of eggs, and care of young are features of reproductive activity in practically all groups of birds, it seems likely that the most primitive cuckoos were nonparasitic as well. From this it follows that a subfamily made up wholly of brood parasites could not be the most primitive section of a family that contains many self-breeding genera and species.

The age of the genus *Clamator* is, of course, unknown, but some suggestive evidence points to its being not later than Pliocene in origin. This is an inference based on the fact that although the genus occurs over a wide area in Africa and in southern Asia, it is absent in the Malagasy Republic (formerly Madagascar). In his study of the history of the African terrestrial fauna, Lönnberg (1929) concluded that Pliocene faunal transfers between southern Asia and Africa generally are absent from the Malagasy Republic regardless of the extent of their range in either of the two continents. The fact that *Clamator* does not occur in Malagasy suggests that the spread of the genus probably took place during, or subsequent to, the Pliocene, at which time Malagasy became completely isolated as an oceanic island. As a result of the present study, it appears that the southern African population of *C. jacobinus* is the oldest, most primitive of existing *Clamator* stocks, and it seems that its species spread throughout much of Africa and thence to Asia. The fact that in southern Asia this stock gave rise to a more involved evolutionary development than in Africa, and eventually produced so different a bird as *C. coromandus,* which, in turn, seems a stage on the phylogenetic road that culminated in *C. glandarius,* suggests a very considerable antiquity for the genus in

Asia. The need for sufficient time makes a Pliocene spread more probable than a post-Pliocene infiltration, presuming, of course, a Pliocene or pre-Pliocene origin of the group stock in southeastern Africa.

The fossil record of the Cuculidae gives no pertinent data. The family is known from the Oligocene of France *(Dynamopterus velox)*, from the middle Miocene *(Necrornis*, only questionably a cuckoo), and from numerous Pleistocene remains too recent to be of any use in reconstructing the history of the family *(Coua, Cuculus, Geococcyx, Coccyzus, Crotophaga, Tapera*, and *Pyrrhococcyx*), but even there nothing close to *Clamator*.

It is not feasible to say, or even to guess, from what stock *Clamator* may have evolved, as there are no living cuckoos that seem likely ancestral forms. Yet I cannot put down the vague thought that something like the Phaenicophaeinae in Asia, or like *Ceuthmochares* in Africa today, may be closer to—less subsequently specialized and hence less deviated from the original—primordial stock of the family, and to this extent may be looked upon as existing representations of the ancestral group that gave rise to *Clamator*.

Recent studies by Berger (1960, p. 82), especially his myological dissections, coupled with his familiarity with what had been written of the breeding habits, parasitic or otherwise, of the genera of cuckoos, led him to write as follows ". . . It would appear that one must discount either myological data or breeding behavior in deciding the relationships among the cuckoos . . . Thus, if we are to place any value on morphological characters, we must assume either that parasitism has developed independently as many as four times in this one family (which seems highly unlikely) or that the parasitic habit (or tendency for it) developed in the primitive cuckoos (all ABXYAm) . . ." Similarly, Darlington (1957, p. 273) concluded from a study of the geographic distribution of the cuckoos as a whole, that the family is probably ancient and had a ". . . complex, undecipherable history."

Although there is fairly good agreement among students that *Clamator* is a primitive genus, there is no such concurrence as to what other living genera it is closest in its phylogenetic relations. The Stresemanns (1961, p. 328) concluded that *Clamator* was only distantly related to the other Cuculinae. Many years ago, Sharpe (1872, p. 68) suggested it was somewhat similar to *Eudynamis*, but this is not substantiated by Berger's anatomical findings (1960). He noted that there were two basic types of cuculine muscle formulae, and that *Clamator* was of one type, along with such genera as *Cuculus, Chrysococcyx, Surniculus, Tapera,* and others, while *Eudynamis* was of the other, along with *Scythrops* and *Dromococcyx.* It must be admitted that it is not wholly clear how significant this myological character may be, as each group contains genera that seem only distantly interrelated. Thus, in the former aggregate, *Tapera* is very different from the rest, and in the latter group all three genera are widely separated.

Berger's anatomical studies, together with earlier work by Beddard, Forbes, Fürbringer, and others, give us our best evidence of relationships within the family. All the characters, osteological, myological, and even ecdysial, have one thing in common—they are all of sufficiently nonfunctional nature as to make them seem relatively removed from the effects of selection. Hence they may be looked upon as phylogenetically conservative, and, to that degree, they are reliable indices of relationship. Breeding habits, parasitic or otherwise, are more amenable to change. In fact, one of the safest deductions that may be made from a study of brood parasitism is that in all the groups in which it occurs it is a secondary situation that arose in stocks that were originally self-breeding.

Inasmuch as all the members of the Cuculinae are parasitic, it would seem that brood parasitism had already become established in their common, remote, ancestral stock before they became differentiated into the genera as we know them today. This differentiation has resulted in a wide variety of end products, some 16 genera with 46 species according to Peters' list (1940), which suggests a long period for its operation. This, in turn, indicates a great antiquity of brood parasitism in the group, an antiquity that the history of *Clamator* suggests must date from pre-Pliocene or not later than Pliocene time.

In studying the genus *Clamator* we are fortunate in that considerable information is available on the life histories of each of its four species. The entire group has been considered by Baker and by Jourdain, two of the principal students of cuckoos' eggs, as one in which adaptive evolution in egg similarity to those of its usual hosts has progressed as far and as successfully as in any genus of cuckoos. *Clamator* is, therefore, a primitive group of highly evolved species, a biological situation that is not infrequent despite its seemingly paradoxical nature. As Baker (1942, p. 3) put it, ". . . perfection or completeness in adaptation or evolution must depend upon time . . . and therefore the most perfectly evolved egg need not and does not belong to the most perfectly advanced Cuckoo. The more primitive forms of parasitic Cuckoo, such as members of the genus *Clamator,* containing the Great Spotted Cuckoo, have probably had an infinitely longer existence in their present form and condition than such beautifully perfected forms as our Common Cuckoo, and we should therefore expect primitive Cuckoos to have acquired a more perfect adaptation in their eggs than those Cuckoos more highly developed."

The phylogenetic relationships of the species of *Clamator,* as suggested by all the data brought together in this paper, ethological, morphological (chiefly plumage coloration and eggshell pattern), and distributional, as shown in the diagram (fig. 2), reveal that *jacobinus* is the most primitive member, and that from it two lines of descent bifurcated. One, rather short one, led to *levaillantii;* the other longer one led to *coromandus* and from this to the "climax" species, *glandarius.* The geographic movements undergone by *Clamator* during its differentiation and dispersal are shown in figure 3.

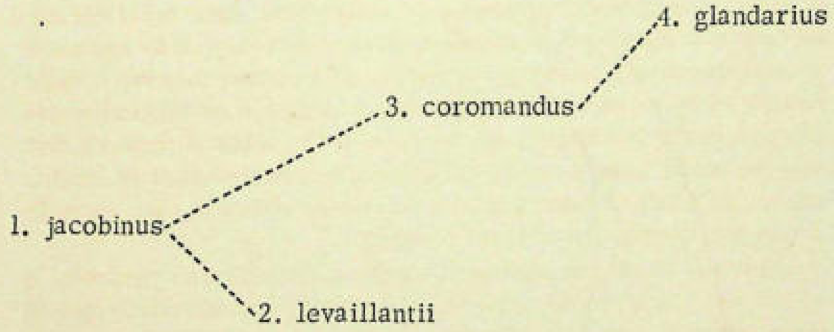

FIG. 2.—Relationships within the genus *Clamator.*

FEATURES OF BROOD PARASITISM IN CLAMATOR

The genus *Clamator* evolved from an earlier stock that was already parasitic, as is indicated by the fact that all of its species are parasitic. It is understandable, therefore, that a comparative survey of their habits affords no clues as to the origin of this mode of reproduction, although it does reveal much of the course of the development parasitism underwent in this particular genus.

Compared with a highly specialized group, such as the species of *Cuculus, Clamator* is relatively simpler and shows none of the development of infraspecific gentes, each with its elaborate, adaptive egg

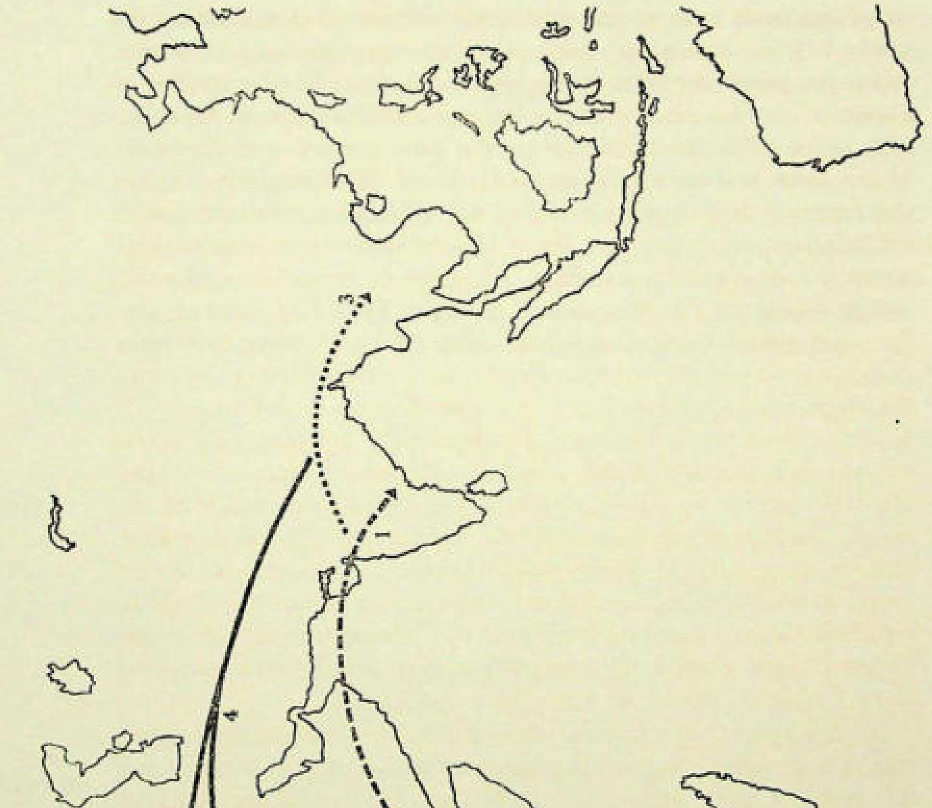

FIG. 3.—Evolutionary dispersal of *Clamator*.

1. Dispersal of *C. jacobinus* from southeast Africa to most of Africa and to India. 2. Dispersal of *C. levaillantii*. 3. Dispersal of *C. coromandus*. 4. Ancient dispersal of *C. glandarius*. 5. Recent dispersal of *C. glandarius*.

morphism, and none of the instinctive eviction of nestmates by the newly hatched young, so characteristic of some species of *Cuculus*. Also, compared with the latter genus, all four of the species of *Clamator* are far more prone to deposit multiple eggs in individual host nests, either multiple eggs by the same cuckoo or multiple use of the same nest by several cuckoos. These differences suggest that the refinements shown in *Cuculus* are evolutionary advances over the basic cuculine stock and that *Clamator* is nearer to the original, common ancestor in these matters. This lack of conformity or control in egg deposition led Mountfort (1958, pp. 54-56) to conclude that ". . . the parasitic behaviour of the Great Spotted Cuckoo is in many respects more complicated than that of our familiar Cuckoo, in which the single nestling merely evicts its foster-brothers from the nest . . ." It seems truer to say that the "uncomplicated" behavior of *Cuculus canorus* is a result of much adaptive evolution, whereas the "complicated" picture in *Clamator glandarius* still retains much of the simpler, less-developed features of the basic primitive parasitic cuckoo that we may postulate as the remote source of both genera. In my introductory statement I mention that the entire literature and thinking about cuckoos is overly dominated by *Cuculus canorus*. If specific evidence were needed to demonstrate this, Mountfort's statement about *Clamator glandarius* would be a case in point.

All the species of *Clamator* have the habit, common to so many parasitic cuckoos, of removing one or more of the host eggs from the nests of their victims either before or after laying in them. Occasionally this does not take place, and in some nests some of the host eggs are dented (equivalent, in survival terms, to destroyed) by the beak or the claws of the adult parasite. There are ample observational data on this in three of the species—*jacobinus, coromandus,* and *glandarius*. The lack of such records for *levaillantii* is not significant. There is no need to repeat here these observations as they are already on record in my earlier (1949a, 1956) accounts, and in that of Stuart Baker (1942). Particular mention may be made, however, of Mountfort's observations (Mountfort, 1958, pp. 54-56; Mountfort and Ferguson-Lees, 1961, pp. 98-99), one of the few detailed recent contributions on this habit in *C. glandarius*. They marked eggs with indelible ink so as to be able to identify them individually on consecutive days; they found that when the hen cuckoos laid they removed one and sometimes two of the magpie's eggs. In no instance did they remove eggs laid by other great-spotted cuckoos, which raises the question as to whether they could recognize the small differences in the eggs. Mountfort and Ferguson-Lees found that as many as three cuckoos laid in one nest.

The various topics of interest in the brood parasitism of *Clamator* are discussed in detail below (pages 14 to 62).

HOST SELECTION AND ITS EVOLUTION

A study of the four species of *Clamator* yields considerable data relevant to the evolutionary changes that formed their present host preferences. Not only are the hosts of each fairly definitely restricted in kind, but two of the four parasites show unmistakable signs of changes in their selection of favored fosterers. To this extent they afford glimpses of the past development of their host orientation, a basic part of their parasitic mode of reproduction. The two that show these signs of evolutionary change are *C. jacobinus* and *C. glandarius,* the most primitive and the most advanced members of the genus. In both species, the change took place together with extensive geographic expansion of their ranges. Furthermore, on the basis of the total survey it is possible to sense the course of host selection in the other two *Clamators* as well.

Clamator jacobinus (figs. 4, 5, pp. 15, 16)

The presumed ancestral home of the pied cuckoo, *C. jacobinus,* is in southeastern Africa, the area now inhabited by the race *serratus.* In this region, ranging from Cape Province, Natal, Transvaal, Orange Free State, parts of South-West Africa, and Bechuanaland, to Southern and Northern Rhodesia and Nyasaland, the cuckoo has been found to lay its eggs in the nests of 22 species, but 13 of these have been recorded as hosts but once, and 2 others but twice. The only species definitely known to be frequent and regular fosterers are four species of bulbuls of the genus *Pycnonotus (nigricans, barbatus, capensis,* and *importunus)* and two shrikes, *Lanius collaris* and *Telophorus zeylonus.* These 6 hosts account for 101 of the total 123 cases of parasitism by *serratus* known to me.

When the pied cuckoo began its geographic expansion, giving rise to the race *pica* in equatorial and northeastern Africa and in India, the population inhabiting these new areas turned from bulbuls and shrikes to babblers as their chief fosterers. The race *pica* has been found to parasitize some 36 species of birds, half of which have been so recorded but a single time. No fewer than 26 of the known hosts are babblers, and all the hosts for which there are 5 or more records are species of this group. More than four-fifths of all instances of

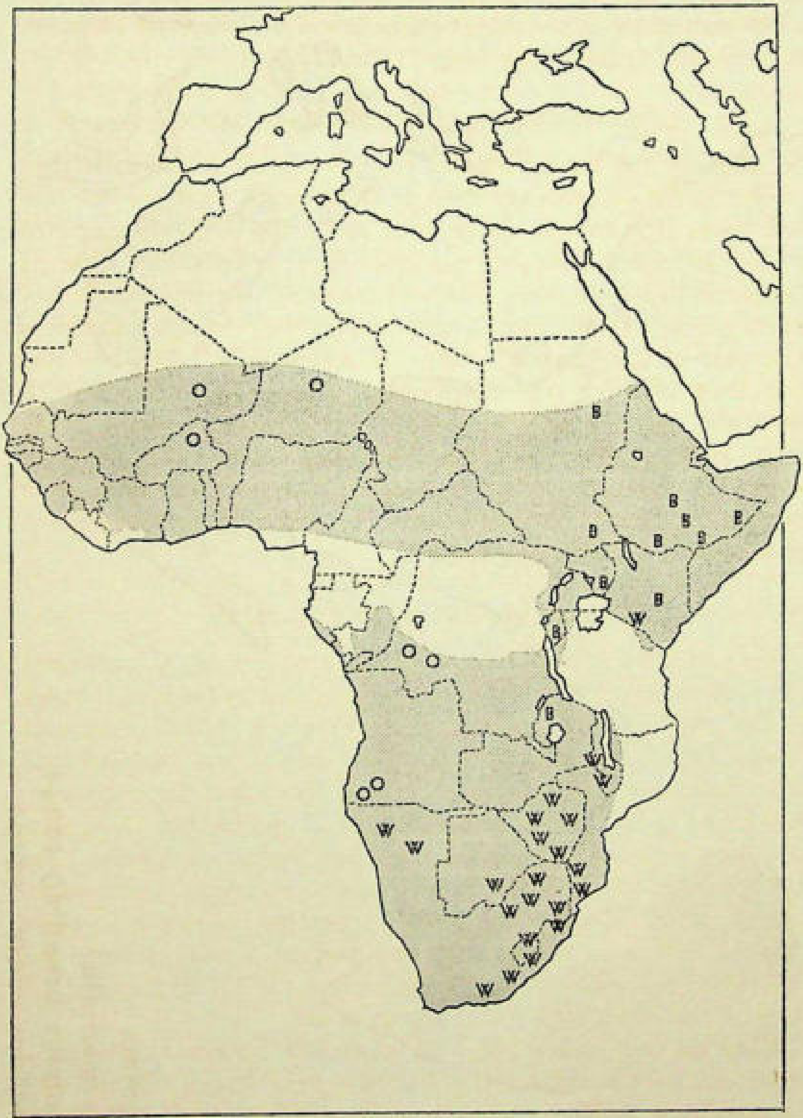

FIG. 4.—African range of *Clamator jacobinus*.
W, White egg record. B, Blue egg record. O, Egg of unrecorded color.

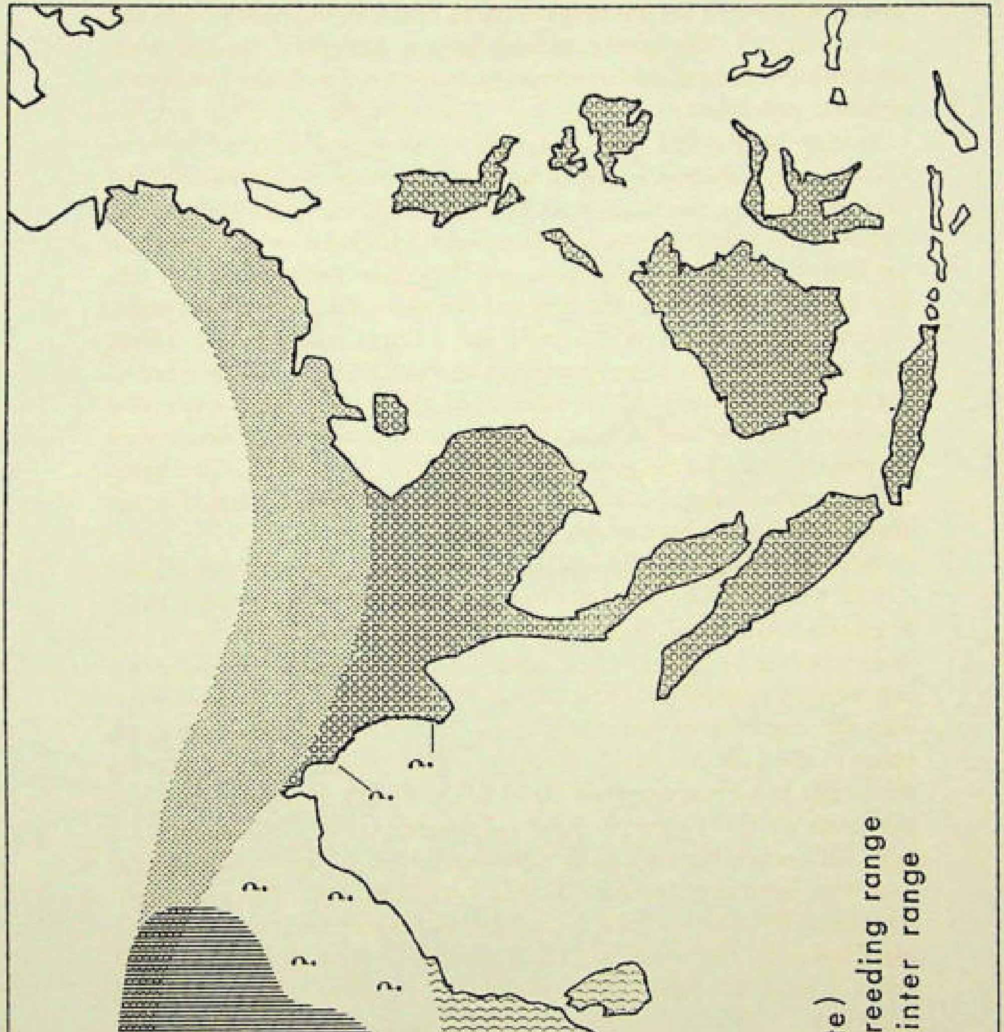

FIG. 5.—Asiatic range of *Clamator*.

parasitism by *pica* known to me refer to 7 species of babblers (94 out of a total of 106 nests) of the genera *Garrulax (moniligerus, pectoralis, delesserti,* and *erythrocephalus)* and *Turdoides (caudatus, striatus,* and *affinis)*.

It may be stressed that inasmuch as several species of bulbuls, shrikes, and babblers occur as breeding birds in considerable numbers throughout the ranges of both races of the pied cuckoo, the difference in host selection is not something imposed on the parasites. In Kenya the race *pica* has been noted by van Someren *(in litt.)* to lay fairly frequently in the nests of a bulbul, *Pycnonotus barbatus,* (3 records), but in India there is but a single instance of a bulbul nest used by the parasite. Inasmuch as Kenya was an early area of invasion in the course of the northward spread of *C. jacobinus,* this tendency there to use bulbuls as fosterers may have been established very early prior to the general shift to babblers. As discussed more fully elsewhere (pp. 51-53) the egg of *pica* is greenish blue whereas that of *serratus* is pure white.

In India, where the pied cuckoo has been studied extensively, Baker (1942, p. 82) had no records of its eggs in central or southern India from any nests other than those of babblers, though a few such had been reported by others. It so happens that this cuckoo, after becoming well established in India, began to expand its range northward into the foothills of the Himalayas. Baker noted that "when we come to the hills . . . we find the . . . Pied Crested Cuckoo placing their eggs in a great range of birds' nests, though in most cases these are nests of the Larger Laughing-Thrushes, nearly all laying blue eggs with which the eggs of the Cuckoos do not contrast. The normal fosterers here are undoubtedly the Necklaced and Black-gorgeted Laughing-Thrushes in the Eastern Himalayas and the Striated Laughing-Thrush in the Western. Of eggs laid in these nests I have 49, while I have 42 deposited in the nests of twelve other Laughing-Thrushes . . . With the exception of the species mentioned . . . I do not believe any of the others could be considered normal fosterers, while even these three can only be considered normal because they have been selected as such by birds breeding outside their own normal Plains area. . . ."

In Africa, when *C. jacobinus* stock gave rise to what has evolved into *C. levaillantii,* that new group, even more than the more northern *jacobinus* (now *pica*), became attached to babblers in its brood parasitism. In these birds, *C. levaillantii* found an abundant supply of fosterers and in their use found an escape from competition with its long-established ancestral relative. To this day *C. levaillantii,* as we shall see, is parasitic chiefly on babblers. In India, when the *C. jacobinus* stock gave rise, apparently in the northern part of its range in the foothills of the Himalayas, to what has become *C. coromandus,* the trend shown in the relatively recent use of laughing-thrushes by northern *jacobinus* became well established in the new group. We find today that laughing-thrushes, chiefly of the genus *Garrulax* are the mainstay of *C. coromandus.*

The tabular list of the known fosterers for each of the three races of the pied cuckoo shows the remarkable degree to which the hosts of the African *serratus* and the Indian *pica* and *jacobinus* differ. The picture is not as clear in the case of the African population of *pica,* as data on it are still rather sparse, and involve only five species of hosts—a bulbul, *Pycnonotus barbatus,* three babblers of the genus *Turdoides (fulvus, rubiginosus,* and *leucopygia),* and a shrike, *Telophorus zeylonus.* It may be expected that more extensive observations will add further Timaliine fosterers to this list, as there is no reason to suppose that African *pica* differ from Asiatic ones in their type of host choice.

HOSTS OF CLAMATOR JACOBINUS

Host	*serratus*	*jacobinus*	*pica*
Stigmatopelia senegalensis aequatorialis..............	x	...	...
Centropus grillii wahlbergi.........................	x	...	...
Halcyon albiventris albiventris......................	x	...	...
Colius striatus minor.............................	x	...	...
Colius indicus indicus............................	x	...	...
Dicrurus adsimilis adsimilis........................	x	...	...
Campephaga phoenicea flava......................	x	...	...
Pycnonotus cafer bengalensis.......................	...	...	x
Pycnonotus nigricans	x	...	...
Pycnonotus capensis	x	...	...
Pycnonotus barbatus layardi.......................	x	...	...
Pycnonotus barbatus fayi.........................	...	...	x
Pycnonotus barbatus tenebrior......................	x	...	...
Pycnonotus importunus importunus.................	x	...	...
Pycnonotus importunus noomei....................	x	...	...
Phyllastrephus terrestris terrestris.................	x	...	...
Aegithina tiphia humei...........................	...	...	x
Turdoides caudatus caudatus......................	...	...	x
Turdoides earlei earlei...........................	...	...	x
Turdoides longirostris	...	x	...
Turdoides malcolmi	...	...	x
Turdoides subrufus subrufus......................	...	...	x
Turdoides striatus sindianus......................	...	...	x

HOSTS OF CLAMATOR JACOBINUS (continued)

Host	*serratus*	*jacobinus*	*pica*
Turdoides striatus somervillei	...	...	x
Turdoides striatus malabaricus	...	...	x
Turdoides striatus striatus	...	x	x
Turdoides striatus rufescens	...	x	...
Turdoides fulvus acaciae	...	...	x
Turdoides rubiginosus rubiginosus	...	...	x
Turdoides jardinei natalensis	x	...	...
Turdoides affinis affinis	...	...	x
Turdoides leucopygia omoensis	...	...	x
Babax lanceolatus woodi	...	...	x
Garrulax moniligerus moniligerus	...	x	x
Garrulax pectoralis pectoralis	...	x	x
Garrulax pectoralis meridionalis	...	x	...
Garrulax striatus striatus	...	...	x
Garrulax striatus brahmaputra	...	...	x
Garrulax leucolophus leucolophus	...	...	x
Garrulax delesserti gularis	...	...	x
Garrulax ruficollis	...	...	x
Garrulax merulinus merulinus	...	x	...
Garrulax caerulatus subcaerulatus	...	...	x
Garrulax cachinnans cachinnans	...	x	...
Garrulax lineatus lineatus	...	...	x
Garrulax austeni austeni	...	...	x
Garrulax squamatus	...	...	x
Garrulax erythrocephalus chrysopterus	...	...	x
Garrulax phoeniceus bakeri	...	...	x
Actinodura egertoni khasiana	...	...	x
Alcippe nipalensis nipalensis	...	x	x
Parisoma subcaeruleum subcaeruleum	x	...	...
Copsychus saularis saularis	...	...	x
Cinclidium leucurum	...	...	x
Enicurus maculatus guttatus	...	x	x
Monticola rufiventris	...	...	x
Myophoneus caeruleus temminckii	...	...	x
Zoothera citrina citrina	...	x	x
Sigelus silens	x	...	...
Terpsiphone viridis perspicillata	x	...	...
Sphenoeacus afer transvaalensis	x	...	...
Motacilla capensis capensis	x	...	...
Motacilla aguimp vidua	x	...	...
Laniarius ferrugineus natalensis	x	...	...
Telophorus zeylonus zeylonus	x	...	...
Telophorus zeylonus phanus	...	...	x
Lanius schach tricolor	...	...	x
Lanius schach nigriceps	...	x	...
Lanius collaris collaris	x	...	...
Petronia superciliaris superciliaris	x	...	...

One important point, not revealed by the tabulation, is the relative frequency with which the different hosts are selected. Out of the total 123 African records, 59 are of species of the genus *Pycnonotus,* and 14 more are of other bulbuls, making a total of 73, or almost 60 percent of the total, that refer to this one family of hosts; 23 are of one species of *Lanius,* and 10 more are of other shrikes, a total for this family of 33, or more than 25 percent of the total; only 5, or not quite 5 percent, are of babblers. On the other hand, out of 106 Asiatic records, only 1 is of a *Pycnonotus,* but over 85 percent are of babblers, chiefly of the genera *Turdoides* and *Garrulax.*

The figures given above for the frequency of parasitism on bulbuls and shrikes in Africa are actually below the truth, as they are based solely on the total of individual instances reported. They make no allowance for the undocumented, general statements of experienced collectors, such as Plowes (1944, p. 93), who wrote that practically every bulbul nest examined was found to contain one or more eggs of the jacobin cuckoo. Also, generally a lower percentage of cases of parasitism on frequent hosts gets into the literature because of their repetitive nature, whereas practically all cases of infrequent ones are apt to find their way into print eventually.

As may be seen from the list of fosterers, in the great majority of cases the pied crested cuckoo lays its eggs in open, cup-shaped nests built in trees or bushes. The one record of its using a kingfisher as a host (Schönwetter, 1928, p. 130) and the two involving the rock sparrow, *Petronia* (de Klerk, 1942, p. 58), are the only instances of its parasitizing hole-nesting species. Another unusual type of nest choice is the lone case of a coucal, *Centropus grillii wahlbergi,* as a host. This bird builds a roofed-over, or domed, nest of fine twigs and grasses, on the ground. Other frequently terrestrial-located nests known to be used occasionally are those of two species of wagtails, *Motacilla capensis capensis* and *Motacilla aguimp vidua,* and of the grass-bird, *Sphenoeacus afer transvaalensis.*

In the present state of our knowledge of *Clamator jacobinus* the only obvious difference in its overall "fitness" to all the aspects of its existence in India and northeastern Africa on the one hand, and in southern Africa, on the other, is the much lesser degree of adaptive similarity of its eggs to those of its common hosts in the latter area. Strangely enough, in the areas where there is adaptive similarity it appears to have value to the parasite, but in the areas where it is nonexistent its absence seems quite unimportant. Baker's data (1942, p. 83) on this cuckoo in India reveal a strong correlation between percentage of host acceptance of its eggs and the degree of egg resemblance involved, and, conversely, between the incidence of rejection when the cuckoos' eggs are deposited in nests of nonadaptive hosts and the degree of difference in the eggs of the two. Thus, of 106 parasitized nests of "normal" (*i.e.*, egg-adapted) fosterers, only 1 was deserted (less than 1 percent); of 48 parasitized nests of "unusual" fosterers, 3, or 6.25 percent were deserted; of 8 parasitized nests of "abnormal" fosterers, 5, or 62.5 percent, were deserted. Similar figures were found (Baker, 1942, p. 85) for the red-winged crested cuckoo, *Clamator coromandus:* of 111 "normal" fosterers' nests, 1, or 0.9 percent was deserted; of 58 "unusual" fosterers' nests, 4, or 6.9 percent were deserted; of 12 "abnormal" fosterers' nests, 6, or 50 percent were deserted.

In the case of the jacobin cuckoo in southern Africa no such correlation has been found. In fact, the most frequently imposed upon hosts in South Africa are two bulbuls, *Pycnonotus nigricans* and *P. barbatus,* whose eggs are salmon to pinkish white, blotched and blurred with reddish brown and grayish lavender, very different from the pure white eggs of the local race of the jacobin cuckoo. Yet these bulbuls accept and incubate these dissimilar eggs. Perhaps the next commonest host in that area is the fiscal shrike, *Lanius collaris,* whose eggs also differ from those of the parasite about as much as do those of the bulbuls, being grayish green rather than pink, but equally speckled and blotched with brown and lilac. The fact that this shrike accepts the strange eggs is even more surprising, as it is an aggressive bird that has been known to attack and to drive off the cuckoos when they come too close to its nest. Yet, in spite of this, once the eggs are deposited in the nest, the seemingly alert, pugnacious host appears to be indifferent to their appearance.

Clamator levaillantii (fig. 6, p. 22)

The stripe-breasted cuckoo is the least known member of the genus, but while the total number of observed instances of its parasitism is less than that of the others, it is sufficient to show a marked preference for babblers as fosterers. The list includes 10 species, 6 of which are babblers, and which, together, account for more than three-fourths of all the records. In fact, one species, *Turdoides jardinei,* alone, with

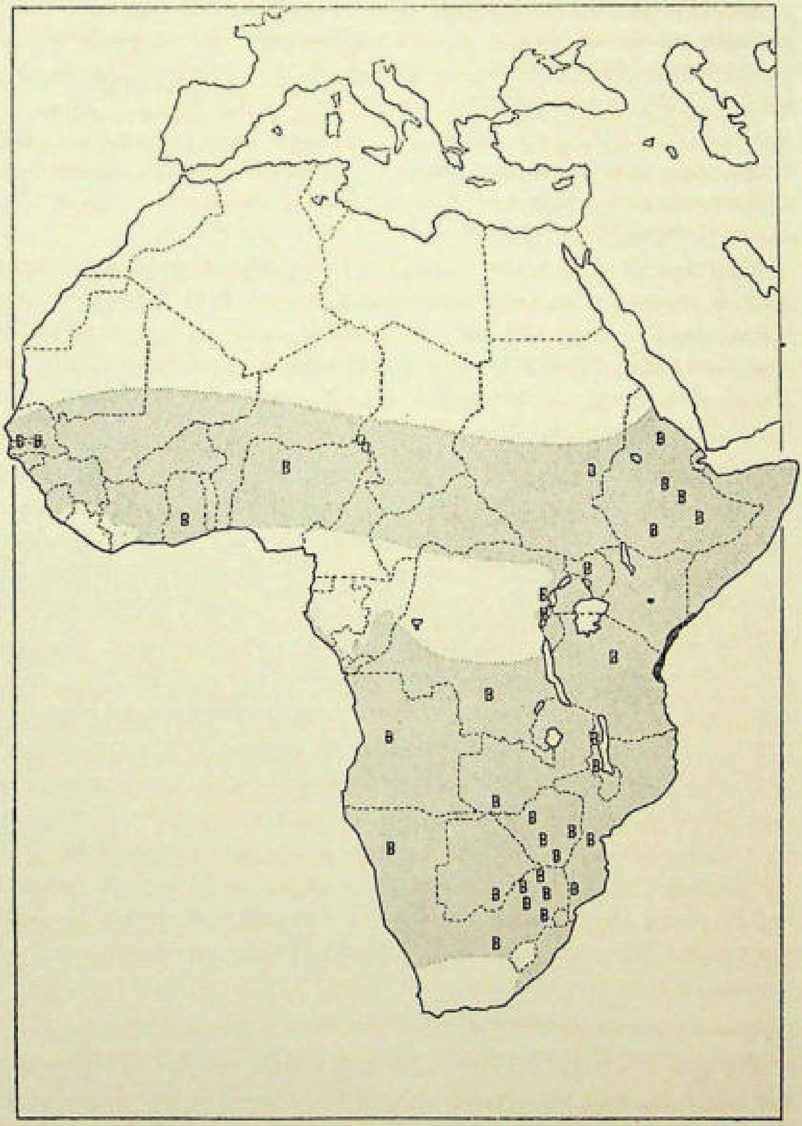

FIG. 6.—Range of *Clamator levaillantii*.
B, Breeding record. Solid black area denotes region of polymorphism.

some 23 records, account for half of the total. The known hosts are as follows:

Phoeniculus purpureus zuluensis
Colius striatus striatus
Pycnonotus barbatus minor
Pycnonotus barbatus layardi
Phyllanthus atripennis bohndorffi
Turdoides plebeja gularis
Turdoides plebeja cinereus
Turdoides plebeja plebeja
Turdoides plebeja platycircus
Turdoides jardinei jardinei
Turdoides jardinei natalensis
Turdoides jardinei kirki
Turdoides jardinei emini
Turdoides jardinei tanganjicae
Turdoides reinwardii reinwardii
Turdoides leucopygia hartlaubii
Turdoides bicolor
Cossypha caffra caffra

Of these 10 species, the first is not more than an accidental choice, and is based on a questionable identification of the parasitic egg (Roberts, 1939a, pp. 10-13). In addition to these it may be added that Bradfield (1931, pp. 7-9) suggested that in Damaraland the Burchell starling, *Lamprotornis australis,* was also parasitized, but he had no evidence other than that he had noted these starlings "mobbing" a stripe-breasted cuckoo.

Clamator coromandus (fig. 5, p. 16)

The red-winged cuckoo is parasitic chiefly on babblers, and, within this group, primarily on the larger laughing-thrushes of the genus *Garrulax,* some 13 species of which have been found to be victimized. Baker (1942, pp. 196-197) listed 265 eggs of the red-winged cuckoo in his collection, taken from nests of 21 species (25 species and subspecies) of hosts. Of these 265, all but 24 were found in nests of *Garrulax,* and no fewer than 109 from nests of a single species, the necklaced laughing-thrush, *G. moniligera,* and 37 from nests of the black-gorgeted laughing-thrush, *G. pectoralis.*

Our knowledge of this cuckoo's fosterers is still largely based on collections and observations from the Indian and Burmese portions of its range. In due time many hosts from other areas will be added to the list. The following list of known victims is based on that of Baker, with a few additions from other sources.

Dicrurus adsimilis macrocercus
Pomatorhinus erythrogenys mcclellandi
Turdoides gularis
Garrulax moniligerus moniligerus
Garrulax moniligerus fuscatus
Garrulax pectoralis pectoralis
Garrulax pectoralis meridionalis
Garrulax striatus striatus
Garrulax striatus brahmaputra
Garrulax leucolophus leucolophus
Garrulax leucolophus belangeri
Garrulax delesserti gularis
Garrulax cineraceus cineraceus
Garrulax rufogularis assamensis
Garrulax caerulatus subcaerulatus
Garrulax ruficollis
Garrulax merulinus merulinus
Garrulax squamatus
Garrulax erythrocephalus chrysopterus
Garrulax phoeniceus bakeri
Actinodura egertoni khasiana

Copsychus saularis saularis
Enicurus schistaceus
Myiophoneus caeruleus temminckii
Zoothera citrina citrina
Turdus protomelas
Lanius schach tricolor

As we have already noted, when the Indian population of pied cuckoos *(pica)* began extending their range northward into the foothills of the Himalayas and found themselves removed from the habitat of the babblers of the genus *Turdoides* that had served them as fosterers in the plains, they began using the larger species of *Garrulax.* This change was probably already incipient in the *pica* stock, as it had become very pronounced and fixed in the earlier evolutionary offshoot from *pica* that resulted in *C. coromandus.* There must certainly have been a considerable time span involved in the evolution of the red-winged from the pied cuckoo, whereas the northward spread of the latter seems to have been fairly recent.

Clamator glandarius (fig. 7, p. 25)

The great-spotted cuckoo is the most advanced of the four species of *Clamator,* and is closer to *C. coromandus* than to either of the others. From the circumstantial evidence of the current situation in the genus, it is justified to conclude that *glandarius* was an evolutionary development from the stock at present represented by *coromandus.* Hence, it seems probable that it originated somewhere near the northeastern portion of the range of that species. Moving eastward, the primordial *glandarius* came into contact with magpies, a group of sizable, suitable, potential fosterers until then unaffected by any parasitic cuckoo, and to them it became adapted with marked success. Advancing farther eastward *glandarius* met with magpies in southern Iran, Iraq, Lebanon, etc., in areas of warmer climate than the Himalayan foothills and slopes of northern Assam, Bhutan, and Sikkim, where its ancestors may have first encountered their magpie hosts. In fact, the presence of the latter birds may well have expedited the eastward shift of early *glandarius.* Being essentially a warm climate form, *glandarius* left its original locus and eventually became a circum-Mediterranean species, still largely in areas of sympatry with the magpie, although becoming allopatric with it in eastern Egypt, where it used crows as hosts instead. At that stage of its history *glandarius* was largely contained within the range of its magpie host, and its great spread to sub-Saharan Africa, completely away from this fosterer, came much later.

It is conceivable, though, in the nature of things not demonstrable, that possible competition from the corvine parasitism of the koel,

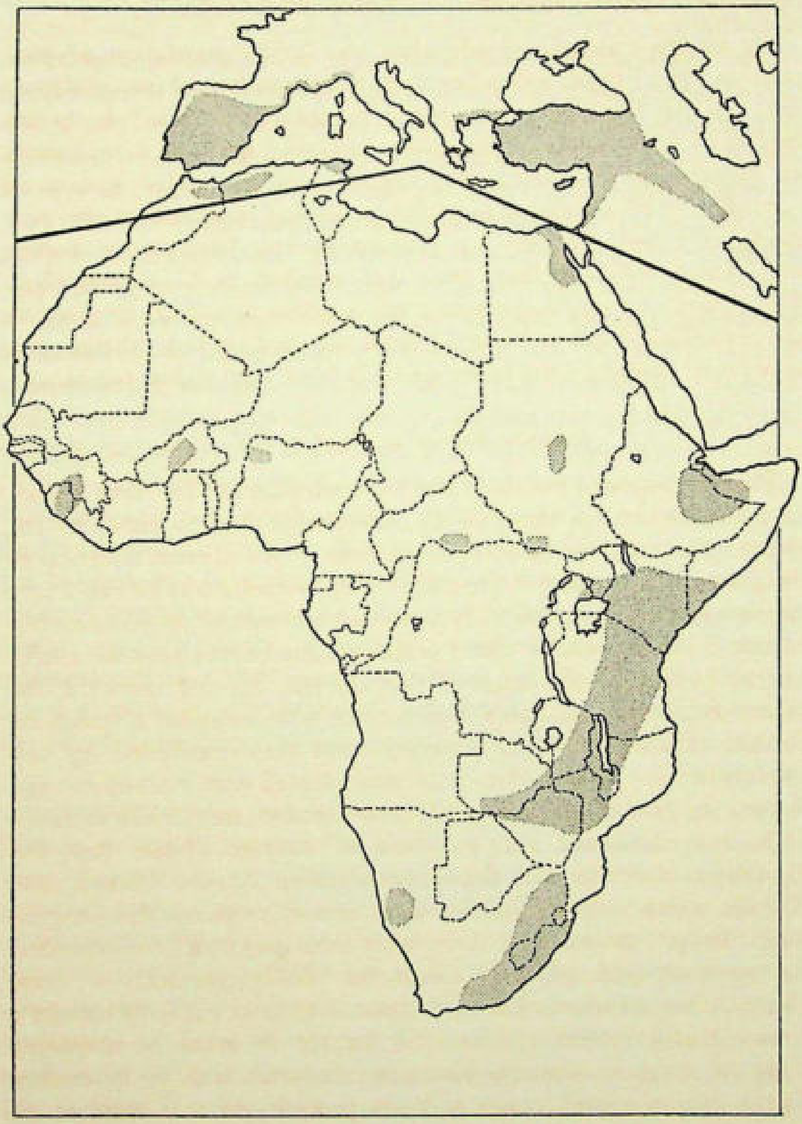

FIG. 7.—Known breeding range of *Clamator glandarius*. Area of sympatry with *Pica* lies north of heavy line.

Eudynamis scolopacea, in northern India, may have influenced the eastward emigration of early *glandarius* to areas free from such difficulties.

The close resemblance between the eggs of the great-spotted cuckoo and of the magpie is evidence of a long continued and very specialized host-parasite relationship. As Baker (1942, p. 85) wrote, the parasite lays, ". . . one type of egg and one type only which is so exactly like in colour, shape, and superficial appearance of texture to that of the Magpie that identification is generally extremely difficult . . ." It may be stressed at this time that the egg, speckled with dusky, is a highly "advanced" egg type for a cuckoo, the basic, primitive egg type in the family being unmarked white, and it has arrived long ago at a stage far beyond the development evinced in any other species of *Clamator.* That it is "fixed" and invariable, and that it now persists unchanged in the vast stretches of sub-Saharan Africa, where it does not match the eggs of the hosts used there, is evidence for the age and the finality of this "end product" of adaptive evolution.

If we were to assume, without documentation, as Voous (1960, p. 154) has done, that *C. glandarius* originated in sub-Saharan Africa and hence, that it there evolved its egg type in the absence of any known host whose eggs it resembled, and then later invaded Mediterranean Africa and the Iberian Peninsula, where its eggs "fitted" so well with those of the magpie, we would have a most remarkable example of extreme preadaptation. It would be so remarkable that it would be difficult to accept it without extremely disturbing doubts and skepticism.

If, on the other hand, it be accepted, as here postulated, that *Clamator glandarius,* having arrived at a perfected stage of adaptive evolution with regard to the degree of similarity of its eggs to those of the magpie, its chief, and almost its only, host in Asia Minor, in the Iberian Peninsula, and in northwestern Africa, then expanded its range southward into areas where this adaptive excellence no longer had its former value, we would have a case of what may be called "repudiative evolution." Part of the species acted as though the matter of egg resemblance no longer mattered, and in its new home used new fosterers to which it was not adapted. In a sense, this amounted to an escape from too specialized a form of host relationship; one which, had it been adhered to, would have markedly limited the parasite geographically, for the cuckoo is a bird of warm climes, whereas the magpie's range extends far to the north where the parasite would not be able to follow it, and the two are sympatric only in a limited area.

The importance of settling the question as to whether *glandarius* was originally sub-Saharan in range and later spread to the Mediterranean areas, or vice-versa, warrants a little further discussion. Voous (1960, p. 154), the only proponent of an African origin for the species, considered the hypothesis for such an origin ". . . supported by the occurrence of at least three other species of the genus *Clamator* in Africa . . ." This is incorrect as there are only two, *jacobinus* and *levaillantii*, while in Asia there are also two, *jacobinus* and *coromandus*. The last named is the species to which *glandarius* is most clearly related and appears to be the stock from which it arose. During a visit to Los Angeles in 1962, Stresemann, who has been studying very carefully the distributional history of the birds of Europe, agreed with me in considering the sub-Saharan range of *glandarius* as a recent expansion from an older circum-Mediterranean one.

In this connection we may recall, in Dobzhansky's (1940, pp. 312-321) words, that ". . . each species, genus and probably each geographical race is an adaptive complex which fits into an ecological niche somewhat distinct from those occupied by other species, genera, and races. The adaptive value of such a complex is determined not by a single or a few genes, but is a property of the genotype as a whole. Furthermore, the adaptive complex is attuned to its environment only so long as its historically evolved pattern remains, within limits, intact . . ." *Clamator glandarius* is highly adapted to the magpie, but yet part of its population has been able to abandon this evolved situation and to become attached to as different a host relationship as that with *Spreo bicolor* in South Africa.

One cannot help but wonder if this exodus of part of the Mediterranean *glandarius* may have been influenced, if not caused, by intraspecific competition in a too populous stock of the species, after its adaptive evolution had seemingly expedited its existence. Haldane (1932, p. 119) pointed out that there is a fallacy in the concept that ". . . natural selection will always make an organism fitter in its struggle with the environment. This is clearly true when we consider the members of a rare and scattered species. It is only engaged in competing with other species, and in defending itself against inorganic nature. But as soon as a species becomes fairly dense matters are entirely different. Its members inevitably begin to compete with one another . . ."

Inasmuch as the other three species of *Clamator* parasitize almost exclusively birds that build open, "saucer-shaped" nests, it may be assumed that a similar host choice is, or originally was, basic in *glandarius* as well, and that the use of hole-nesting starlings is a relatively recent development. The surprising thing is not only that it was able to make this change, but that it had previously gone so far in the road of adaptive specialization to a host with which its area of sympatry was so limited.

The magpie genus *Pica* occurs throughout Europe, including the Mediterranean islands, and Asia north of the tropics (*i.e.*, north of the Arabian Peninsula, Baluchistan, Pakistan, India, Burma, Assam, and the Malayan countries), east to the western part of North America, and south from Gibraltar to northwestern Africa (Morocco, Tunisia, Algeria). In all the vast extent of this primarily Holarctic range, it is sympatric with its "highly adapted" brood parasite, *Clamator glandarius,* only in the Iberian Peninsula, adjacent portions of northwestern Africa (Morocco, Tunisia, Algeria), parts of southeastern Europe, Cyprus, and the Near East as far as Iran. This area of sympatry is thus a somewhat peripheral part of the range, both of *Pica* and of *Clamator glandarius* (whose geographically most extensive range is African south of the Sahara all the way to the Cape, and in eastern Egypt). An instance of the degree of sympatry of *C. glandarius* and *Pica* in southwestern Europe is the absence of both from the Balearic Islands although both occur in the Iberian Peninsula and in Morocco.

If the egg coloration of *Clamator glandarius* evolved to match that of *Pica,* this must have taken place in this limited area where the two occur together. The bulk of informed opinion regards the close egg resemblance as something arrived at by adaptive evolution, and not as a fortuitous coming together of a parasite and a host whose eggshells were similar in color, pattern, and size. The latter interpretation would assume an improbable and unlikely happening, although it cannot be ruled out as a possible explanation. The fact that throughout its range, the great-spotted cuckoo lays only this one type of egg suggests that its original range was just those areas where its egg type was adapted to a prevalent host. This further suggests that the *Pica*-allopatric portions of its present range in Egypt and in Africa south of the Sahara must have been a more recent extension of its distribution.

Amadon (1947) ascribed a marked change of bill form and of feeding habits in a Hawaiian honeycreeper, genus *Hemignathus,* to a sudden ecological shift of its ancestral population. Mayr (1959, pp. 177-178) considered that such a shift into an entirely new ecological niche may well have been the type of occasion attendant upon the emergence of many major evolutionary novelties. When

Clamator glandarius extended its breeding range into sub-Saharan Africa, the ecological shift was one that involved a marked change in host choice, even a virtual repudiation of a previously highly evolved egg adaptation, but, as it did not involve any apparent, drastic alteration in the daily life or feeding habits of the adult cuckoo, no comparable evolutionary change transpired.

It follows from this that, whereas in the case of self-breeding birds the entire biology of the species is a closely coordinated unit (almost what in current commercial jargon is referred to as a "package deal") on which selection may operate, in the case of brood parasites there is cleavage resulting in two fairly separate parts. The evolutionary climate ambient to the egg and nestling stages is that of the host species and has relatively minor connections with, and repercussions upon, the selective factors surrounding the life of the adult parasite. This may have helped make it possible for *Clamator glandarius* to invade vast new areas and to remain unchanged. Concurrently, it must be assumed that the new, non-egg-adapted hosts, suddenly parasitized by the newcomer, had no previous need to evolve any particular acuity of discrimination and thus were relatively easily susceptible to parasitism.

As far as casual observations go (and these are all that have been recorded in the literature), the great-spotted cuckoo seems equally successful in the various portions of its range. It might be expected that the wide discrepancy in the degree of host adaptation it shows in tropical and southern Africa on the one hand, and in the Mediterranean area on the other, would be reflected in its local numerical status, but the available evidence does not point to any such effect. It must be admitted, however, that the data are still very superficial and imperfect. If anything, the fact that unusually large numbers of its eggs are often found in single nests of its corvine hosts in the areas where the cuckoo is nonadapted might even suggest a relatively greater abundance of the parasite in proportion to the available host population there.

The known hosts of the great-spotted cuckoo, as listed here, are primarily birds of two families, the Corvidae (crows, jays, magpies, and piapiacs) and the Sturnidae (starlings). The other three included species are a kestrel, which was probably an "unintended" host choice as the bird was using an old magpie nest, and two South African ground-tunnel nesters, the hoopoe and the ground woodpecker, which may have been "acceptable" to the parasite because of their general similarity to the nesting tunnels of the pied starling, *Spreo bicolor,* a favored and frequent host there.

The predominant role played by members of the Corvidae as fosterers of this cuckoo is indicated by the fact that of a total of 172 nests parasitized, 141 were of various corvids; 89 nests belonged to crows of 6 species *(Corvus corax, corone, ruficollis, albus, rhipidurus,* and *capensis)*; 1 was of a raven, *Corvultur albicollis,* 48 were of 2 species of magpies *(Pica pica* and *Cyanopica cyanus),* 1 was of a piapiac *(Ptilostomus afer),* and 2 were of a species of jay *(Garrulus glandarius).* Of the remaining 31 parasitized nests, 28 belonged to 7 species of starlings. Of these 14 were of the pied starling, *Spreo bicolor;* 5 of the red-winged starling, *Onychognathus morio;* 4 of the glossy starling, *Lamprotornis nitens;* while of the other species single instances only have been reported so far.

Falco tinnunculus tinnunculus
(in an old *Pica* nest)
Upupa epops africana
Geocolaptes olivaceus
Corvus corone sardonius
Corvus corone corone
Corvus ruficollis edithae
Corvus corax corax
Corvus albus
Corvus capensis capensis
Corvus capensis kordofanicus
Corvus rhipidurus
Corvultur albicollis
Cyanopica cyanus cooki
Pica pica pica
Pica pica bactriana
Pica pica galliae
Pica pica melanotos
Pica pica mauritanica
Garrulus glandarius krynicki
Ptilostomus afer
Acridotheres tristis tristis
Onychognathus morio morio
Spreo bicolor
Spreo albicapillus
Lamprotornis nitens phoenicopterus
Lamprotornis caudatus
Lamprotornis chalybeus cyaniventris
Lamprotornis chalybeus sycobius

As we have seen in the case of *Clamator jacobinus,* in the present species also, it is the sub-Saharan segment of its total membership that is the less well adapted in its egg coloration. However, in both these species, the available observational evidence gives no grounds for assuming that the sub-Saharan birds are less "successful" than their more completely and more perfectly adapted northern segments, insofar as "success" may be implied from ability to survive in numbers over a vast area.

We cannot, however, deduce from this that adaptation has lost its value and significance in one geographic portion of the total distributional range of this one genus of birds, while remaining advantageous elsewhere in the same genus, as well as in most of the rest of the animal kingdom. Certainly the case for the natural selective value of adaptation generally is so strong, so well-nigh invariable, that we cannot easily accept its apparent unimportance here. At least part of the answer to this puzzle lies in the fact that because these two cuckoos were studied earlier in India and in the Mediterranean lands than in sub-Saharan Africa we have come to accept the adaptive excellence reported for them from those areas as an essential and necessary aspect of their natural economy. But now we know that, advantageous as this may be, it is not essential, and that the two species can and do survive without it. Actually, this is implied even in the course of the evolution of the climax adaptation in the areas where it has transpired, as countless less completely adapted generations had to survive to provide the material out of which was achieved the greater perfection, which in time supplanted the less adapted birds.

We have, then, a superficially similar situation in southern Africa in both the great-spotted and the jacobin cuckoos, but one which appears, on more careful study, to be due to opposite evolutionary trends. In the jacobin it seems probable that the southern population, *serratus,* is the original, primitive segment of the species that has remained as it was while giving rise to the more advanced *pica* and *jacobinus,* an evolution involving primarily the change from unpigmented to pigmented eggshell. On the other hand, the fact that in sub-Saharan Africa *glandarius* is not only bereft of the adaptive advantage its egg evolution had given it in Mediterranean lands, but further that in its southern range there is a striking difference in the numerical relationship of parasite-host eggs in parasitized nests in the two areas causes the southern population of this species to seem relatively so inept that it may only be explained on the basis of the recency of its invasion into that area.

What has happened with *C. glandarius* is paralleled by a similar, though less extensive, move in the jacobin cuckoo. Although the geographic spread of *C. jacobinus* from Africa to India is something that happened relatively early in its evolutionary history, the species has expanded its range in India more recently by advancing higher into the hills. Thus, Baker (1942, p. 83) considered it possible that its present breeding in the hills up to 6,000 feet and even higher in Assam and in the central Himalayas was a "modern extension of its breeding habitat. In the Plains . . . its normal fosterer, or group of fosterers is so completely established that exceptions are very, very few. In the lower hills the Cuckoo adheres closely to the Necklaced and the Striated Laughing-Thrushes, but above the normal elevation of the breeding areas of these birds or where these birds are not found, or are rare, it launches out into the use of all kinds of nests which bear some resemblance to those they usually cuckold . . ."

The timespan involved in the southward spread of *Clamator glandarius* to sub-Saharan Africa need not have been great. The case may well have been similar to the recent rapid, almost "explosive," spread of the cattle egret, *Bubulcus ibis.* In both instances the advancing birds filled vacant ecological niches. The cattle egret had no competition from other herons because it was a dry land bird and lived largely on insects, not an aquatic feeder on fishes, tadpoles, etc. The great-spotted cuckoo was parasitic on corvids, a group until then unmolested by any parasitic birds in Africa. The spectacular spread of the collared turtle dove, *Streptopelia decaocto,* in Europe during the past 50 years is a parallel example.

It seems that the relatively recent, but very extensive, geographical expansion of *C. glandarius* originally was motivated by the bird rather than by its environment. This statement may require a little elaboration to make its meaning clear. Evolutionary changes are often the result of a double process of selection; selection by the environment of the most advantageous, best adapted structural, functional, or behavioral organization in the organism, and also selection by the animal of the most comfortable, the most nearly optimal environment. The capacity for making a choice among available environments is inherent in all animals that are able to move about freely. In effect, this results in a process of sorting out the members of a species environmentally instead of selectively eliminating the less fit in the original ecological situation.

Implied in the phrase "sorting out" is what appears to have been behind the great move to sub-Saharan Africa. The part of the original circum-Mediterranean population of *C. glandarius* that was relatively less completely "fit" was the part that moved on to new territory—in this case, to equatorial and southern Africa. That it was less delicately, or less nicely, adapted to its original hosts than was the part that stayed in the Mediterranean area is still evidenced by its lack of adjustment in its egg deposition to the size of the total resulting clutches in the nests of its victims. This significant difference in the two geographic segments of *C. glandarius* is discussed in detail in our account of the intensity of parasitism (see pp. 38-47), but a little additional comment seems called for here.

While it is obviously impossible to state precisely what factor, or factors, motivated the dispersal of part of the *glandarius* population from its Mediterranean homelands, it seems likely that it was growing population pressure, such as we have seen recently in the case of the cattle egret, mentioned above. The latter bird had increased greatly in numbers in Africa prior to its sudden geographic advance. Coincident with a situation of overpopulation, it may be remembered that the nature and the intensity of natural selection varies with different degrees of abundance of a species. When a species is numerically uncommon the selection pressure it experiences is exerted chiefly by the environment, whereas when it is more abundant the selection is often between members of its own species. It was selection of the latter kind that seems to have been involved in the emigration of the less adapted members of the *glandarius* population.

.The lack of any fine control in the intensity of parasitism, as evinced by multiple-egg deposition and the resulting uncorrelated egg complements in parasitized nests, in sub-Saharan *glandarius* is more than a matter of an as-yet-unachieved adaptation. It is also an indication that the cuckoo is a recent arrival and is increasing in numbers, because at a time when the size of the population of a species is growing, selection is usually relatively weak, and such excesses as extreme multiple parasitism would be tolerated, whereas in a stable, "climax" situation this would be less apt to succeed.

Conversely, selection is apt to be stronger when the population of a species is decreasing. This must have been the case in the Mediterranean *glandarius* when part of the species emigrated southward, thereby reducing the intraspecific competition and permitting a more active environmental selection. This may actually have contributed to the development of an even better controlled host-parasite relationship there. As Carter (1954, p. 255) has stated, ". . . the population that survives the decrease of numbers will be a selected, and not a random, sample of that at the preceding maximum. Only the better adapted are likely to survive . . . It follows from this that adaptive evolution will be accelerated at the time of decrease . . ."

As the great-spotted cuckoo extended its range into sub-Saharan Africa, where there were no magpies, it undoubtedly used at first the nests of various species of crows for its egg laying, just as it had already done in eastern Egypt and the Near East. However, while it continued to use the arboreal nests of corvine hosts throughout its new domain it also extended its host choice to include such very different types of nest structures as those of an earth-tunneling starling, *Spreo bicolor*. It is known that in some animals specific types of nest structure may act as isolating mechanisms, preventing mismating. So marked a change as that between the arboreal, bulky nests of masses of twigs and sticks of the magpies and crows, and the terrestrial nesting tunnels of the pied starling might seem more than sufficient to have functioned in its impact on the behavioral patterns of the cuckoos in much the same manner as an isolating mechanism. However, the differences involved, real as they are to human eyes, did not appear to affect the parasite.

In this connection I may say that I have tried to find a place where both the pied starling and one or more species of crows were present in numbers as breeding birds and where the great-spotted cuckoo also bred, but have not been able to do so. Such a locality might give an observer the opportunity to study the host choice of the parasite where both types of hosts were equally available.

The matter of host nest selection appears to affect the life and activities of the cuckoos only during the brief moments of actual ovulation by the hens. It may be remembered that mating or copulation by the cuckoos does not take place in or at the nests of any of the hosts, and that the cock cuckoos do not necessarily even know which nests receive the eggs they may have fertilized.

While the difference between the two extreme types of egg depositories used—the open, dish-shaped, arboreal, stick nest of a crow and the long earth-tunnel of a pied starling—are great, the change probably was not as abrupt as it might seem. To begin with, the host to which the great-spotted cuckoo's evolution has made it most adequately adapted is the magpie, a bird which customarily makes large nests of small branches, twigs, and sticks, roofed over, with an entrance on one side, and usually constructed in large thorny bushes or on the upper branches of tall trees. From this it was not a great change for the parasite to use nests of the crow in eastern Egypt and the Near East, the chief difference being that the nests of the latter were open, not roofed over, but were constructed of similar materials and in generally similar types of situations. From one species of crow to another (from *C. corone* in Egypt, Iraq, etc., to *C. albus* and others in sub-Saharan Africa) involved no vital change for the parasite, but the change from these to hole-nesting starlings seems quite marked. However, even this was neither abrupt nor as drastic as one might assume. In former British Somaliland (now a part of the Somali Republic), a somewhat intermediate stage has been reported by Archer (1961, *in* Archer and Godman, pp. 649-659). He found several eggs of the great-spotted cuckoo in nests of the white-capped starling, *Spreo albicapillus,* a species that builds bulky, domed nests of twigs and coarse grasses high up in trees—nests quite similar in their main features to those of the magpies, the parasites' primary fosterers. From laying eggs in these domed, internally dusky, if not dark, somewhat tunnellike egg chambers of *Spreo albicollis* it was not a great step to using the darker nests of true tree-hole nesters, of other species of starlings, such as *Lamprocolius nitens* and *L. caudatus* and *Acridotheres tristis.* More of a change was involved in the shift from these to terrestrial burrowing hosts such as *Spreo bicolor,* but even here there may have been a transition stage, as this starling is said to nest in a variety of sites such as are used by *Sturnus vulgaris* as well as in its more usual earth burrow. Priest (1948, p. 118) indicated that this variety of nesting sites includes crevices on walls, under the eaves of houses, in trees, as well as breeding in tunnels in soft river banks or cuttings, or in mine shafts. I am informed by Dr. Winterbottom that the nest record files of the Percy Fitzpatrick Institute of African Ornithology extend this list of sites to include haystacks and even a crevice of a concrete platform in the sea (obviously near shore).

Once the cuckoo had become used to the pied starling as a fosterer, it could be expected to be attracted to it regardless of just where the nest was built. From terrestrial burrow nest-sites of this starling it was no great change to utilizing other similar nests, such as that of the ground woodpecker, *Geocolaptes olivaceus.* The pied starling is the most frequently used host in eastern South Africa today.

A partial parallel to what transpired in *Clamator glandarius,* as outlined above, has also been reported occasionally for the Indian koel, *Eudynamis scolopacea,* a cuckoo parasitic also very largely, in fact almost solely, on crows. Baker (1942, p. 197) listed two starlings, *Acridotheres tristis* and *Graculipica nigricollis,* among its known hosts, the former one or two times, the latter more often. However, as far as known, the koel has not adapted itself to terrestrial-nesting hosts. Baker listed 209 eggs of the koel in his collection. Of these, 16 were laid in nests of the black-necked mynah, *Graculipica nigricollis,* 2 were with *Acridotheres tristis,* 6 in nests of 2 species of magpies, and the other 185 in nests of 2 species of crows.

Even the European cuckoo, *Cuculus canorus,* has been known to lay occasionally in the underground nests of the wheatear, *Oenanthe oenanthe.* Furthermore, and more directly pertinent, it may be recalled that one egg of *Clamator jacobinus* has been reported from a ground-tunnel nest of a kingfisher, *Halcyon a. albiventris,* and another from a tree-hole nest of a sparrow, *Petronia superciliaris.*

Also, *Clamator levaillantii* has been known to lay in the hole nest of a kakelaar, *Phoeniculus purpureus.* The tendency to utilize such nesting sites has certainly not developed in *jacobinus* to the extent it has in *glandarius,* but these instances show that it is not outside the range of possibilities even in the former.

One further thought emanating from a consideration of this problem of host selection may be added here. Recent studies on many species of self-breeding birds, particularly in North America and Europe, have shown that nest-site selection is fairly rigid and fixed in its major elements. Slight vegetational differences often are critical to various species in the precise location of their nest sites. So widespread is this tendency that it is only proper to apply it to a review of the situation in brood parasites as well. In these birds nest-site selection would be altered to host selection based on the types of nest-sites used by the latter, and would be expressed in terms of host specificity as far as the parasites are concerned. On the whole, avian brood parasites fall into three main categories in this respect. Some exhibit little or no such specificity; others are specific in their host choice as individuals only ("individual-host specificity," as found in the European cuckoo, *Cuculus canorus*); and in still other parasites the entire species is specific on one or a small group of related hosts ("species-host specificity").

Inasmuch as nest-site selection does reflect trenchant and remarkably uniform criteria in each species of self-breeding birds (potential hosts), and inasmuch as there is no reason to assume that parasitic species, especially early in their evolutionary history, were necessarily different from self-breeding birds in their response to familiar and uniform environmental details, it may be that species-host specificity, as opposed to individual-host specificity, was the original situation in brood parasites and that a broader range of host choice developed from it later. This would imply that the broad spectrum of hosts subsequently arrived at may have evolved even as a negation of the original selection pressure that operated in an earlier atmosphere of species-host specificity. From this concept it would follow that rigid, if not actually "obligate," parasite-host specialization is a basic rather than an ultimate condition. This is quite the reverse of the often assumed pattern of species-host specificity arising from individual-host specificity.

In this connection it may be pointed out that the one species of brood parasite whose descent from a self-breeding form is most obvious and clear, the screaming cowbird, *Molothrus rufoaxillaris,* started with, and has not deviated from, a fixation upon a single-host species, its close and antecedent relative, the bay-winged cowbird, *M. badius.* Furthermore, the parasitic Viduinae are still in the original stage of limited range of hosts, their Estrildine relatives, the waxbills. It also seems not improbable that the great-spotted cuckoo, *Clamator glandarius,* early became involved with, and went through its eggshell evolution with a single host, the magpie, *Pica pica;* the same is true of the stripe-breasted cuckoo, *Clamator levaillantii,* with its chief host, the babbler, *Turdoides jardinei,* and of the koel, *Eudynamis scolopacea,* with its use of crows. The evolution of host egg similarity obviously is facilitated by species-host specificity.

INTENSITY OF PARASITISM

By intensity of parasitism two quite separate things are implied. The percentage of the total nests of frequently used hosts that are parasitized gives one aspect of the parasite-host situation. The frequency with which individual parasitized nests are found to contain more than one egg of the cuckoo adds still another element of the total picture. On the whole, increase in frequency of multiple-egg parasitism on the same pair of hosts is something that is superimposed on the basic situation. While in some areas where the host nests are very numerous the incidence of multiple parasitism appears to be lower than in places where there are relatively few hosts for the number of cuckoos, this cannot yet be demonstrated convincingly, as in no area have the data been sufficiently extensive and intensive to give a precise survey of the numerical status of the hosts and of the parasite, or of the percent of nests of the favorite fosterers that are parasitized. Perhaps the nearest approximation to the kind of information needed is that afforded by Mountfort (1958, p. 54). In his fieldwork in Spain, he examined 7 nests of the magpie on one afternoon and found that 5 of them were parasitized by the great-spotted cuckoo, an incidence of simultaneous parasitism of 71.4 percent in a circumscribed area. Mountfort did not list the numbers of eggs or of young of either the host or the parasite in each of these nests, so his observations tell us something of the percent of magpie nests parasitized but not how intensively they had been affected. However, a compilation of all the cases he mentioned shows that of eight parasitized nests, none were found to have only a single cuckoo egg apiece. His figures are quite different from those given below for 28 other parasitized magpie nests, all also from Spain. Mountfort found some 50 occupied magpie nests in that country in 1956, but did not specify if the 8 parasitized ones that he discussed were the only ones so affected.

The lack of sufficiently comprehensive or detailed quantitative observational evidence makes it necessary, at least for the present, to rely on the available data on multiple parasitism of individual nests as our primary method of evaluating the host-parasite relations. Of all the species of *Clamator* the one that is most revealing of evolutionary change in this important regard is the great-spotted cuckoo, *C. glandarius,* and we may, therefore, begin with it. The data on this species are as follows.

Clamator glandarius

Of a total of 172 parasitized nests, containing 407 eggs of the cuckoo, 82 had a single one each, 41 had 2, 13 had 3, 13 had 4, 10 had 5, 5 had 6, 1 had 7, 4 had 8, 2 had 10, and 1 had 13. In other words, some 47 percent of the nests contained single eggs of the parasite. However, considering that the first cuckoo egg laid in a nest was a "single" one at that time, and counting only the subsequent eggs as "multiples," the total is 172 singles and 235 multiples. In other words, multiple eggs were almost 50 percent more frequent than singles. While this is a general condition, it does not give a representative picture of the situation as it really is in any one geographic fraction of the total range of the parasite.

To make the data more comparable, we may eliminate for the moment all cases involving hosts other than species of crows. Six species of the genus *Corvus (corone, corax, albus, capensis, ruficollis,* and *rhipidurus)* are parasitized, and together account for more than half of all the records (fig. 8). Out of 43 parasitized crow nests found in Spain, Asia Minor, and Egypt (the bulk of the records are from Egypt) containing a total of 54 cuckoo eggs, we find that 33 nests had 1 each, 9 had 2, and 1 had 3. In other words, over 75 percent of the nests contained single eggs of the cuckoo, and, all in all, multiple eggs of the parasite were less than 25 percent as frequent as were singles.

Out of 35 parasitized crow nests from south of the Sahara—from former Italian Somaliland (now a part of the Somali Republic) to Nigeria and south to South Africa—only 5 had single cuckoo eggs, 7 had 2, 3 had 3, 6 had 4, 7 had 5, 2 had 6, 2 had 8, 2 had 10, and 1 had 13; a total of 148 cuckoo eggs for the 35 nests as compared with 54 eggs from 43 nests in the Mediterranean lands. In tropical and southern Africa less than 20 percent of the nests had single eggs of the cuckoo, and, all in all, multiple eggs of the latter were three times more frequent than single ones.

In the Iberian Peninsula it is definitely established that crows are only infrequently parasitized and that magpies are the principal hosts. In Egypt, and in Africa south of the Sahara there are no magpies, and the various species of *Corvus* are regularly victimized. Judging from all the records available it appears that multiple eggs of the great-spotted cuckoo in Mediterranean lands are found more frequently in the nests of magpies than in those of crows. Thus, in Spain, Lilford (1866, p. 184) found a magpie nest with eight eggs of the cuckoo and five of the host, while Saunders (1869, p. 401) reported others with four and six cuckoo eggs in them, although he noted that other magpie nests had only one or two of the parasitic eggs apiece. As mentioned above, Mountfort (1958, pp. 54-56) found eight parasitized magpie nests in Spain. The number of eggs or young of the great-spotted cuckoo in these were as follows: One nest had six; two had five; two had three; and two had two.

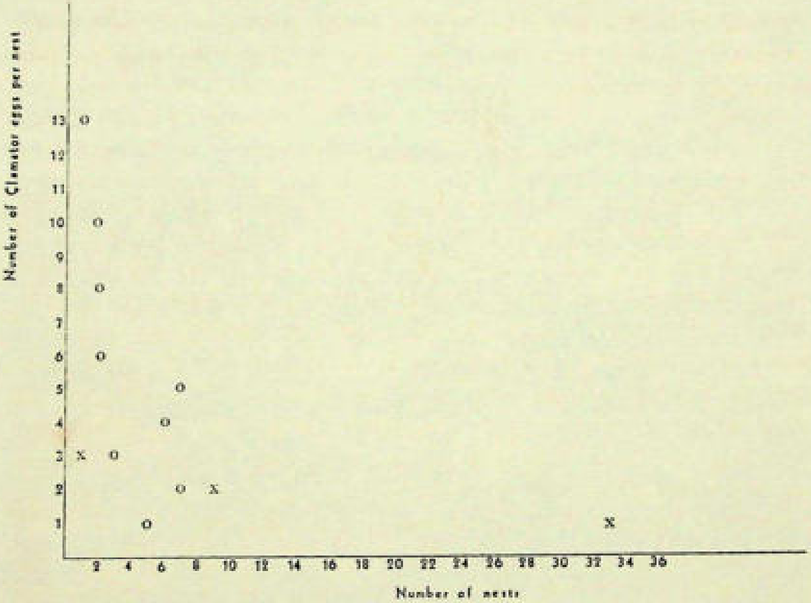

FIG. 8.—Frequency of multiple *Clamator* eggs in nests of *Corvus*. O, In sub-Saharan Africa. X, In Mediterranean area.

In reply to my inquiry, J. D. Macdonald very kindly sent me the data on 28 parasitized sets of the magpie, all taken in Spain, and now in the British Museum. In these the combinations of eggs of the parasite and of the host were as follows: 1 cuckoo egg in each of 10 nests with from 1 to 6 eggs of the magpie; 2 cuckoo eggs in each of 12 nests with from 2 to 8 of the magpie; 3 cuckoo eggs in each of 3 nests with from 1 to 3 of the magpie; and 4 cuckoo eggs in each of 3 nests with from 0 to 6 of the magpie.

Data are at hand on nine parasitized nests of the Spanish blue-winged magpie (*Cyanopica cyanus cooki*) from the Iberian Peninsula, *ex* Rey (1872, p. 143) and others, plus three sets in the British Museum; all of these had only single eggs of the cuckoo, with from one to five of the host. It is not possible, however, to say whether there is a significant difference in the intensity with which the two species of magpies are parasitized, although the available data appear to suggest that there may be. In both sets of data *(Pica pica* and *Cyanopica cyanus),* few of the sets approach the maximum size recorded for complete, unparasitized clutches—up to eight or nine eggs of either of the magpies. It can only be conjectured if this may have been due to elimination of host eggs by the parasite.

However, in the total count of instances of all host species, the recorded numbers of eggs of the fosterers in the individual nests do not consistently follow any variation directly proportional to the number of parasitic eggs found with them. We may recall that in his discussion of the great-spotted cuckoo as a parasite on species of magpies and of crows, birds larger than itself, Lack (1947, p. 323) reasoned that it might ". . . be anticipated that the host could raise more young than a single Cuckoo, and in fact, the young *Clamator* does not eject the members of the host brood, which are raised with it. However, the argument of this paper is that the full clutch of the Corvid host is determined by the average maximum number of young which the parents can successfully raise, hence even one additional nestling should upset the balance. It is therefore interesting that, according to Baker (1942) and Jourdain (*in* Witherby, et al., 1938-41) the parent *Clamator* removes one egg of the host species. Jourdain states further that a *Clamator* sometimes lays more than one egg in the same nest, in which case it is thought to remove one host egg for each egg of its own."

Jourdain (1925, p. 657) did expressly state that the female great-spotted cuckoo usually removes an egg of the fosterer when laying one of her own, but in a later paper (1936, p. 739) he further wrote that ". . . in some cases the eggs of the Magpies are removed by the Cuckoos, for on one occasion I met with a Magpie's nest containing four eggs of the Cuckoo but none of her own. Occasionally a Magpie manages to keep her clutch apparently intact, though unable to prevent the Cuckoos from depositing an egg or two. Thus, one bird was flushed from a nest with ten eggs, eight of her own and a couple of Cuckoos' eggs . . ." It seems from this that Jourdain's evidence was not unvarying, but still pointed to regular egg removal. Mountfort (1958, pp. 54-56) has added more evidence in support of this habit. He marked with indelible ink all the eggs in a number of parasitized magpie nests. ". . . The notes made subsequently at these nests . . . proved clearly that not only as many as three different hen cuckoos were laying in one Magpie's nest but that, as more eggs were laid, so the number of the host's eggs diminished. Moreover, on at least two occasions the addition of one Great Spotted Cuckoo's egg coincided with the disappearance of *two* Magpie's eggs . . ."

The picture revealed by the present data may be viewed graphically in figures 9, 10, and 11, in each of which is shown the distribution of the actual records, the number of instances of each particular combination of egg numbers being indicated in the graphs. By contrast, to emphasize the scattering, uncorrelated nature of this distribution, the dotted line represents the theoretical arrangements we should expect ideally from Lack's postulated clutch-size relationship.

All cases falling to the left, or below, the dotted diagonal line can only be interpreted as in agreement with the Lack relationship, as they represent clutches of eggs either collected or observed, but in all cases it is not only possible, but even probable, that had they been watched for subsequent days they would have had more eggs of either the host or of the parasite, or both, and would thus have moved closer to the line. The cases above and to the right of the dotted line are instances of disagreement with the postulated relationship, and it is their frequency with relation to those that concur with the diagonal line, and the degree by which they exceed this relationship that indicates the lack of adjustment between the parasite and its hosts.

It may be noted that the great-spotted cuckoo is relatively well adjusted in the intensity of its parasitism to magpies (fig. 12), very well adjusted to crows in Mediterranean lands, especially in eastern Egypt, and quite obviously little or not at all adjusted to crows and starlings (fig. 13) in sub-Saharan Africa. Because of the historical accident by which this cuckoo came to be studied in Spain earlier and more extensively than elsewhere, we have come to think of it as primarily a parasite on magpies and, because of that, we are apt to think of its use of other hosts almost as relatively unusual. This concept is, as we now know, erroneous. As a matter of fact, the parasitism of this species on the magpie is remarkable in two very dissimilar ways. For one thing, the adaptive resemblance in egg coloration between them is so close as to imply a lengthy evolutionary relationship between the two birds. On the other hand, at least in terms of their respective present distribution, the two are sympatric only in a very small, peripheral portion of the range of each.

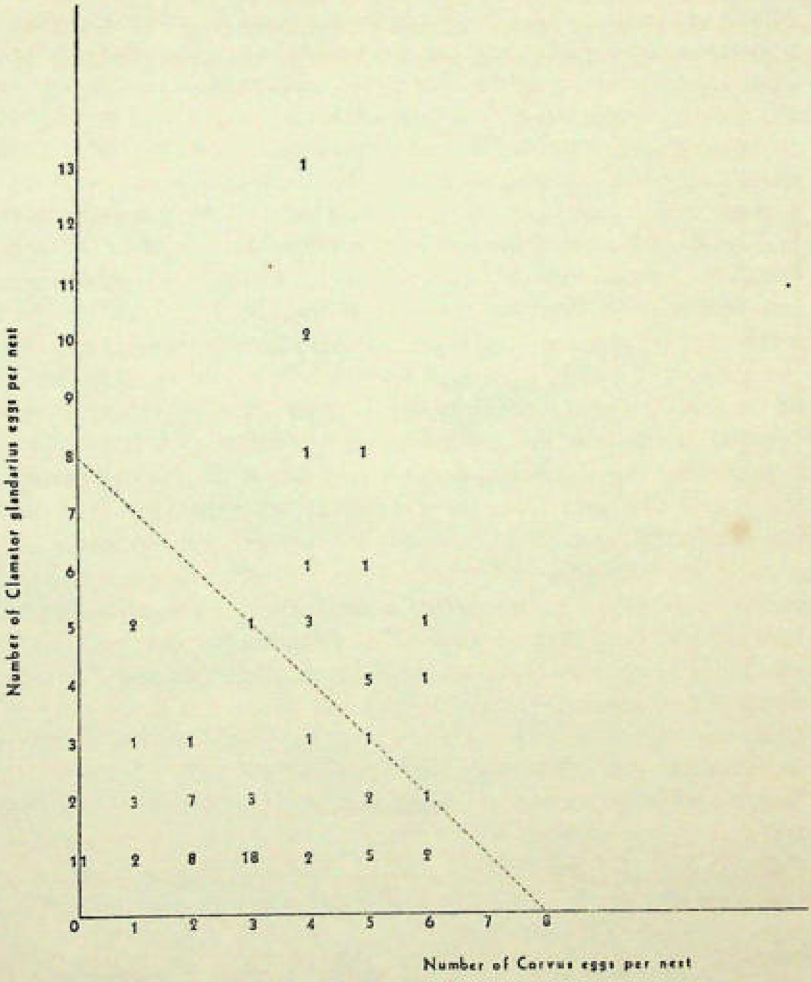

FIG. 9.—Distribution of *Clamator glandarius* eggs in nests of *Corvus*, and the number of instances of each particular combination of egg numbers.

A question that may arise from a perusal of this situation, and that merits some discussion is the following. It may be asked whether the striking difference in the degree of correlation between the egg numbers of the great-spotted cuckoo and of its hosts in the parasitized nests of the latter on the two sides of the Sahara might be explained by assuming that the sub-Saharan cuckoos do not have the habit of removing one or more of the hosts' eggs when laying in the nest, as their Mediterranean counterparts are known to do. Against this explanation we may note that the egg-removing habit is also known in *C. jacobinus,* the most primitive member of the genus, and in *C. coromandus,* while lack of evidence on this habit in *C. levaillantii* cannot be looked upon as implying its absence. In other words, it appears to be a basic part of *Clamator* behavior, and it would be surprising if one population of the most advanced member of the genus no longer showed it. Furthermore, in numerous parasitized

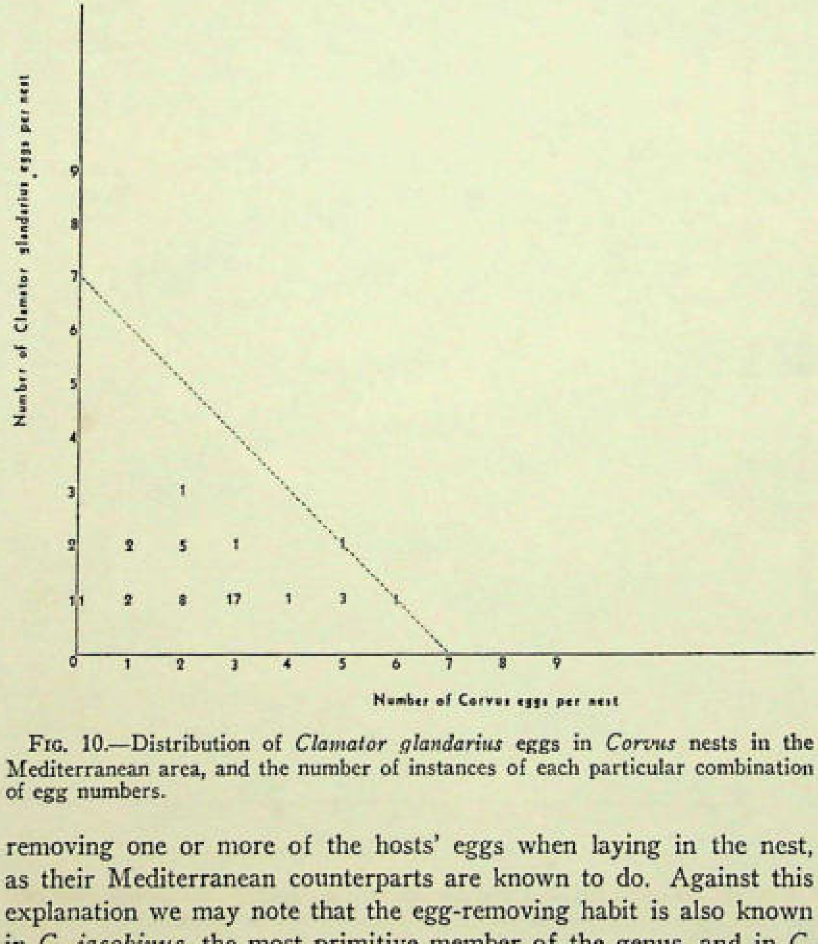

FIG. 10.—Distribution of *Clamator glandarius* eggs in *Corvus* nests in the Mediterranean area, and the number of instances of each particular combination of egg numbers.

nests of *Spreo bicolor* in South Africa, many of the hosts' eggs were found to be pecked prior to the hatching of the parasites, and hence this damage, comparable to egg removal, could only be attributed to the cuckoo. In the case of the long, narrow tunnels of the *Spreo* nesting sites it might be difficult for the parasite to remove the eggs, and pecking them may be a "substitute" behavior. To this extent it is evidence of the basic egg-removing habit in sub-Saharan *glandarius*.

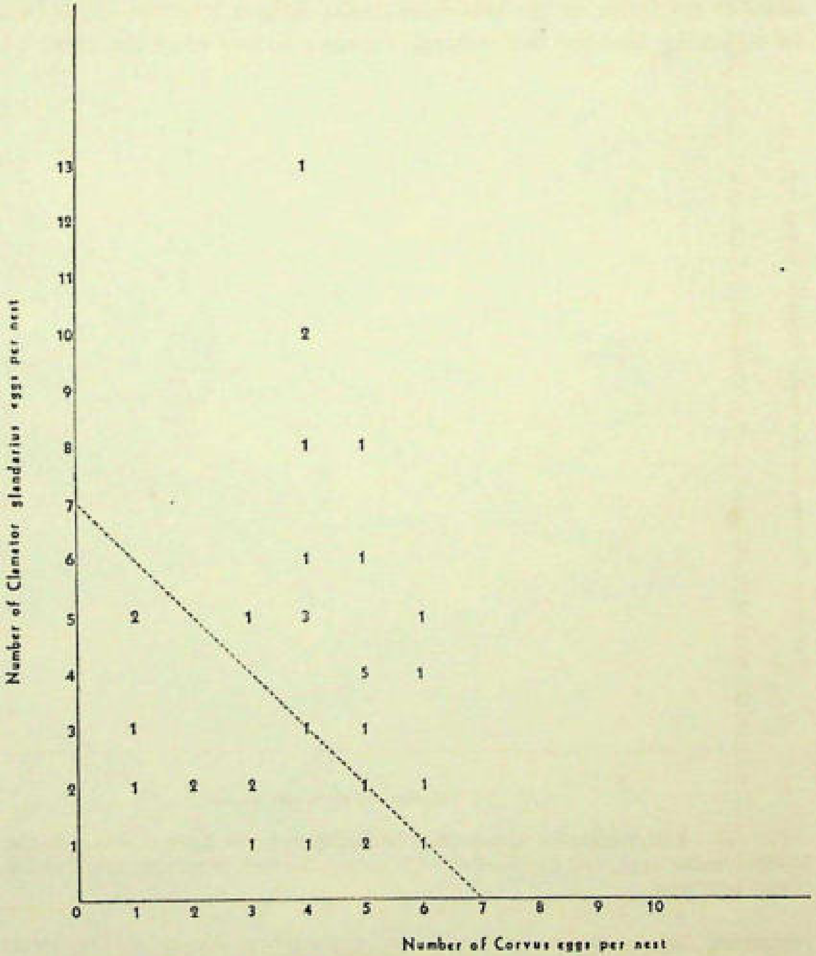

FIG. 11.—Distribution of *Clamator glandarius* eggs in *Corvus* nests in sub-Saharan Africa, and the number of instances of each particular combination of egg numbers.

Furthermore, out of 13 of the parasitized nests of the Cape rook, *Corvus capensis*, in southern Africa, described later in this paper (p. 99), 6 instances, containing a single cuckoo egg apiece, held from 1 to 4 eggs of the host, while in 7 nests with 2 cuckoo eggs apiece, there were from 1 to 3 eggs of the rook. This suggests at least a certain frequency of host egg removal, although it is true that other more intensively parasitized nests of the same species of host in southern Africa did not bear this out.

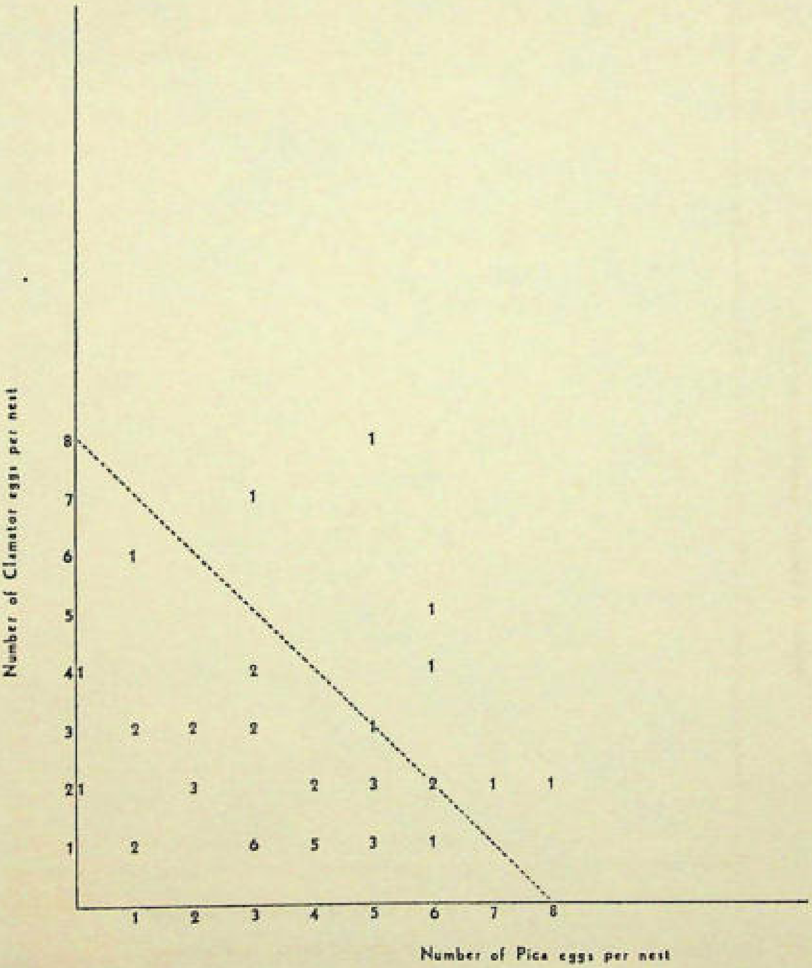

FIG. 12.—Intensity of *Clamator* parasitism to *Pica* indicated by number of instances of each particular combination of egg numbers.

Recent knowledge gives us no reason for assuming any density dependent genetic factor that may operate in such a way as to control and to maintain a proper "spread" of multiple parasitism with reference to the resultant combined clutch size of the parasite and the host. Indeed, it is difficult to imagine just what such a factor or factors might be. The available evidence, incomplete as it is, suggests that it is not chiefly a matter of differential development of the habit of host egg removal by the parasite that is responsible for the striking difference we have found in the circum-Mediterranean and in the sub-Saharan populations of *Clamator glandarius.*

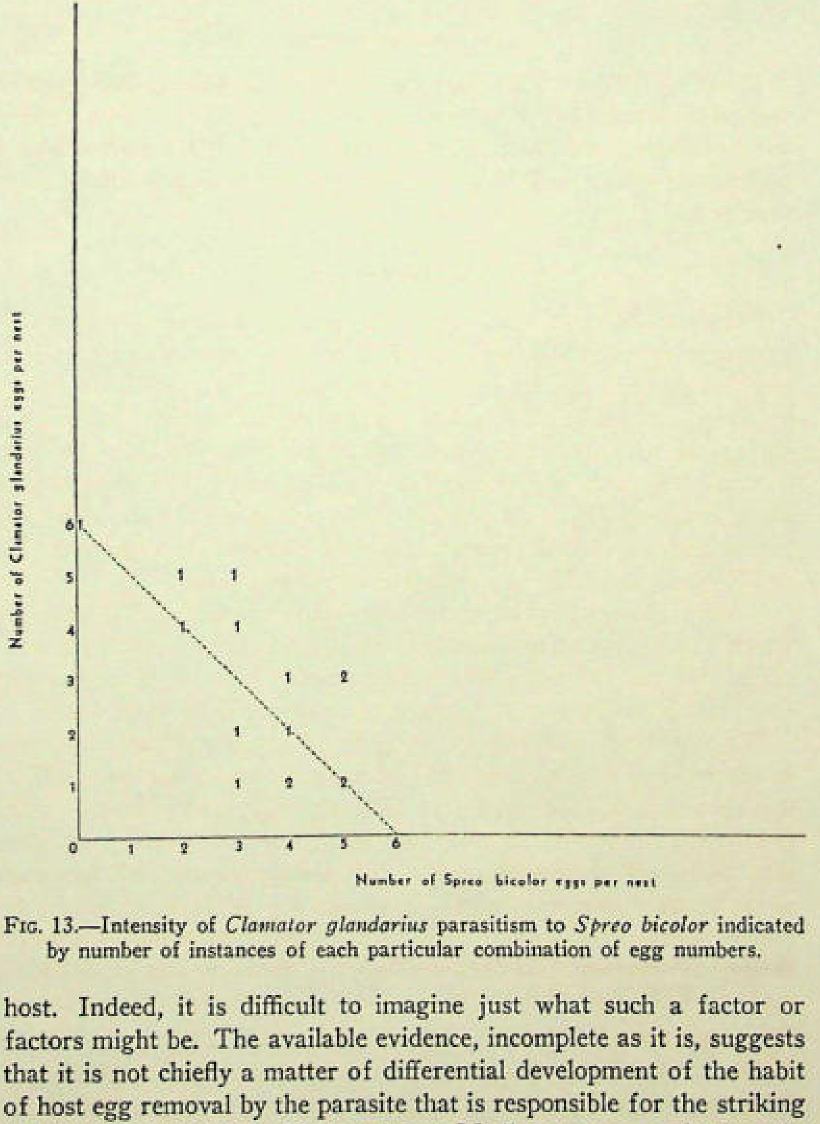

FIG. 13.—Intensity of *Clamator glandarius* parasitism to *Spreo bicolor* indicated by number of instances of each particular combination of egg numbers.

The high incidence of multiple eggs in *Clamator glandarius*, particularly in sub-Saharan Africa, raises the question as to the situation in the other members of the genus. A summary of all the available data gives the following figures, none of which comes up to those we have just considered.

Clamator coromandus

Baker's (1942, p. 152) data on 171 nests containing 225 eggs of this cuckoo reveal 171 were singles when laid, and 54, or 31.5 percent were multiples. Of the parasitized nests 139, or 81.3 percent had 1 cuckoo egg apiece, and 32, or 18.7 percent had been parasitized more than once.

Clamator jacobinus

Data on 220 nests containing 290 eggs of this species show 220 were singles when laid, and 70, or 24 percent, were multiples. Inasmuch as this is a species which has extended its range (from Africa to Asia) and is, in this regard, somewhat comparable to *C. glandarius*, we may treat the Asiatic separately from the African data.

Asia: 106 nests containing 142 eggs, of which 106 were singles when laid, and 36, or 25 percent, were multiples. Of the 106 nests parasitized, 84, or 78.2 percent, had but a single cuckoo egg each; 22, or 21.8 percent, had been parasitized more than once.

Africa: 114 parasitized nests were found containing 152 eggs, of which 114 were singles when laid, and 38, or 25 percent, were multiples. Of the 114 nests, 98, or 86 percent had a single cuckoo egg each, and 8, or 14 percent had been parasitized more than once.

We may point out that the absence of any significant difference in the ratio of multiple-egg deposition in the two great segments of this species is decidedly different from the comparable picture in the great-spotted cuckoo. It adds one more support to the contention that the great geographic spread of *glandarius* and of *jacobinus* were, in an evolutionary sense, quite opposite of each other. In the former species it was a very recent (late) advance after a high evolutionary development had been achieved; in the latter species it was an early spread prior to the evolution of egg adaptation. In *glandarius* the geographic "advancers" still reveal a lesser degree of efficiency in their host relationship than do their "stay-at-home" ancestors; in *jacobinus* this is not true. Of the total 220 nests parasitized by the latter species, throughout its range, 182 contained 1 egg each of the cuckoo, 21 had 2, 9 had 3, 5 had 4, 2 had 6, and 1 had 7.

Clamator levaillantii

Data on 23 nests containing 28 eggs of the stripe-breasted cuckoo reveal that 23 were singles when laid, and 5, or a little under 20 percent, were multiples. Of the 23 parasitized nests, 20, or 87 percent, had but a single cuckoo egg each, while 3, or 13 percent, had been parasitized more than once (2 had 2, and 1 had 4 cuckoo eggs).

Other Genera

A still higher incidence of multiple eggs is known to characterize the brood parasitism of another genus of cuckoos in southeastern Asia, the koel, *Eudynamis scolopacea*. This large, sexually dimorphic cuckoo is parasitic chiefly on crows, to the eggs of which its own show much resemblance. In its host selection it is, thus, comparable to *Clamator glandarius*. Baker (1942, p. 153) gives the following data on the koel, culled mainly from observations in India.

Out of 223 koel eggs laid in 93 parasitized crow nests, 93 were singles when laid, and 130, or a little over 58 percent were multiples. Of the 93 nests, 36, or 38.7 percent, held a single koel egg each; 57, or 61.3 percent, contained multiple eggs. The greatest number of parasitic eggs in any one nest was 16, but in 75 percent of the nests 1, or not more than 2, koel eggs were present; 8 nests had 3 koel eggs each, 7 had 4, 4 had 5, 1 each held 6, 7, 9, 11, and 16 koel eggs respectively. That Baker's data are not atypical is shown by many published observations on this cuckoo by others. Thus, to take only a single such note, Hopwood (1912, pp. 1211-1212) found koels to be unusually abundant at Arakan, Burma, and to be "wasteful" of their eggs. In one crow nest, apparently forsaken by its builder, he found seven koel eggs, which appeared to have been laid by at least three different individuals, and none of the crow.

In the European cuckoo, *Cuculus canorus*, by contrast, we find the birds almost always lays but one egg in a nest and it is relatively seldom that more than one hen uses the same nest. Thus, Baker listed 3,711 eggs of several races of this cuckoo in his collection, and from his various statements it is possible to estimate that in only 86 out of 3,617 parasitized nests were there more than a single cuckoo egg. To put it a different way, out of 3,711 eggs of *Cuculus canorus* 3,617 were singles when laid, and 94, or about 2.5 percent, were multiples.

While in *Cuculus canorus*, with its wide range of egg variability, it is possible to distinguish multiple eggs from the same hen, from eggs of multiple hens, this usually is not readily feasible in some species of *Clamator*. Baker (1942, p. 152) has claimed otherwise, and he had behind him many years of experience, even if not of the most critical sort, when he wrote that ". . . several eggs of all the species of the genus *Clamator* . . . may be found in the same nest, obviously the production of two or more Cuckoos . . . For instance, in the set with six Pied Crested Cuckoos' eggs it is easy to see that they must have been laid, two each, by three different cuckoos . . ." Yet, elsewhere in his work he stressed the fact that each species of *Clamator* lays a single, invariable egg type. The only variations that might be expected would be quite minor, and in many cases these would hardly suffice to distinguish the eggs of individual parents.

In the case of *C. glandarius* the greater variability of eggshell pattern makes it possible to distinguish between multiple eggs of the same hen and eggs of different individual cuckoos. Here there are acceptable records of more than one parasite laying in the same nest. Mountfort and Ferguson-Lees (1961, pp. 98-99) found as many as three cuckoos laying in single nests of magpies in Spain. What is true of *glandarius,* and, it seems, of *coromandus,* may or may not be true of *jacobinus* and *levaillantii.* There are not yet the necessary, careful observations to prove or to disprove this in these two species.

Because of this it is not profitable at this time to attempt to particularize our discussion of multiple parasitism in *Clamator* below the species level. In instances of maximal numbers of eggs in single nests it is highly probable that multiple hens were involved, but in cases of two, or even three, eggs in a nest, there is no certain way of telling.

Brood parasitism is a more precarious mode of reproduction than is self-breeding, as it involves all the risks normally attendant upon the nests it utilizes plus the elements of desertion of the nests or destruction of the eggs by the hosts. It is therefore plausible that any improvement, or any increased discrimination, in the matter of egg deposition would provide a basis on which natural selection would operate and, conversely, a basis from which the effects of such selection might be inferred. By and large, the chances of success for the parasite tend to decrease when more than a single egg is laid in the same nest. Many hosts may stand for a single imposition but not for repetitive ones without deserting the nest; others simply could not hatch and rear more than one or two of the parasitic young. It follows, therefore, that an original tendency to lay multiple eggs in the same nest would eventually be modified by natural selection, and that the relative frequency of such multiple eggs would tend to decrease in areas where selective pressure was in operation.

The situation we have just outlined in *Clamator glandarius,* especially in Africa south of the Sahara, and in *Eudynamis scolopacea* in southern Asia, appears, at first glance, to go counter to this idea. However, one important factor that enables their excessively multiple egg deposition to continue as a reasonably well-functioning habit is that both of them use large hosts, mostly birds as large as, or even larger than, themselves, that are capable of incubating successfully more of the eggs and of rearing more of the young of the cuckoos than is the case with other species of cuckoos, regularly parasitic on birds smaller than themselves. In the latter situation one cuckoo egg is often close to the limit of the hatching potential of the host, and in such cases multiple-egg deposition would merely bring about the loss of the nest and its contents. In other words, the fact that in the case of the great-spotted cuckoo and the koel the parasite-host size ratio tends to favor the host has the effect of lessening, if not eliminating, any selective pressure against multiple parasitism. This has made it possible for sub-Saharan *glandarius* to become established over a vast area. It seems, however, that as the frequency with which it selects smaller birds, such as starlings instead of crows, as fosterers increases, it will again be committing itself to the selective pressure to which it is temporarily fairly immune.

EGG MORPHISM

The great development of egg morphism in *Cuculus canorus,* with its connotations of adaptive evolution, could only have come about from a basic wide range of original variations in eggshell coloration. However, this is a highly specialized species, far removed from the situation in the crested cuckoos of the genus *Clamator.* In fact, the very simplicity of the whole matter of eggshell coloration in *Clamator* permits some suggestive glimpses into the early stages of a process that has not gone far in this genus, but that has not only advanced, but, in doing so, has obscured its past history, in *Cuculus.*

The basic, primitive, unspecialized type of eggshell in the cuckoos, as a family, is unpigmented, unmarked white. In this character the cuckoos agree with the doves, the parrots, the owls, the touracos, and also with the bulk of the scansorial and picarian families. The eggs of the relatively unchanged, nonparasitic cuckoos are either plain white or tinged with plain, unmarked, pale bluish, and this may be looked upon as the original, basic type in all cuckoos. However, numerous kinds of cuckoos lay eggs that are pigmented in a plain, overall tone, and, in the most highly specialized species, we find some that lay eggs that are patterned, speckled, or blotched as well. The situation in the species of *Clamator* is discussed below in detail for each of the four forms, but in general it may be said that each species has but a single egg type, except for *C. jacobinus,* where we find two types, but which are geographically distinct, so that even there, in any one area there is but a single type. In *C. levaillantii* there is some, as yet not wholly satisfactory, evidence for incipient egg morphism; in *C. coromandus* and in *C. glandarius,* only one type apiece occurs.

Clamator jacobinus

So evident does it seem that uniform white is the primitive eggshell type that I am influenced by it in considering the southeast African (*serratus*) population of *C. jacobinus*, with its pure white eggs, as the old, primitive portion of that species, and its other two races, *pica* and *jacobinus,* with their pale greenish-blue eggs, as more advanced. There is no other character that lends itself to judging their relative phylogenetic positions. In all the great number of eggs of this cuckoo taken in Ethiopia, the Somali Republic, Uganda, most of Kenya, and in India, not a single one has been found that was not plain, greenish blue. One white egg, taken from the oviduct of a collected female, was reported from Doinyo Narok, in southern Kenya, by Jackson (1938, pp. 495-496). One other white-shelled oviduct egg obtained near Timbuctu in Mali (formerly part of French Equatorial Africa) by Paludan (1936, p. 292). In an earlier study (1949a, p. 20) I suggested that the white color of this particular egg might have been due to the fact that it was "unfinished," an oviduct egg not quite ready to be laid, and that it might have been about to receive some bluish pigment. This has been countered by the results of Harrison's recent study (1963, pp. 154-155), which show that the pigment is distributed throughout the thickness of the whole shell in bluish eggs of this cuckoo. The example from Timbuctu, therefore, must be looked upon as a definitely white egg. The white Doinyo Narok example appears to have been even closer to laying time when collected. These two are puzzling records that cannot be "explained away" easily. The Doinyo Narok one is separated from the nearest (more southern) record of a pure white *jacobinus* egg by over 600 miles, the closest ones being from Nyasaland! It may be mentioned that the species has not yet been found to breed in Tanganyika or in the northern half of Mozambique, so there are no records of blue eggs between Doinyo Narok and Nyasaland either. The Timbuctu specimen is even more remote from known white eggs of the species. Blue eggs are known from near Nairobi (Ngong), not too far to the north of Doinyo Narok. Clancey (1960, p. 29) has identified a breeding male specimen of the cuckoo from Lake Magadi, quite close to Doinyo Narok, as of the subspecies *pica,* a race whose eggs are bluish.

In South Africa, South-West Africa, Bechuanaland, the Rhodesias, southern Mozambique, and Nyasaland, the known eggs (and there are many) are pure white, except for one blue oviduct egg from Bulaya, 8°33'S., 30°07'E., near Lake Mweru, in northeastern Northern Rhodesia. It is possible that the local race of the cuckoo there is *pica* and not *serratus,* as it cannot be said, on present evidence, that *pica* may not be the breeding form of Ruanda-Urundi (now the Republic of Ruanda and the Kingdom of Burundi) and the eastern part of the Republic of the Congo near Lake Tanganyika, and that its range may extend south to Bulaya. On the map of the breeding ranges of the races of this cuckoo the egg color has been indicated, B for blue, W for white.

Several recent authors have considered *pica* inseparable from *serratus,* but while close I prefer to keep them distinct, as did Clancey (1960). As far as our immediate problem is concerned the only difference is that if they were merged we would have two egg types in one race, although geographically separate from each other, whereas in our present arrangement, each race has one egg type, but still the species has two. Inasmuch as *C. jacobinus* is the only species of the genus that has developed two distinct, and constant, egg types, it may be pointed out that the more "advanced" of the two, the pigmented, or greenish-blue, type is apparently the type developed in the stock that gave rise to *C. levaillantii* and to *C. coromandus,* both of which lay similar, unmarked bluish or bluish-green eggs.

The origin of two egg types, or, more precisely, the advent of the pigmented one in a species originally laying only unpigmented white eggs, is a problem for the solution of which no real clues exist, although we have already noted that nonparasitic cuckoos lay eggs that are either white or bluish white, and that there may be a tendency in the basic, primordial cuculine stock as a whole to produce some blue eggshell coloring. However, a parallel case has recently been described in a totally unrelated, primitive parasitic cuckoo, the Neotropical *Tapera naevia.* This bird, parasitic primarily on furnariids and dendrocolaptids, all of which lay white eggs, was known to lay white eggs as well. Haverschmidt (1961, pp. 353-359) has found, in Surinam, that this cuckoo lays two types of eggs, both unmarked, one white, the other bluish green. Of 13 eggs taken near Paramaribo, 6 were white, 6 were bluish green, and 1 was white with a bluish tinge. In other words, in *Tapera naevia* we have a comparable trend, but without geographic separation of the two types as in *Clamator jacobinus*. Other examples, among nonparasitic birds, of two such egg types sympatrically, are *Diplootocus moussieri* and *Phoenicurus ochrurus gibraltariensis*, (Etchecopar, 1942). In this connection it may be noted that Etchecopar (1946, p. 160) suggested that the blue egg color might be a result of the greater humidity in the more tropical areas. He cited no evidence in support of this notion, and, indeed, it is not clear that the more equatorial birds do experience more humidity than do their more austral relatives. It is not clear just what he had in mind when he referred to the ". . . grande facilité la coquille à se tacher sous l'influence d l'humidite, il nait alors de grandes macules bleu fonce tres particulieres a ces oeufs. . . ." The blue eggs are not blue spotted; they are uniform in their blue coloration.

Clamator levaillantii

The eggs of the stripe-breasted cuckoo are uniform, glossy, pale bluish to greenish blue, somewhat pitted, and average 26 x 20.4 mm. Most of the recorded eggs are of this type, but there is evidence of some egg morphism in this species. Pale pink eggs, finely and faintly speckled with slightly darker pink, attributed with strong presumptive evidence to this cuckoo, have been taken in two nests at Kafanchan, Northern Nigeria, by Serle (1939, p. 689) and at Balgowan, Natal, by Bell-Marley (Friedmann, 1949a, pp. 44-45). Searle was of the opinion that the pink eggs were an adaptation to the similarly pinkish eggs of the local fosterer in Nigeria, *Turdoides plebeja;* no such seeming adaptation was involved in the Natal records, where the host (two cases) was the Cape robin chat, whose eggs were not pinkish, but pale greenish blue flecked with brown. It is true that in some instances the eggs of this bird are almost covered with light salmon-pink flecks.

To these two egg types we may add that it has been suggested in print that this cuckoo may occasionally lay pure white eggs. The evidence, if it may so be termed, is far from conclusive, but the case may be given here. Milstein (1954, pp. 4-5) observed two *Clamator levaillantii* showing much interest in a yellow-vented bulbul's nest. They repeatedly came toward the nest and each time were attacked by the bulbuls. The cuckoos, fluttering wildly, never attempted to fight back, even when one of the bulbuls yanked out a tuft of whitish breast feathers from one of the intruders. Milstein watched this repeated series of attacks for over an hour and a half. Several hours later he returned and examined the nest which he found contained two eggs of the bulbul and four larger, pure white eggs of a cuckoo. One of the white eggs was on the rim of the nest, almost falling out; this one Milstein was inclined to assume had been laid by the stripe-breasted cuckoo during his absence. It was very slightly pinkish, which he interpreted as indicating extreme freshness. The white eggs measured 25.2 to 27 by 20.7 to 22.2 mm., agreeing with known eggs of both *levaillantii* and *jacobinus* in size, and with *jacobinus* eggs in color. If they were laid by *levaillantii*, they add a third egg type to the known range of its egg colors.

Clamator coromandus

The red-winged crested cuckoo lays but a single type of egg, uniform greenish bluish, slightly glossy, and averaging about 26.9 x 22.8 mm. According to Baker, who has studied it more extensively than anyone else, its eggs show good adaptive resemblance to those of its usual hosts, laughing-thrushes of the genus *Garrulax*.

Clamator glandarius

The great-spotted cuckoo also lays but one egg type, pale greenish white to pale greenish gray, abundantly spotted and flecked with fairly evenly distributed tiny dots and larger markings of various shades of yellowish brown, reddish brown, umber, grayish brown, and slate gray, many of the blotches with a pale lilac tone or undermarking. In many eggs the blotches tend to be more numerous toward the large pole and in some they almost fuse to form a ring there, but in others there is no such local concentration. In size they vary from 29.1 to 35.2 by 22.6 to 26.5 mm.

This is definitely an "advanced" egg pattern, more developed than the uniform ones of the other three species of *Clamator*. In a sense the pinkish eggs of *levaillantii* with their faint speckling of darker pink may be looked upon as foreshadowing the development that took place in *glandarius*. Makatsch (1955 pp. 218-220) has discussed the evolution of spotted from uniform egg coloration in cuckoos, and concluded, as I do, that these patterned eggs represent the climax stage, and not, as Baker and von Boxberger did, the early stage.

The eggs of the great-spotted cuckoo are smaller than those of its corvine hosts, although as large as, or larger than, those of its sturnid fosterers. In the other species of *Clamator* their eggs are generally larger than those of their victims.

The egg pattern of the great-spotted cuckoo is so closely adapted to that of the magpie, its primary host in Spain, that it has often been mentioned as an example of perfected adaptive evolution. As we have had occasion to discuss elsewhere in this paper, there can be little doubt that it developed with the magpie as the chief host, and that the range of the cuckoo has subsequently been extended to areas outside the range of this fosterer.

As is so frequently the case, adaptations that seem, to the investigator, obviously functional, and, hence, readily understandable, suddenly seem to be unimportant and unnecessary when the organism possessing them moves into a different situation. In Portugal, and also in parts of Spain, the great-spotted cuckoo parasitizes the blue-winged magpie, *Cyanopica cyanus cooki,* and, in Egypt and in sub-Saharan Africa it uses even more divergent hosts. Etchecopar (1946, p. 165) admitted the striking similarity in the eggs of this parasite and those of *Pica pica,* but was moved to state that when the host was *Cyanopica* it was difficult to see any special resemblance (". . . ou il est difficile de voir la moindre trace d'adaptation . . .").

Recently Tomlinson (1962, p. 260) has stated that he found the great-spotted cuckoo parasitized the black crow (*Corvus capensis*) and the pied crow (*Corvus albus*) in South Africa, and that its eggs varied in color to match those of the host, pinkish in the case of *capensis,* greenish in *albus!* Fraser (1962, p. 343) and Calder (1962, p. 344) rightly questioned the identification of the pink "cuckoo" egg noted by Tomlinson. In the light of all we know at present there is no reason for thinking that the great-spotted cuckoo lays more than one type of egg. However, as I discussed in my earlier account (1949a, pp. 44-45) and in the description of egg morphism in *Clamator levaillantii* in the present paper, there are on record some four instances of pinkish eggs attributed with some presumptive evidence to the stripe-breasted cuckoo. In addition to these, Priest (1934, vol. 2, pp. 238, 245-247) reported a speckled, pinkish egg, supposedly of a cuckoo, in a nest of a pied crow (which lays greenish eggs that contrasted very strongly with it). He suggested that it might be either the stripe-breasted or the great-spotted cuckoo, and noted that its size, 29 x 23 mm., favored the latter identification. In discussing this record I suggested that it might have been a "runt" egg of the black crow; this suggestion would be even more appropriate in Tomlinson's record, as there the nest and the egg would both be identified to the same species.

The problem of egg morphism, is, as we have seen, not a prominent one in the genus *Clamator*. Still, by virtue of what it reveals in *Cuculus,* where it is well developed, it raises one further point that is worth discussing here. In the European *Cuculus canorus* we have a species with a wide range of eggshell coloration, and we have reasonably good evidence for the existence within the species of numbers of different gentes, each specific on a definite host species. The existence of two or more gentes sympatrically increases the efficiency of each in exploiting host egg mimicry, and allows a greater population of cuckoos to exist in a limited area. Regardless of the reality of these gentes, and no doubts as to their existence are here implied, it is true that the only way in which we may be made aware of them is by the fact that each individual hen cuckoo lays a single egg type, and is specific in its host choice, while the species lays a wide range of eggs and uses many species of hosts. From this it follows that if *Cuculus canorus* laid but a single type of egg it could still have gentes, but we would be unable to sense their existence and would have no reason even to conceive that there might be any. In the crested cuckoos of the genus *Clamator* we have seen that each species has but a single egg type, except for incipient variation in *levaillantii* and geographic variation in *jacobinus.* Consequently, no suggestion of gentes has ever been raised in studies of this genus, and, indeed there would seem to be nothing on which natural selection might have favored the development of such infraspecific categories. Still, we cannot rule out the possibility that the hens of each of the four species may be individually host specific (as in *glandarius* in the Iberian peninsula, where all the hens are essentially specific on the same host, the magpie). If this should prove to be the case, we would have, in effect, undistinguishable but yet actual gentes in the species of *Clamator.*

In this connection we may recall Southern's (1954, p. 223) conclusion about gentes in *Cuculus canorus* to the effect that those gentes which are highly adapted in egg mimicry probably thereby sacrifice a certain degree of what plasticity their ancestors may have had, and with it the ability to turn successfully to new and very different hosts. In effect, *Clamator glandarius* in the Iberian Peninsula and in adjacent parts of western Mediterranean Africa is comparable to a single highly specialized gens in *Cuculus canorus.* Yet it has been able to utilize remarkably dissimilar hosts in sub-Saharan Africa.

Whereas in *Cuculus* there is a definite trend for small egg size, relative to the size and weight of the adult bird, a trend which has enabled the members of that genus to parasitize birds much smaller than themselves, no such reduction in relative egg size is found in *Clamator*. For that matter, diminution of egg size is found in all species of *Cuculus*, but not in other genera of parasitic cuckoos. Within the species *Clamator jacobinus* we do find a slight geographic reduction in egg size, but nothing comparable to the situation in *Cuculus*. The greenish-blue eggs of *C. j. pica* average slightly smaller than do the white ones of *C. j. serratus*, but the difference, while significant and, in an evolutionary sense, suggestive, is not trenchant as there is extensive overlap in the sizes of the two groups. Thus, eggs of southern African *serratus* vary from 24.1 to 28 by 20.8 to 23 mm., with an average of 25.5 by 22 mm.; while those of *pica* from Ethiopia vary from 22 to 25 by 20 to 22 mm., with an average of 23.5 by 20 mm., and eggs of *pica* from India range from 21.9 to 28 by 17.6 to 21.4 mm., with an average of 24.3 by 19.4 mm. The eggs of south Indian, nominate *jacobinus* are slightly smaller still, in keeping with the lesser size of the birds of that race.

The development of brood parasitism and the varying features it exhibits in different genera of cuckoos make it clear that each genus needs to be studied independently before we may attempt to generalize. In *Clamator* the evolutionary history of the egg size and coloration differs from that in *Cuculus;* it reveals no marked reduction in size and while it has achieved remarkable adaptive similarity to those of its hosts in color it has done this without developing any extensive egg morphism within any of its species.

INCUBATION PERIOD

Rapid development of the embroyos, or shortening of the incubation period of the eggs, is generally considered as advantageous to a parasitic bird, as it may result in the parasite hatching before its nestmates and thereby gaining a "start" on them. This would seem particularly pertinent to parasites that do not attempt to evict their nestmates but grow up with them. If this concept were infallible we might expect to find a slight, but significant, change in this direction from the most primitive species of *Clamator,* the pied cuckoo, *C. jacobinus,* to the most advanced, the great-spotted cuckoo, *C. glandarius.* The few facts available, are, surprisingly enough, contrary to this postulated condition. The incubation period for *jacobinus,* as worked out carefully by Liversidge (1961, p. 624) in four instances, was between 11 days ± 14 hours and 12 days ± 12 hours, while in *glandarius,* Mountfort (1958, pp. 54-56) found it to be 14 days. As yet, no data are available on the other two species.

It should be kept in mind that even with its longer incubation of 14 days, *glandarius* averaged 3 to 4 days less in its incubation period than the magpie hosts it used in Spain, where Mountfort studied it. This would be true for its other corvine hosts as well. It may be that the greater size of *glandarius,* as compared with *jacobinus* is reflected in its longer incubation period, but this is by no means established. The incubation periods of the various hosts—shrikes, bulbuls, and babblers—that are used by *jacobinus* are shorter than those of the magpies and crows used by *glandarius*. It may be that the change in host choice in the latter offset any advantage that more rapid embryonic development might otherwise have given it.

HOST-PARASITE NESTLING RELATIONSHIPS

The development of brood parasitism in *Clamator* has not included the development of eviction by the newly hatched young.

In some parasitic cuckoos, notably those of the genus *Cuculus,* the newly hatched bird, while still featherless and with still unopened eyes, evicts from the nest in which it finds itself other nestlings and eggs. This it does by pushing against them and slowly burrowing under them until it gets them on its back, when it climbs slowly to the rim of the nest, where with a final and violent, muscular effort it heaves them out of the nest. Thereupon, it falls back into the nest, where it rests momentarily before tackling the next nestmate. This evicting behavior usually lasts only until the fourth day of life, after which the nestling cuckoo tolerates anything that may be in the nest with it.

This highly peculiar, and obviously instinctive, behavior is one of the features associated with brood parasitism that has not been developed by the species of *Clamator*. In *C. glandarius* and *C. coromandus* we have ample numbers of observations to be able to state that usually eviction by the newly hatched cuckoo does not take place. In *glandarius,* the elimination of the host young that often happens is due to their being either starved or smothered by their parasitic nestmates, and their dead bodies removed by their own parents. Thus, Mountfort (1958, pp. 54-56) wrote that in only one magpie nest in Spain did he find young of the host and of the great-spotted cuckoo together, and this was only for a very brief period, as the nestling magpie was gone 2 days later. It had hatched 3 days after the eggs of the parasite, and the emerging nestling was never able to overcome this disadvantage. Mountfort concluded that the shorter incubation period of the cuckoo (shorter by 3 days) doomed the young magpie, and that only such young magpies as hatch from eggs laid well before those of the parasite can have any chance of surviving.

Similarly in South Africa, Miss M. Courtenay-Latimer (*in litt.*) watched a nest of a hoopoe, *Upupa e. africana,* that originally contained four eggs of the host and one of the parasite. The cuckoo egg hatched on the same day as the first host egg; the other three hoopoe eggs hatched on the following 2 days. The young hoopoes disappeared 3 days later, but their eviction or removal was not observed. The fact that they did not disappear until 3 days after hatching argues against eviction by the young cuckoo, and makes it appear likely that they perished in the matter of food competition with it.

Another case in point is one reported by Meyer (1959, p. 85). Near Que Que, Southern Rhodesia, he found a nest of a glossy starling, *Lamprotornis chalybeus,* containing a young great-spotted cuckoo several days old (the quills just appearing on the wings and tail), a young starling, fully feathered and estimated to be 10 to 14 days old, a dead young starling, estimated to have been dead for from 2 to 3 days, and trampled into the bottom of the nest, and one cracked, unhatched starling egg. Three days later the young cuckoo and the young starling were still in the nest; on the following day only the parasite was there and was seen being fed by the foster-parents; there was no trace of the missing young starling. Six days later the cuckoo, still in the nest, was fully feathered; the following day the nest was empty, but two days later the starlings were seen feeding the fledged parasite. Here we have another example showing the absence of eviction by the young cuckoo. In this particular instance it would appear that the starling must have hatched some days before the cuckoo.

In *C. levaillantii* we still lack such observations but there is no reason for thinking that the picture there is any different. Actually there are unpublished data of N. R. Hyslop (editorially referred to in Bokmakierie, vol. II, 1959, p. 19) that are said to confirm the absence of evicting behavior in this species. In the case of the pied crested cuckoo, *C. jacobinus,* alone, has anyone even suggested that eviction may take place and even here there is no conclusive evidence for it. In the few instances where this has been suggested it was not possible to establish that the ejection was deliberate or even that it was done by the nestling cuckoo.

Skead (1962, pp. 72-73) observed a nest of the forktailed drongo, *Dicrurus adsimilis,* containing a young jacobin cuckoo and three drongo eggs. Two days later one of the eggs was found on the ground below the nest; the following day another egg was found there; still 4 days later the drongo chick, which had hatched in the meantime, was lying below the nest. The finding of these eggs and of the nestling drongo under the nest suggested (but only suggested) that the eviction was done by the young parasite. Skead was careful to point out that this inference required proof.

The estimated age of the young cuckoo was three days when the first of the host's eggs was found below the nest, and 8 days when the drongo chick was so recorded. If the eviction was done by the young cuckoo, this would imply a much longer duration of the evicting instinct than occurs in *Cuculus,* a genus in which the habit is well established.

It is impossible to state that the young cuckoo was not responsible, but there are other cases known where eviction definitely did not take place. Skead himself (1951, pp. 172-173) described a case in which a nestling jacobin cuckoo tolerated eggs and young in the same nest for up to 4 days, and another nest in which another young parasite made no attempt to evict the eggs for 4 days during which the nests were under observation. It not infrequently happens in a crowded nest that activity by one of the nestlings may sometimes result in the accidental pushing of one of the eggs or young out of the nest. Also, in parasitized nests, the young parasite often is larger and grows relatively faster than its nestmates and by successful competition with them for the food brought by the adults may starve them to death. In such cases the dead young are removed, not by the young parasite, but by their own parents as a matter of nest sanitation.

Furthermore, there are observations of still other nests in which the host young and the young jacobin cuckoo grew up together to the fledgling stage, and were seen together even after leaving the nest (Godfrey, 1939, p. 3; Bates, 1938, p. 125). These are clearly cases in which no eviction by the young parasite took place. In the two instances described by Skead, if any eviction by the young cuckoo might have been involved, it did not occur for some days after hatching, which is not the case in *Cuculus.* On present evidence it is doubtful that young *Clamators* have the habit of methodically and deliberately ousting their nestmates during the early stages of their nestling life.

An unusual type of host-parasite nestling relations was observed in India by MacDonald (1960, pp. 174-175). He watched a nest of a jungle babbler, *Turdoides striatus somervillei,* that contained a nestling jacobin cuckoo and a young babbler. The young parasite was more advanced in its development than its nestmate and it was found to leave the nest and forage and then return to it to be fed by the foster-parents, who were more or less bound to the nest by the presence in it of their own less advanced chick. This was noted repeatedly, and suggested a degree of resourcefulness quite unexpected in a bird at the nestling-fledgling stage. It also was another instance of mutual survival, or, in other words, of the absence of evicting behavior by the young cuckoo.

FLEDGLING FEEDING BY ADULT CLAMATORS

The feeding of well-grown, fledged, young crested cuckoos by adults of their respective species has been reported for two of the four species of the genus. In no case has convincing, corroborative evidence been placed on record, but inasmuch as such behavior has an evolutionary interest as atavisms it is necessary to mention them here. The data are as follows:

In India, Gill (1925, p. 283) claimed that he had often watched adults of the jacobin cuckoo, *C. jacobinus* feeding fully fledged young of their own kind, and that koels, *Eudynamis scolopacea,* do this even more often and regularly. If this is correct the observations have not been reported subsequently by other field students, and it is possible that Gill mistook an adult female for a fully grown young merely because he saw it being fed by another jacobin cuckoo. It is known that this cuckoo does indulge in courtship feeding and it may be this was what Gill really saw. Thus, in South Africa, Godfrey (1939, p. 26) watched a melanistic and a pale morph of the jacobin cuckoo feeding on caterpillars on the ground. The pale bird was seen to pick up a caterpillar, pass it a few times back and forth along its beak, and then to approach the black-phase bird with this in its bill. It mounted the latter, gave it the caterpillar, and then mated with it.

Similarly, many years earlier, in northeastern Africa, von Heuglin (1869-1873) wrote of the great-spotted cuckoo, *C. glandarius,* that he thought it occasionally took care of young of its own kind. It is not possible to decide from his wording exactly what actions he witnessed, but it may have been more a matter of premigrational flocking, as no evidence of actual feeding of the young by the adults has been noted since anywhere in its range. That this may be the real condition from which von Heuglin gathered his impression is suggested by an observation of Ivy's (1901, p. 22), who, in eastern Cape Province, found a pair of adults with five young birds late in February. He considered that ". . . the old birds collected their broods previously to migrating . . ." The most that may be said in the case of this cuckoo is that fledgling feeding is yet to be proved.

The mere act of courtship feeding, as shown in the jacobin cuckoo, is in itself an atavistic behavior, and if it should eventually be found to be coupled with even occasional feeding of fully fledged young (other than by mistaking them for adult females) this would further strengthen the suggestion that *Clamator* is a fairly primitive genus of parasitic cuckoos.

PLUMAGE VARIATIONS AND THEIR SIGNIFICANCE

Before we discuss the polymorphisms which have been well established in two of the four species of *Clamator, jacobinus* and *levaillantii,* it is necessary to review the extent and the nature of the variations found in the "normal" plumages as well as in their melanistic phases.

Although not pertinent to the immediate problem of polymorphism, the plumage variations of the climax species *C. glandarius* also may be described and discussed in this section of the paper, as they have pertinent evolutionary implications as well. *C. coromandus* calls for no comment here.

Clamator levaillantii

The "normal," i.e., the white-breasted, plumage has the entire underparts from chin to vent white, with black streaks on the chin, throat, breast, and upper abdomen, these streaks narrowing to shaft lines on the feathers of the sides, flanks, and undertail coverts, the streaks heaviest on the throat and upper breast; all the rectrices with broad white tips crossing both webs, and with a white patch on the outer eight primaries, this patch not visible from above in the closed wing because of the overlapping secondaries; underwing coverts white with very variable amounts of black markings. The entire upper surface of the head and body is solid black.

Here we find variations in the mental and pectoral stripes from specimens in which these dark marks are narrower than the white interspaces (the lateral portions of the feathers are here involved) to others in which the dark marks are broadened to the degree that they become practically coalesced to form almost solid black areas on the chin and upper throat. Although no geographic races of the stripe-breasted cuckoo are recognizable, much attention has been paid by authors to the degree of the variation, especially in the heaviness, the length and width, and the darkness of the blackish stripes on the throat and breast of the adult birds. Gyldenstolpe (1921, pp. 246-247) considered some of this variability to be a matter of age, the stripes being narrower in younger birds than in older ones. He also thought the stripes were broadest and darkest in the males. Examination of large numbers of specimens, especially in London, convinced me that no correlation with age or sex may be maintained. Chapin (*in litt.*, 1961) wrote that while these stripes were variable throughout Africa, they seemed to average heaviest in specimens from the northeastern part of the continent—Ethiopia and Somalia. In five specimens from there in the American Museum of Natural History the throat was so broadly streaked as to be almost completely black. Examples of this extreme type came from Giamo, Bissidimo, Godja-Mariam, and Maraco, in Ethiopia, and from Warsangli-Mush Hated, 5,000 feet, in the Somali Republic. Another equally dark bird came from much farther to the south, from Machame, Tanganyika; in it the chin was fairly solid black, the throat less solidly so. In the British Museum I have seen specimens just as heavily marked with black from Mount Lotuke, in the Didinga Mountains of Sudan; also from Usambara Mountains, Pangani River, Tanganyika, and even one from as far to the southwest as Damaraland. All of these examples were adult males. Furthermore, in all the areas involved, other examples were much less heavily striped than those mentioned here.

One of the palest birds seen was from Tembura, in the Bahr-el-Ghazal Province of Sudan. It had only narrow black streaks on the chin and throat, these disappearing on the upper breast, in marked contrast to the Mount Lotuke dark extreme which not only had the black streaks almost coalesced on the chin and throat, but had these markings continuing very broadly over the entire breast, tapering caudally, but with narrow black shaft streaks on the entire abdomen, sides, flanks, and thighs. These abdominal shaft streaks were even more pronounced in the Usambara birds. Perhaps the extreme variant in this character of all the birds seen was a female from near Mombasa, collected together with five in the melanistic "*albonotatus*" plumage phase. In it the entire underparts were heavily streaked with black, from chin to vent. One from Kyambu, near Nairobi, Kenya, described by van Someren (1922, p. 51), was said to have the black stripes reaching the abdomen as well.

Turning now to the opposite extreme, a male from Gunnal, in Portuguese Guinea, from the other side of the continent, was almost as lightly marked as the Tembura bird. Recently, in a report on Gabon specimens, Rand, Friedmann, and Traylor (1959, p. 271) noted the great variation in the underwing coverts and axillars; from almost wholly dull white to largely blackish. The Tembura specimen in London had no blackish at all under the wings. Years ago, a specimen from Danger River, Gabon, was used as the basis for the description of a very pallid "race" *caroli.* This specimen was studied in 1962 together with the Tembura one, as well as with a very extensive series of others. It was found to be paler, less streaked with black on the chin and throat, but the difference between it and the Tembura bird was not great enough to suggest that it might represent a distinct race. The type of *caroli* had the terminal white spots on the rectrices larger than in the Tembura specimen. The extreme pallor of *caroli* suggests, if anything, that just as in coastal Kenya *levaillantii* may produce completely melanistic phases (*albonotatus*), so elsewhere it may almost approach *jacobinus* in its lack of dark ventral markings. Certainly the geographic distribution of color extremes—darkest birds from Ethiopia, Somali Republic, Kenya, Sudan, Tanganyika, and Damaraland in South-West Africa, and lightest ones from Sudan, Gabon, Portuguese Guinea, and Rhodesia—indicate that they are haphazard in their occurrence, and hence not significant taxonomically. In none of these areas are the birds uniform in their variational trends.

Another variable character of the "normal" phase of *levaillantii* is the length of the feathers forming the crest. Here again, examination of long series from all parts of the range, tends to rule out the supposed significance of any local extremes. At one time in these investigations it seemed that birds from Ethiopia tended to have on the average longer crests than birds from elsewhere, but measurements failed to corroborate this.

The melanistic phase, originally described as a separate species under the name *C. albonotatus,* has been found (with one exception) only in the narrow coastal belt of Kenya, south to Usambara Hills, in Tanganyika, and north to southern Jubaland in the Somali Republic. I have been able to examine 21 of the 26 recorded specimens known to me. Since relatively few investigators have examined this plumage, and none with as ample material, the following notes on its variations are here recorded.

In general this phase may be described as being black all over, except for terminal white spots on the outer rectrices (this varies from the two outermost pairs to the four outermost pairs in different individuals), and a white patch on the inner webs of the eight outer primaries. However, in four of the specimens there was some whitish, in the form of edges on the feathers of the throat, breast, abdomen, and undertail coverts. The amount of such whitish areas varied individually; in one unsexed example from Takaungu the feathers of the abdomen and the undertail coverts were broadly edged with grayish white; in another from the same place these pale edgings were very narrow. In this connection, it may be recalled that in our discussion of the variations in the normal phase, we described (*supra*) one example, collected together with melanistic birds, in which the entire underparts were white, heavily streaked with black from chin to vent. This specimen might equally well be described as a melanistic polymorph in which all the ventral feathers had white edgings.

The white spots at the tips of the outer tail feathers not only vary in the number of rectrices on which they occur, but also in the size of the individual spots; in some cases they are restricted to the outer web, in others they extend across both webs of these feathers. The presence of these tail spots is the only constant difference, aside from the total size of the bird, and its corresponding wing and tail dimensions, between this phase of *levaillantii* and the corresponding melanistic morph of *C. jacobinus serratus*. Very occasionally a specimen of *levaillantii* may lack these white tail spots, as in one taken near Lake Chahafi, Kibwezi, southwestern Uganda, reported by Pitman (1931). He implied that there was another similar one from former French West Africa in the British Museum, but I failed to find it when I examined the series there in 1962.

A number of the specimens of this black phase studied were in various stages of molt. They revealed that the juvenal plumage (or, at least, subadult plumage) is uniformly dull fuscous brown on the entire upper side of the body and head. In some examples the entire underparts, as well, were of this color, but in others the abdomen and sides were paler, more of a dirty brownish white. Even these young specimens had the white wing speculum as in the adults.

Clamator jacobinus

Unlike *C. levaillantii*, this species varies geographically in its plumage characters, and has been divided into three recognizable races. Typical *jacobinus*, a small race (wings 135.5 to 150; tail 146 to 172 mm.), with white throat and breast, the feathers of the lower throat and breast with the faint, dusky shaft streaks either practically wanting or pale and very narrow, hairlike lines, occurs in southern India and Ceylon, and is partly migratory as some of its members winter in

Africa. Another race, *pica,* similar in color characters, but larger in size (wings 149 to 164 mm.; tail 173 to 197 mm.), has two disconnected breeding ranges; one part breeds in Baluchistan, and in northern India from the Kashmir Himalayas west to West Pakistan, and Nepal, south to United Provinces, and Kutch, and winters largely in Africa, south of the Sahara; another large segment of the subspecies breeds in sub-Saharan Africa from Senegal east to Ethiopia and the Somali Republic, southward to Angola, northern portions of Northern Rhodesia, and southern Kenya. The third race *serratus,* similar in size to *pica,* is dimorphic in the southeastern portion of its range. Its pale morph is like *pica* but with the shaft streaks of the throat and breast feathers darker and often heavier, and the entire pectoral area and the sides of the body tinged lightly, or more heavily, with grayish. The dark morph is black except for the white wing patch. This is the race of Africa south of the Zambezi River, where it occurs only during the breeding season, October to March, wintering in tropical Africa along with *pica* and *jacobinus.* In the western part of its breeding range, especially in South-West Africa, it approaches in coloration the race *pica;* but the birds breeding there agree better on the average with pale *serratus,* and, furthermore, they lay white eggs like *serratus* (*pica* and *jacobinus* lay blue-green eggs). There is reason to believe that *serratus* may breed north to southern Kenya, but no form of the jacobin cuckoo has yet been found to breed in Tanganyika.

The chief evolutionary interest in the facts discussed in this section is that the range of variation in *C. levaillantii,* from the heavily striped pattern to the almost unstriped anterior underparts, as in the type example of *"caroli"* and in the Tembura example, comes very close to bridging the gap in this character between this species and *C. jacobinus* (fig. 14). We have also seen that the range of variation in the pale morph of the latter varies from birds with the chin, throat, and breast entirely white, devoid of any streaks or marks, to others with well-developed, but narrow, dusky shaft lines on the feathers of these parts. The lack of greater difference between the most definitely lined *jacobinus* and the least striped *levaillantii* almost establishes a variational continuum. There is a more sizable break between the dimensional characters of the two, but here again, the gap between the smallest *levaillantii* and the largest *jacobinus* is not very great in proportion to their size. Also, the juvenal plumages of the two species, and the melanistic phases are extremely similar, save in dimensions. The eggshell color of *C. jacobinus* in India and in northeastern Africa is similar to that of *levaillantii.* It is true that in the more southern population of *jacobinus* (*serratus*) we find a markedly different egg type, but the difference here is just as great between sections of this species as between it and *levaillantii*. There can be no reasonable doubt as to the close relationship of the two species.

Inasmuch as it is thought that the southern *serratus* is nearer to ancestral *C. jacobinus* than are the other races of the species, it would follow that the evolutionary trends in plumage pattern involved a loss of the pectoral shaft stripes giving rise to *C. j. pica* and *C. j. jacobinus* on the one hand, and a great intensification of the same character giving rise to *C. levaillantii*. From the *serratus*-like primordial stock both developments arose and diverged.

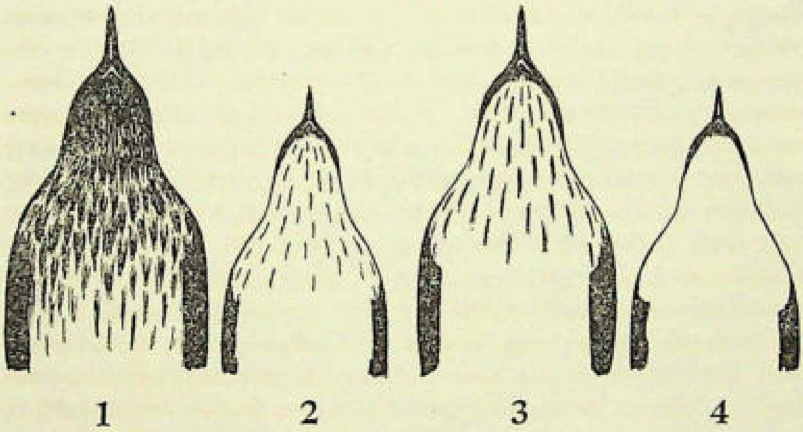

FIG. 14.—Variation in pectoral markings.
Clamator levaillantii: 1, Darkest; 3, palest.
Clamator jacobinus: 2, Darkest; 4, palest.

It may be remarked that it seems (to human eyes) that some plumage characters of no great biological significance are tenaciously retained during evolutionary changes while others of no more obvious utility are altered. An example of the former is the white wing patch found in both the pale and the melanistic morphs of both *jacobinus* and *levaillantii*, although this may have a recognition and a releasing function in both species.

Clamator glandarius

The one feature of greatest evolutionary significance, or, to put it in a different way, the one phylogenetic clue of greatest interest in the plumages of this, the climax species of the genus, is the fact that its juvenal plumage has the remiges extensively reddish, suggesting a relationship with *C. coromandus.* Aside from this, there is only one point worth mentioning in any detail, the possible geographic variation in the adult *C. glandarius.*

Clancey (1951, p. 141) separated the population breeding in Africa south of the Sahara from the nominate, Mediterranean basin birds, and gave them the name *choragium.* The characters of this southern race were smaller size and warmer buff on the throat and breast with less pronounced dark shaft streaks on the feathers. Judging by Clancey's account, Gilliard examined for him the material, totaling 101 specimens, in the American Museum of Natural History and apparently agreed in considering the two populations as distinguishable. In the course of my studies I have examined nearly 200 additional examples, including 177 in the British Museum, and I found that there was very extensive overlapping in all these characters. The buff tone of the throat and breast in fully adult birds may average very slightly warmer in *choragium,* but great care must be taken to compare birds of the same age, as the young of both populations are warm tawny buff on the throat and breast and adults of both largely lack this color and are not more than pale buffy cream with a slight ashy tinge. I could not find any constant difference in the development of dusky shafts on the feathers of this area in the two groups of birds. Furthermore, the size characters showed more overlapping than the figures given in Clancey's paper, and at best were not more than a slight average difference, hardly enough to warrant nomenclatorial recognition.

Using only breeding season examples, to eliminate possible migrants of the other population, I found that in males the wing length varied from 190 to 223 in Mediterranean birds, from 185 to 218 in southern ones: The tail length in these males varied from 186 to 226 in Mediterranean examples, from 181 to 219 mm. in southern ones. The females showed similar overlapping. Finally, as a test, I found myself unable to relegate the majority of specimens to subspecies without looking at the localities on their labels. I therefore do not accept *choragium* as a valid race, at least not as a race of utility in taxonomic work.

It may be mentioned that I examined these birds with the expectation that *choragium* would be corroborated, as I was aware of interesting differences in the host relations and host-parasite adaptations in the two populations. I can only look upon the results as providing unexpected support for the relative recency of this cuckoo as a breeding bird in sub-Saharan Africa, a conclusion already suggested by a study of their relatively poorly adjusted host relations in the African part of their range.

The situation present in the sub-Saharan *Clamator glandarius* as compared with that in the circum-Mediterranean segment of the species is reminiscent of Thorpe's (1930) biological races in insects. He called attention (p. 189) to instances among species of insects and allied groups in which geographically isolated populations with little or no structural or pigmentary differences were definitely differentiated biologically or behaviorally. These he considered essentially the same as subspecies, but in which the racial characters are aspects of the living rather than of the preservable parts of the specimens. As I have already indicated I do not think it advisable to give separate taxonomic or nomenclatorial rank to the two sections of *Clamator glandarius,* as the size and color characters ascribed to *choragium* are too slight and the overlap too great to make it a "usable" subspecies, although *choragium* does reveal a trend toward differentiation, as yet not well developed, and there is in its life history a biological difference in its host relations and in its range of host selections. The very fact that its behavioral character results in relatively poor coordination in its host relations, coupled with the independent fact that its structural modifications are still only faintly developed, suggests that *"choragium"* is a new, possibly as yet only an incipient, race.

One further item in the plumage cycle of *C. glandarius* deserves mention. Its juvenal plumage is blackish on the top of the head and nape, not gray as in the adult. Because of this, Jourdain (1925, p. 661) suggested that this might have been produced through adaptive evolution to achieve some degree of resemblance to the plumage of the nestlings of its Palaearctic corvine hosts. Jourdain stressed that the only conspicuous parts of the young bird while in the nest are the crown and nape, and he accordingly discounted the pale tawny chin and throat coloration. However, it may be recalled that the critical moments for the nestling are when the foster-parent comes with food. At such times the young cuckoo, as well as host young, raise their heads and open their mouths widely and clamor for food, and at such moments the throat would be no less visible than the crown and nape. I cannot help but consider Jourdain's suggestion as an "armchair speculation," and it certainly does not apply to the sturnid hosts the parasite uses in Africa. On the other hand, Cott (1940, p. 422) was convinced enough to write that the nestling of this cuckoo has a plumage ". . . whose crown has been influenced by natural selection, but whose throat has been neglected—so that while the latter resembles that of its parents, the former imitates that of its nest-mates . . ."

POLYMORPHISM

Two of the four species of *Clamator* have produced well-established melanic morphs or plumage phases in restricted portions of their respective ranges. These two are *C. jacobinus* and *C. levaillantii,* and it so happens that the black phases of the two are extremely similar. Their geographic ranges are quite dissimilar in extent, however; that of *jacobinus* occupies a large area of southeastern Africa, while the corresponding one of *levaillantii* is restricted to a narrow coastal strip of northeastern Tanganyika and of Kenya.

Both of these morphs appear to be, in every way, good examples of polymorphism in the sense defined by Ford (1945, p. 73). In his definition a polymorphic species is one in which there are two or more distinct phases or forms simultaneously in the same habitat, even in the same deme and the same local population, and in which these forms occur in sufficient numbers that even the least common of them is too numerous to be accounted for by a continuous series of recurrent, identical mutations. To this basic concept may be added, as was pointed out by Carter (1954, p. 259) the further thought that the characters of these polymorphs must be such that they do not blend on crossing; in other words, they must be controlled by single genes, or at least by small groups of genes that are closely linked in their mode of inheritance. Otherwise, the normal interbreeding that goes on in any local population of a species would tend to transform these polymorphs into a broad but continuous spectrum of variation. In the case of *C. jacobinus* we have ample field evidence that crossing between the two color morphs takes place frequently and yet no intermediate plumages are known. For *C. levaillantii* we still lack field observations of similar crossing between the morphs as little work has been done in the restricted area of its polymorphism.[1] In

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[1] As described in our discussion of migratory behavior (p. 86) Lamm noted seeing two *levaillantii,* one in the normal and one in the black phase, at Vila Luisa, southern Mozambique. There can be no reasonable doubt as to his identification of the pale morph, and if the two were really a "pair" this would be a case suggesting that the situation between morphs in this species is the same as in *jacobinus.* The fact that the locality is so far south of the known range of the melanistic morph of *levaillantii* makes this sight record somewhat uncertain. Furthermore, Lamm's notes are not conclusive as to whether the two birds were really a pair. He merely saw a black-plumaged bird near the normal *levaillantii;* he observed no sign of mutual interest between them, although he wrote, "probably a pair."

this connection it may be recalled that Stresemann (1947, pp. 518-519) suggested that the ". . . allele-producing mechanism has besides some physiological effect increasing viability in this special environment (but not elsewhere) which results in its being favoured by selection . . ." In support of this suggestion he pointed out that a shrike, *Laniarius ferrugineus sublacteus,* also has a melanistic morph (*L. nigerrimus*) in the same limited area of coastal Kenya and the lower portion of the valley of the Tana River.

While the restricted geographic coincidence of melanistic polymorphism in two widely dissimilar and unrelated birds as a cuckoo and a shrike may be suggestive, it remains that in neither species do we have as yet any observational data as to the relative abundance of the two plumages, to say nothing of the frequency of crossing between their phases. In the absence of such information we can only interpret the situation in *C. levaillantii* as probably similar to what we know in the related *C. jacobinus* in southeastern Africa, and in that species it is difficult to see that either morph has any selective advantage over the other. In connection with Stresemann's suggestion, it may be recalled that *C. jacobinus* also occurs in coastal Kenya and the Tana Valley, and has produced no melanistic morphs there although it has done so far to the south. If there were something in the ecological situation of coastal Kenya that might favor such melanisms we might expect it to have produced some visible manifestation in *C. jacobinus* as well. That local ecology is not directly important in the establishment of polymorphism is further indicated by the fact that in the extensive area of southeastern Africa where *jacobinus* has two phases, *levaillantii* occurs in a single, "normal" or "pale" phase. In other words the two species are sympatric in the two areas where one and not the other is polymorphic.

The melanistic morph of *C. jacobinus* occurs as a breeding form throughout Natal, the eastern Cape Province, the eastern half, or more, of the Transvaal, the Orange Free State, and to Bechuanaland (Mahalapye), Southern Rhodesia (Bulawayo), Northern Rhodesia (Livingstone), and Nyasaland (Misanje). It is decidedly rare in the Rhodesias and Nyasaland, and finds its greatest abundance in Natal, the eastern Cape Province, and eastern Transvaal. It also occurs in southern Mozambique, but I know of but one actual specimen record from there, and it had no exact locality other than "Mozambique" on its label.

The corresponding black phase of *C. levaillantii* is known, as far as I have been able to learn, from some 26 specimens in the museums of the world. Of these, no fewer than 18 were collected within 50 miles of Mombasa (Mombasa, Kilifi, Mazeras, Takaungu, Rabai Forest, Sokoke Forest); 1 came from Malindi; 3 from the lower portion of the Tana Valley (Kosi, Kau, and near Lamu); one example was recorded from southern Jubaland (Jebeir), the most northern locality from which the black morph has been reported; the type specimen (of "*albonotatus*," under which name this morph of *levaillantii* was first described as a new form) was collected in the Usambara Hills, northeastern Tanganyika, and another was taken not too far away, on the Pagani River. The one remaining specimen, now in the collection of the Academy of Natural Sciences, Philadelphia, was taken at an altitude of 10,000 feet on Mt. Kenya, in February 1919! This locality is far removed geographically and ecologically from all the others. The specimen was originally in the Blayney Percival Collection, and since Percival is generally considered to have been a careful and reliable labeler of his birds, there is no valid reason for questioning this record.

It does, however, point out an interesting fact, namely that the tendency to produce melanistic morphs is not absolutely restricted to the area where these have become well established. While it cannot be proved that this specimen from the high slopes of Mt. Kenya was not a migrant from the coastal lowlands, this is extremely improbable. It would be a strange migration indeed for a bird of the hot coastal belt to migrate to an altitude of 10,000 feet on Mt. Kenya. Furthermore, we have no other evidence of the melanic morphs spreading out from their restricted habitat, such as we might expect if they were regularly migratory. Yet, it must be admitted that Percival (in Bannerman, 1910, p. 704) wrote that "*albonotatus*" seemed to visit the coastal belt of Kenya for about 6 weeks only in the year, which suggests seasonal movement. On the other hand, he collected two examples there in March, only a few weeks different in season from his Mt. Kenya bird. It seems, from all these considerations, more likely that the latter was a case of an individual melanism cropping up as an isolated occurrence. It may be mentioned that there is evidence of similar, sporadic, widely spaced cases of melanic polymorphism in *C. jacobinus* as well.

In the latter species occasional black-phase birds, indistinguishable from southeast African melanistic *serratus,* have been taken at Port Gentil, Gabon (November 3), south of Lake Tchad (in July), at Kulme, Darfur, Sudan (July 11), Kordofan, Sudan (no date) and at Sagon River, Ethiopia (June 4). Reichenow (1902, p. 78) listed the Kordofan record in the synonymy of the pale-vented *jacobinus,* not of *serratus.* However, Strickland (1850, p. 219) was aware of the difference, and commented that to his knowledge this ". . . Cape bird has never before, I believe, been obtained to the north of the equator . . ." Certainly the November bird from Gabon, in very fresh plumage, cannot have been a migrant from southeastern Africa, where at that time of the year *serratus* is breeding. Furthermore, the Kulme and Lake Tchad birds, taken in July, and the June specimen from Sagon River, are all in the same stage of molt as Natal birds are in February. This indicates that whether they were resident in the areas of capture, or whether they wandered there from elsewhere, they may not have come from southeastern Africa, where the molting season differs by a third to a fourth of a year from theirs.

The ranges of the melanistic phases of *C. jacobinus* and *C. levaillantii* are not readily expressed in terms of vegetational areas. Thus, if we take Keay's 1959 Oxford "Vegetation Map of Africa south of the Tropic of Cancer," we find that the black-plumaged *C. j. serratus* overlaps in its breeding range, the "Relatively Dry Woodlands and Savannas" (characterized by savannas of tall grass with *Acacias* as well as other trees) and the "Temperate and Subtropical Grassland" (pure grassland above 3,500 feet). The melanistic phase of *C. levaillantii* appears to be contained within, but is not coextensive with, the "Coastal Forest Mosaic" area.

To clarify the recorded data, it may be stated at this point that the old report of a black-phase *serratus* from Denkera, Fantee, Ghana, listed by a number of authors in their compilations, is based on an error. The actual specimen involved, examined by me in London in 1962, is not a *Clamator* at all, but a black cuckoo, *Cuculus cafer.* Similarly, the supposed record of melanistic *serratus* from Lamu, Kenya, cited by several writers on east African birds, is actually based on an example of the black phase of *C. levaillantii,* to which it is properly referred in the present study.

To return to Ford's illuminating appraisal of the whole question of polymorphism, it appears that the situation in the two species of *Clamator* fits the definition of what he terms neutral polymorphism. It may be explained that Ford distinguishes three types—transient, neutral, and balanced polymorphism. The first is, as its name suggests, a polymorphism in the process of spreading through a population, but once it becomes fixed and ceases to spread it is no longer to be termed transient, but becomes either neutral or balanced. When a variant phase, or morph, has a selective advantage only as long as it does not dominate numerically the total population in which it occurs, and loses this advantage when it becomes more widely prevalent, it is said to be a balanced polymorphism. However, when such a form appears to be without obvious selective value or adaptive advantage, it is termed a neutral polymorphism. It is not clear that the distinction between neutral and balanced polymorphism is biologically factual; it might be better to say that the neutrality of certain balanced polymorphisms is merely an observational inference rather than an established genetic fact. It is in this restricted sense that the situation in *Clamator* may be described as neutral. In the light of present evidence, at least as far as *Clamator jacobinus* is concerned, the "normal" morph and the black phase seem equally well adapted to their common environment. The birds interbreed freely and act as though they recognize no differences between them, and furthermore the black form is not noticeably spreading geographically or becoming increasingly numerous where it occurs together with the white-breasted form (and it is not known to occur anywhere as the sole morph). In some localities it is apparently as common as, and in a few spots even more numerous than, the pale morph, but there is no evidence to suggest that the ratio has changed appreciably in the past half century or more of observations. It must be admitted that this absence of evidence is not nearly as good a support as would presence of negative evidence have been. The "evidence," if it may so be termed, is chiefly the memory and recollections of observers of long residence, unsupported by critical records and notes.

In the case of *C. levaillantii* we can only assume that the situation is also one of neutral polymorphism, as we do not have the direct evidence available in *C. jacobinus*. It seems, however, a safe assumption.

Polymorphism is an expression of gene frequency, and neutral polymorphism implies a fairly stable frequency picture. Inasmuch as the occurrence of melanistic morphs of both *levaillantii* and of *jacobinus* away from their geographically restricted areas of developed neutral polymorphism is so sporadic and infrequent, it follows that these two wide-ranging species, each with geographically continuous, uninterrupted, nonfragmented distribution patterns, have local populations whose gene pools seem to be fixed and seem to be kept unavailable to adjacent populations of their own kind.[2] There

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[2] In the case of *C. jacobinus* this statement is intended to cover only the African part of its range; its extensive Asian population is of course effectively cut off from the larger African one. No black-phase birds of this cuckoo have ever been noted in Asia (from which area I have examined at least 200 examples, as well as read and checked the many observations and records in the literature).

may possibly be some unknown and, as yet unsuspected ecological factor in the area of polymorphism of each of these species that has made possible a local decrease in selective pressure and thereby enabled two morphs of each to develop in a state of passive neutrality. This may be something akin to what Stresemann vaguely suggested, although transposing the factor from the "allele producing mechanism" to the environment. There is no evidence even tangential to this concept that may be cited, and the thought is merely inserted for its suggestive value. Considering that both species are highly migratory, at least in their southern sections (exactly the section where *jacobinus* is polymorphic), it is difficult to account for this apparent genetic isolation in the light of present knowledge. It seems that in coastal Kenya, Percival's statement (*cit. supra*) notwithstanding, *levaillantii*, with its local black phase, is relatively nonmigratory, but no such assumption can be maintained for either in southeastern Africa. The absence of migrant, or of "wintering" examples of black-phase *C. jacobinus serratus* from equatorial Africa during the southern winter, when it is known that both phases are absent from their relatively well-observed austral breeding range and have presumably gone north, is a real puzzle. This is discussed more fully in our account of migratory behavior (see pp. 84-85). In the present connection it may be hypothecated that, wherever they may "winter," all the individuals of southeastern *serratus* return to their home area for breeding, and thus remain unmixed with their adjacent conspecific populations.

Aside from the well-developed melanistic morph in the adults of *jacobinus* and *levaillantii*, the latter species also has a rufescent juvenal morph, reminiscent of the hepatic phase of the young in *Cuculus canorus.* I know of only two examples of this rufescent phase, both from the northeastern portion of the Republic of the Congo (former Belgian Congo). One such bird, a young male, taken at Poko, in the Uelle district on July 31, now in the British Museum, is bright cinnamon rufous above and below, only the remiges and retrices being darker, less reddish, as in the "normal" juvenal. The other one came from near Beni, in the Ituri district. Another, possibly partial, rufescent bird may be one mentioned by Granvik (1934, p. 24) as having the undertail coverts pale rufous, although the rest of the plumage was probably "normal" as it evoked no comment from the describer.

MIGRATORY BEHAVIOR

The evolutionary picture of migratory behavior in the genus presents some peculiar features. All four of the included species are strictly migratory in some parts of their respective ranges and not in other parts. (In the case of *C. coromandus,* the available evidence is not conclusive about an area of permanent residence, and, hence, of a population of nonmigratory birds.) The extent of migratory movement varies from none at all to thousands of miles. All three of the species breeding in South Africa (*glandarius, jacobinus,* and *levaillantii*) are absent from that area during the southern winter; all three have resident populations in tropical Africa. The first named of these is present in its Mediterranean breeding grounds in the Iberian Peninsula and northwestern Africa only during the northern summer, and then migrates to equatorial parts of Africa, apparently chiefly in the eastern half of the continent. The migration of this section of the species is thus exactly the opposite, both in direction and in time of the year, from that of the South African *glandarius.* In other words, we find in these cuckoos that geographic segments, not necessarily even subspecifically distinct, differ markedly from other conspecific segments in their migratory behavior. It need hardly be added that in the majority of birds that have spatially distinct breeding and nonbreeding quarters, migration is an important, well-formulated and patterned, presumably evolved and inherited, part of their annual life cycle. Yet in the crested cuckoos of the genus *Clamator,* this migratory behavior is manifested only in sections of each of the included species.

In this geographic fragmentation of migratory behavior within the members of each species, we have something that may be likened to partial migration, with the difference that here the "partial" element is geographic, not individual. Partial migration is a term used chiefly for species in which some individuals are regularly migratory while others, breeding in the same area, are nonmigratory, resident birds. Inasmuch as there is no evidence to prove that the migratory South African populations are ecologically or geographically cut off from their nearest resident counterparts in tropical Africa, we cannot postulate an interference effectively isolating them into discrete, non-intercommunicating colonies or gene pools. Even allowing for a reduced frequency of such intercommunication, we may come back to something akin to partial migration (in an overall species view) as a valid way to express their migratory tendencies.

Partial migration of the more usual sort has been studied in the North American song sparrow by Nice (1937), and in a variety of European passerine species by Lack (1943-44). Their findings are of interest here. Nice (1937) found that in the song sparrow, *Melospiza melodia,* in the Columbus, Ohio, area, migratory and nonmigratory behavior was not correlated with age, and apparently was not a matter of inheritance. Thus, nine resident fathers had seven resident and two migratory sons, and nine migratory fathers had seven resident and four migratory sons. Among 61 males, it was found that 24 remained consistently resident, 31 were consistently migratory, and 6 changed from one to the other of these behavior groups. Among 43 females, 5 were consistently resident, 37 always migrated, and 1 changed from resident to migrant. Some years later Lack (1943-44) reported on a study of partial migration in a number of species of European birds, and showed that in all cases the females and the young of the year showed a noticeably greater tendency to migrate south in the autumn than did the adult males.

Baker (1942, p. 4) was aware of the partial nature of the migration of cuckoos other than *Clamator.* He went so far as to conclude that ". . . most genera and, indeed, most species of migratory Cuckoos include a race which is more or less sedentary. For instance, the Common Cuckoo, the most migratory form of Cuckoo, has a race, the Khasia Hills Cuckoo, which can hardly be called migratory at all. It breeds in the eastern sub-Himalayas and spreads into the plains of Burma and India in winter, while some individuals remain all the year round in their summer quarters. If . . . migration has in many cases been forced upon birds because of the insufficiency of food supply during the breeding season it may well be, . . . that cuckoos were originally tropical or sub-tropical oriental birds and their extreme limits, East and West, are those to which they have extended under this pressure . . ."

In his recent (1962) survey of bird migration, Dorst noted that a considerable number of species of birds are composed of sedentary, migratory, and partially migratory populations, which could be looked upon as "physiological races" or sections of the total population of each species. From this he drew the logical conclusion that migration cannot be regarded as a specific character as it really belongs within the framework of populations within the species.

In some species of other birds migration is a characteristic of one race or subspecies and not of another. A case that may be mentioned is the Oregon junco, a North American finch studied experimentally by Wolfson (1942). This bird has a migratory and a purely resident race in northern California. To test their migratory tendencies Wolfson experimentally subjected groups of individuals of each kind to increasing numbers of hours of light, either natural or artificial, but only the individuals of the regularly migratory race responded by becoming restless. This indicated that not only was a predisposition for migratory behavior necessary but that it could be manipulated. What can be manipulated experimentally by the investigator may also be effected out of laboratory conditions by "natural" causes.

At this point it seems useful to note the results of some recent studies because they correct a concept of migration based too largely on what has been recorded in north-temperate areas of the world. The pattern of migration there, with its easily accepted geographic inferences and correlations, is usually expressed in terms of Pleistocene climatic fluctuations. However, Moreau (1951) has shown that bird migration is probably as old as bird flight and that what happened during the Pleistocene in Europe and North America merely determined the geographic details of the migrations of individual species; but not the migratory behavior itself. It is true that most of the major, "best organized" migrations of considerable geographic magnitude seem to have reflections of Pleistocene events, but we realize that migration may have begun anywhere, anytime, with different groups of birds (Drost, 1950, p. 231). Pleistocene glaciation was not its cause. Moreau (1951) and Mayr and Meise (1930) indicated that migration may have originated in any localities where seasonal food scarcity may have caused some birds to move away seasonally and thus have a better chance of survival. Ostensibly, it would seem that this would be acted upon by natural selection, and in this way migratory behavior would become established, with or without any influence of Pleistocene glaciation, and, in some cases, probably was much earlier than Pleistocene in origin. In defense of this argument Moreau (1951, p. 247) cited cases of migration entirely within warm areas, and mentioned among them ". . . the Indian population of the cuckoo, *Clamator jacobinus,* which travels all the way to East Africa after breeding . . ."

Cuckoos, as a group, are birds with a great tendency or predisposition toward migration. Many years ago, W. L. Sclater (1906) calculated that of the 814 species of birds then known to occur in South Africa, 731 were resident, and only 21 were to be considered as African migrants (as distinguished from European and Asiatic winter visitors), and of these 21 no fewer than 9 were cuckoos. Many years prior to Sclater, Emin Pasha, prior to 1888, (published by Schweinfurth, et al., 1888, p. 392) noted the seasonal wanderings of a number of purely African savannah birds in "Equatoria" (the southern part of the present Sudan and the adjacent area of the Republic of the Congo), among which he mentioned *Clamator.*

It is among the cuckoos, purely insectivorous in their feeding, that we find some of the most remarkable of geographic migrants. We may take, as an example, the long-tailed cuckoo, *Urodynamis taitensis,* that makes an unusually long, and largely nonstop, overseas journey from its New Zealand breeding grounds to the islands of Polynesia, some of which are as much as 4,000 miles away. (Bogert, 1937). Another notable example is the little bronze cuckoo, *Chrysococcyx lucidus,* also a New Zealand bird, that goes more than 2,000 miles across the South Pacific to the Solomon Islands (Fell, 1947). The common cuckoo of Europe makes a similarly impressive journey from its northern breeding area to tropical and even to southern Africa. In fact, numerous writers have made particular mention of the fact that the young of the year of this species make this spectacular trip by themselves with no possible aid from, or accompaniment by, the adults of their own kind, with whom they have had no experience.

The concepts of migratory tendencies, even if they are not more than a periodic psychobiological restlessness, originally not rigidly correlated with, or controlled by, heredity, and of migration apart from the rigid seasonal climatic fluctuations of Pleistocene glaciation-induced patterns, make it possible to look upon the *Clamator* situation as less enigmatic and less paradoxical than it first seemed to be. Considering the pronounced migratory tendencies of its relatives in the subfamily Cuculinae, it would be surprising if the species of *Clamator* were not also somewhat migratory. The extent to which this behavior is developed differs in the four species of the genus. To explore these differences further, we may now turn to the situation in each species, as far as the present, still incomplete, data will permit coordinated presentation.

Clamator jacobinus

It is definitely known that the population (subspecies *serratus*) that breeds in Natal, Transvaal, Cape Province, and Southern Rhodesia, is absent from those areas from late March to October (southern "winter"), and that individuals of the pale morph of this race have been collected during these months in Nyasaland, in the open grasslands of the southern and eastern parts of the Republic of the Congo, former Belgian Congo, (Aru in the Upper Uele, Mahagi Port in the Ituri, and near the base of Ruwenzori) and in Uganda (Mohokya, Fajao, and Kebusi in May, Butiaba in November). In Darfur, Lynes (1925, p. 354) found *serratus* (recorded by him as *jacobinus,* but corrected by Jackson and Sclater, 1938, p. 497) in June and August.

In Sudan the pied crested cuckoo generally is reported by Cave and MacDonald (1955, p. 174) to be a fairly common nonbreeding visitor from March to October in the southern part of the country, from June to late August in Darfur. It may be noted, however, that many years ago Emin collected an egg of this cuckoo at Lado (Hartlaub, 1881, p. 114) while Butler (*in* Sclater and Mackworth-Praed, 1919 p. 642) stated that it breeds near Khartoum, where he found newly fledged young on October 5 (Butler, 1908, p. 245).

In British Somaliland (now part of the Somali Republic) Archer and Godman (1961, pp. 663-668) reported it as present in May and June, the main breeding season of many potential passerine hosts. There are as yet no definite breeding records from that area but the pied cuckoo may well prove to breed there.

In Ethiopia, *serratus* has been collected as early as April 7 to 8, at Gato River, near Gardula (Friedmann, 1930, pp. 268-272) together with examples of the race *pica,* and at Sagon River, June 4. In Eritrea, K. D. Smith (1957, p. 309) classed it as a migrant, present from June to September, possibly breeding there in summer.

In Angola this cuckoo (subspecies *pica*) is found only from October to May, from Huila and eastern Moçãmedes to Cuanza Norte to Luanda and along the coast from Benguela to Cuanza; it migrates north of the equatorial forest in "winter." For these summary data I am indebted to M. A. Traylor of the Chicago Natural History Museum, who further informs me that there are breeding records from Chibia in February and from Huila in December, and that some of the Huila specimens show an approach to the pied phase of *serratus.*

In Tanganyika, Moreau (1937b, pp. 22-23) noted that while no race of *C. jacobinus* had yet been found to breed in that country, pied morphs of *serratus* were known to appear there as migrants, as well as the paler, white-breasted *pica,* some of the latter race presumably coming from India. He further noted that examples of this cuckoo from extreme western portions of Tanganyika may belong to a ". . . population different from that occurring in the rest of the territory; the date of the influx accords with a possibility that they might be birds coming south from spending their off-season in Darfur and the Sudan." Thus, at Kigoma, in late October, Packenham found *pica* became abundant, and he found that a female collected as a specimen record had an enlarged ovary, ostensibly a bird on its way to its breeding grounds.

In another paper, Moreau (1937a, pp. 5-7) reported that white-breasted birds (*C. j. pica*) had been collected in northern, central and southern Tanganyika between December and April. All his own northern Tanganyika records were of ". . . silent non-breeding birds in worn plumage or very slow and irregular moult like the February birds of extreme southern Tanganyika . . . This influx of non-breeding birds into northern Tanganyika fits in strikingly with Whistler's hypothesis that the Indian population migrates to Africa after breeding in the northern summer; and clearly the birds, also non-breeding, that are so common in Darfur June to September must have quite a different origin . . ."

In Kenya and Uganda, Jackson (in Jackson and Sclater, 1938, pp. 495-496) found *pica* to be a local migrant, rarely if ever remaining long in one locality, arriving in November and leaving in April and May. He noted these birds, apparently traveling north, from March 20 to April 16 at Nimule, Uganda, and moving south in November at Lake Albert. In the Nyando Valley he found them common early in May and scarce at the end of that month. "The same influx and departure after a few weeks' sojourn takes place in the coast and bush-veld regions of Kenya Colony . . . It is particularly plentiful in the Taru wilderness in November and December, and again in April . . ." However, there is now definite evidence that *pica* breeds in Kenya (Ngong) and in Uganda, so here it appears that there are resident birds, migrants from elsewhere in Africa, and migrants from India, making the resulting situation difficult to interpret with certainty in many specific instances. The intra-African migrants appear to be of both *pica* and *serratus* stocks. Similarly, there is some evidence that both *pica* and *jacobinus* wander to Africa from India.

It is unfortunately true that, so far, we have no direct proof, of marked individual birds, demonstrating the migration of pied cuckoos from India to Africa, but there are inferential considerations that strongly point in this direction. Long ago Whistler (1928) compiled an account of the postulated migration in the hope that it might stimulate observers in India to fill in the gaps in the information he was able to bring together. He showed that the bird (*pica*) is extremely numerous in northern India during the rainy season, when it breeds there, and that it is definitely absent from there the rest of the year. He expressed his attitude by stating that if the birds do not leave India and go to Africa ". . . we cannot say at present where so great a mass of individuals can winter unrecorded; it can only be in southern or southeastern India or in Ceylon . . . Legge's evidence appears to have ruled out Ceylon. As to southern and southeastern India, we have no definite evidence either for or against the supposition . . ."

In a later paper (1931, p. 193) he pointed out that the absence of examples of north Indian birds (*pica*) in the extensive series collected in southern India (*jacobinus*) at all times of the year ". . . virtually settles that our northern migrants go to Africa . . ."—a conclusion which has been accepted and implemented, without definite proof, by many others since Whistler's paper. Smythies (1953, p. 326) found that the jacobin cuckoo ". . . seems to leave Burma altogether in the winter, possibly migrating to Africa." In his recent compendium on Indian ornithology, Ripley (1961, p. 175) stated that *pica* (*serratus* of his book) reaches, on its winter migration, Gujarat, Bombay, Andhra, and northwestern Madras. ". . . The main wintering range appears to be to the west, south of the Sahara in Africa. Rainy season wanderings of this form and the next (*jacobinus*) prevent exact definition of the breeding zones in central India." Meinertzhagen (1954, p. 308) reported that in Arabia, a presumably logical area through which migrants between India and Africa might be expected to pass, the species was known as a migrant in the southwestern part of that peninsula, where specimens were obtained near Aden on March 31 and April 22, in the Amiri district in May, at Hadda near Mecca on April 2. He noted that a pair was obtained in Asir on June 26, which "may denote breeding." If these were breeding birds, and not delayed migrants, they constitute the only evidence for the pied crested cuckoo in Arabia other than on migration. On the basis of extensive personal experience with both Asiatic and African birds, Meinertzhagen concluded that some of the birds that breed in northern India and Baluchistan appear to go to Africa in the northern winter.

Grant and Mackworth-Praed (1948, pp. 171-172) attempted to study the migration of these birds on the basis of the dates of molting specimens in the British Museum. They started with the opinion that Indian specimens should be in molt from September to November, South African breeders, from April to June, and birds from other parts of Africa, from June to August. The fact that in India birds taken from September to November were in molt was in line with these dates, and from all these considerations it was thought that any molting examples taken in Africa during September, October, and November should be Indian migrants. Their examination failed to find any such material and they were forced to conclude that none of the African records could be considered definitely as migrants from India, and they ended with the statement that the ". . . only evidence we still have of this species visiting Africa from India in the nonbreeding season is the fact that it does leave India . . ." In 1962 I went over the material in the British Museum with a hope of finding some clues that Grant and Mackworth-Praed might have overlooked, and to examine recently acquired specimens that they had not seen. My results suggested a greater spread of months for molting of African birds, which clouded or obscured the whole picture to the degree that it was not feasible to demonstrate Asiatic origins by molting dates.

Clancey (1960, pp. 27-31) has, I think, made the only convincing contribution to this problem. He stated that not only do north Indian birds (*pica*) migrate to Africa, but he found that so do many of the smaller, typical *jacobinus* of southern, peninsular India and Ceylon. The birds of this subspecies are identifiable by their smaller size and consistently white throats and breasts (like *pica* in this latter character), and they are known to breed only in India, Assam, Burma, and Ceylon, but they occur in Africa as far south as Nyasaland, Southern Rhodesia, and southern Mozambique. The African records fall between September and April, which agrees with the fact that the birds should be back in India for the breeding season. Unlike north Indian *pica*, the race *jacobinus* is only partially migratory, some individuals remaining throughout the year in southern India and Ceylon while others reach Africa where they disperse over a wide area. The fact that some south Indian birds do migrate to Africa increases the probability that similar movements occur in north Indian *pica* as well.

The migration of *C. jacobinus* between India and Africa, does have some peculiar features. Ali (*in litt.*) has informed me that as far as he knows no other long-distance land migrant arrives in India at the commencement of the southwest monsoon season as this cuckoo apparently does. He further assured me that there is no evidence that any seasonal lack of insect food could operate as the reason for this bird to leave India after the close of the breeding season.

As discussed elsewhere in this report (p. 51) it seems that the southern African population (*serratus*) of *C. jacobinus* is the oldest, most primitive segment of the species, and of the genus, as it exists today, and that after it gave rise to *pica* in equatorial Africa, the latter spread to Asia and became established there. The present migration of *pica* between northern India and Africa thus is an annual reflection of an original movement in the past history of the species, a situation existing (or, at least, so interpreted) in many other migratory birds. Ticehurst (1922, p. 531) postulated a route from northern India to Africa for a number of Indian breeding species that are absent from there in winter; among them are *Agrobates g. familiaris, Caprimulgus e. unwini, Merops apiaster, Glareola pratincola, Cuculus canorus,* and others. To these may be added another cuculine species, the lesser cuckoo, *Cuculus poliocephalus,* that breeds in Asia, beyond the Himalayas, and winters in numbers in East Africa (Moreau, 1937b, p. 42), while Ali (*in litt.*) informed me of similar migratory behavior in Indian breeding *Merops superciliosus persicus, Coracias garrulus semenowi,* and *Muscicapa striata neumanni.*

Before leaving *C. jacobinus,* it is necessary to discuss the melanistic morph of the race *serratus* in connection with its migratory movements. This black phase is frequent in the eastern parts of the breeding range of *serratus*—Natal, Cape Province, Orange Free State, etc., and, like the pale morph, this one is absent from South Africa during the southern winter. These melanistic individuals are, in a sense, critical material, as the pale morphs could not be distinguished from similar birds resident in more tropical areas to which they presumably migrate. Yet, aside from a small number of black-plumaged birds (four), this phase has been conspicuously absent from collections made throughout Africa outside of their southeastern breeding range. The four black-phase birds, indistinguishable from southeast African *serratus,* that have been taken are as follows: At Port Gentil, Gabon (November 3), south of Lake Chad (July), at Kulme, Darfur (July 11), and at Sagon River, Ethiopia (June 4). These pose a very puzzling problem that cannot be completely resolved. These have been discussed briefly in our account of polymorphism (see p. 71) but our interest in them at this point is in their implications concerning their geographic movements. The November Port Gentil, Gabon, specimen, in very fresh plumage, can hardly have been a migrant from southeastern Africa, where at that time of the year *serratus* is breeding. The dates and the respective stages of molt and of feather wear of the other examples do not fit closely the seasonal chronology of the southern birds, and in this respect they suggest that they might be considered as individual (and rare) instances of melanism of the more northern race *pica.* In southeastern Africa *serratus* is dimorphic, and the melanistic phase is common, but if the four northern records of black-phase birds, listed above, are not *serratus,* or, at least, are not unquestionably of that subspecies, it would follow that not a single completely convincing example of the black morph of *serratus* has yet been collected away from its breeding range. There is no inherent reason why *pica* may not produce an occasional melanistic individual as *serratus* does in such numbers, although breeding examples of such have not been found as yet. If the Gabon, Lake Chad, Darfur, and Ethiopian black examples are looked upon as *pica,* where do the black *serratus* go when they leave their breeding range? If they are *serratus,* why have so few of this phase been collected during the southern winter while so many more of the pied phase have been taken? The discrepancy in numbers of winter specimens of the two is not at all consistent with their numerical status (almost equivalence in some localities) in southeastern Africa during the southern summer. Is it possible that the bulk of eastern *serratus,* which would include most of the black morphs, migrate a relatively short distance into Mozambique, an area where relatively little collecting has been done, and where Lamm (1955, p. 33) found this cuckoo (recorded binomially by him, but almost certainly *serratus*) from December through February? The only evidence, if it may be called that, suggesting that some of the melanistic *serratus* from southeastern Africa may wander far beyond Mozambique, even as far as southern Ethiopia, is that Mearns (in Friedmann, 1930, pp. 272-274) not only collected one bird, already mentioned, at Sagon River, on June 4, but saw four there, June 3 to 6, and two others at Turturo, June 15 to 17. If Mearns was correct in his identification of these sight records, this is the only instance known of a substantial, as opposed to a casual or individual, movement of these dark *serratus.* It is certainly not likely that the breeding *pica* of southern Ethiopia frequently produce melanic morphs in a limited area, or we would have had some other evidence of it by now, and, hence, if these records of Mearns are accepted they must be looked upon as migrant *serratus.* In support of this latter interpretation it may be noted that Mearns collected two examples of the pied plumage phase of *serratus* at Gato River, near Gardula, southern Ethiopia, April 7 to 8, together with other examples of the white-breasted race *pica* (*ibid.,* pp. 268-272). That pied morphs of *serratus* could reach southern Ethiopia as early as April 7 suggests either a very rapid migration, which is not very likely, or that some of the southern birds must start north considerably before others.

In Southern Rhodesia, where we might expect to find the black phase with some regularity either as a breeder or as a migrant, M. P. S. Irwin informs me that he has never seen one in life, and that the collections in Bulawayo contain a single Southern Rhodesian example, taken at Forest Vale, near Bulawayo, on November 20, and another from Livingstone, Northern Rhodesia, collected on October 19. These, and one other from Nyasaland, are the only black *serratus* out of a series of 64 skins from the Rhodesias and Nyasaland in the collections of the National Museum of Southern Rhodesia. In Nyasaland, Benson (1953, p. 35) noted two reliable sight records of the black-phase *serratus,* one from Fort Johnston in March, the other at Monkey Bay, in November. Benson assumed that these birds were transients in Nyasaland, and called them migrants from the north. I presume this means that they were looked upon as migrants coming from (November) their more northern wintering grounds on their return to their southern breeding area, or (March) returning to the north for the off-season.

To return, in our discussion, to southern Mozambique, Lamm (*cit. supra*) mentioned that in early December he saw both color phases of *Clamator levaillantii;* however, without the specimens (which were not collected), it is impossible to be certain that the black individual was really *levaillantii* and not *serratus,* for the dark morph of the former has not been found south of extreme northeastern Tanganyika. In reply to my inquiry, Lamm has informed me that this sight record was made at Vila Luisa on December 10, 1950. His notebooks record an ". . . all black cuckoo with white wing patch; near it another, black above, white below heavily streaked on the chest, probably a pair . . ."

It may also be mentioned that Pakenham (1948, p. 99) saw a black crested cuckoo in Zanzibar, April 10, which he considered as probably *C. j. serratus.* On the basis of the geographic proximity of Zanzibar to the known range of the black phase of *levaillantii,* Pakenham's bird may have been of this species. The mere sight record, unfortunately cannot be identified, and remains relatively useless.

To summarize, the peripheral populations of the jacobin cuckoo, *serratus,* in Africa south of the Zambezi River, and *pica* in northern India, are highly migratory; typical *jacobinus* of southern India is partly migratory, and *serratus* and *pica* in much of tropical Africa are apparently fairly resident in some places and move about without obvious correlation with season, climate, rainfall, or other noticeable factors in other localities. In large areas of tropical Africa a breeding form and two or more migrant, either transient or "wintering," populations often occur together. The movements of southeastern *serratus,* as evidenced by its melanistic morphs, are still unclear, but there is no question as to their going north during the southern winter.

Clamator levaillantii

As in *C. jacobinus,* the population of the stripe-breasted cuckoo breeding south of the Zambezi leaves that area after the end of the southern summer in late March, and does not return until October. Elsewhere in Africa it has been noted as a local migrant, or at least as a fluctuating element in the avifauna, locally present one day and absent the next. In Nyasaland it has been recorded from early October to May and even to June, and has been known to breed there. It is assumed by Benson (1953) that it migrates to somewhere to the north for the rest of the year. In the Rhodesias, where it also is known to breed, it is also seasonal, although further data are needed, especially from Northern Rhodesia, to clarify the local picture. Thus, in that country the earliest spring date is given as November 8, a month later than in South Africa (!) and the latest autumn date as May 4. Grant and Mackworth-Praed (1952, p. 506) wrote that it passes through Northern Rhodesia in November and December to breed farther south, and concluded that "there is certainly a northern and a southern breeding bird but this is probably not the whole story."

The seemingly haphazard occurrence of the species in localities where it has been found to be present or absent without obvious seasonal correlations, was stressed by Jackson (1938, pp. 497-498) in both Kenya and Uganda, although the species has been recorded there throughout the year. In Tanganyika the picture also is still confusing. Moreau (1937b, p. 23) noted that the only localities in that country where the species had been recorded as breeding were Iringa, from February to March; the east side of Lake Nyasa, in May; at Kilosa, in April. He recorded that it had been seen at Kigoma and at Uvinza in November, when it was molting. He considered it not unlikely that the nonbreeding birds in Kenya and northern Tanganyika may have been migrants from Ethiopian breeding grounds, while the southern Tanganyikan birds ". . . in the east up as far as the Central Line represent a different population breeding there and with their own movements . . ."

In coastal Kenya and the adjacent parts of northeastern Tanganyika, Percival (*in* Bannerman, 1910, p. 704) concluded that the stripe-breasted cuckoo was present as a "visitor" for a matter of only about 6 weeks in the year. However, this is erroneous, as specimens of the local melanistic morph have been taken in that restricted area in every month of the year except July and August, and the present lack of records for those 2 months is not indicative of absence. Further evidence of the nonmigratory status of this cuckoo in that area is afforded by the fact that during the more than half a century since Percival's work many and very comprehensive collections and observations have been made in practically all parts of Kenya at all times of the year, and not a single example of the black morph (the so-called *"albonotatus"*) has ever been collected outside of the coastal strip, except for one very surprising, but apparently acceptably authenticated record, taken by Percival, at 10,000 feet on Mount Kenya. As mentioned in our discussion of polymorphism (pp. 70-75) this last record would seem better interpreted as an unusual local melanism of the population of *C. levaillantii* resident on Mount Kenya, than as a migrant from the coastal lowlands.

In the Republic of the Congo (former Belgian Congo), Chapin (1939, pp. 181-182) treated it as a resident bird in the Uele and in most other lowland savannahs, absent from forested areas, but known to breed in May and October (fledglings taken). Further to the north, in the Sudan, Cave and Macdonald (1955, p. 174) found it to be a common nonbreeding visitor between March and October, while in Darfur Lynes (1925, p. 354) concluded it was a rather infrequent summer visitor to the West Basin. In Mali, according to Malzy (1962, p. 34) the stripe-breasted cuckoo is a local migrant, common at the close of the rainy season, seen at Bamako from July to November.

It is not clear as yet if the species leaves its Ethiopian breeding grounds (where it breeds from June to September) during the northern winter, but it may well do so in the highlands, thereby adding to the confusing population in Kenya to the south and in Sudan to the west. In Eritrea, K. D. Smith (1957, p. 309) called it a "presumed resident" but had only scanty evidence.

The movements of the species in West Africa are still uncertainly known. Bannerman (1933, pp. 108-110) could only say that a ". . . corresponding movement to those which take place in East Africa certainly occurs in West Africa, but observers being fewer we have less data . . ." He found from his compiled records that it appeared to have been met with only seldom between July and November south of latitude 12°. It is known to breed in Ghana (February) and in Nigeria (July). In the latter country, Marchant (1953, p. 45) found it to be an uncommon transient from December to February. By this he probably meant to infer that it wintered somewhere to the south and bred to the north, but he made no geographic guesses as to how far in each direction its migration extended. The species is present throughout the year in Gambia, but the local population is increased by migrants in June.

Insofar as it is possible to summarize all these data, we may say that the species is clearly seasonal in Africa south of the Zambezi River; occurs throughout the year in equatorial Africa, where, however, its numbers are swelled during the southern winter months, and where it appears to comprise several populations, each with its own movements. It has not yet been ascertained to breed north of Ethiopia, the Republic of the Congo, Nigeria, Ghana, and Liberia, but probably does so. Inasmuch as it is not possible to separate, taxonomically, any geographic forms of this cuckoo and inasmuch as the known breeding records show a general, although spotty, distribution, it follows that the picture is somewhat like that in *C. jacobinus,* but wholly contained within the African continent.

The species seems to be scarcer now than formerly in the southeastern portion of its range. Thus, in the late years of the 19th century the Woodwards (1899) found it at the Umfolozi River, in Zululand, while today Clancey (*in litt.*) informs me that he has never met with it in Natal and considers it a very rare bird in the southern portion of its range. I also never encountered it in Natal, but only in the northern Transvaal (at Moorddrift, in December), where it was breeding. Even where it is common it is usually less numerous than the jacobin, although there is local variation in its numbers. In the Ashanti forest and the northern sections of Ghana, Lowe (1937, p. 635) reported it as abundant and present everywhere in the grass savannahs and in the open clearings in the forest.

Clamator coromandus

This is the one species of the genus that may have no nonmigratory populations or individuals, but available information is insufficient to establish this. The species ranges over an area where there never have been many resident observers and, as a result, our present data depend largely on specimens collected and deposited in museums. I have examined a large number of documented specimens of this cuckoo, and these, together with what has been published, yield the following picture. The species is known to breed in the Himalayan foothills from Garhwal and Nepal east to Assam at elevations of from about 2,000 to 8,500 feet, and in Burma at elevations of from 1,500 to 6,000 feet; north to southeastern China (Kwangsi, Kwangtung, Kiangsi, Fukien, Chekiang, and Hupeh Provinces; possibly also in Kweichow and Hunan); and southeast (rarely) to northern Thailand (Deignan, 1945, p. 158).

In the nonbreeding season it wanders to Chota Nagpur, Madras, Mysore, and Karala in India, to Ceylon, to Thailand (where it is a transient in spring and autumn, never found in winter), to the entire length of the Malay Peninsula (except the eastern side), the Indo-Chinese countries, Lingga Archipelago, Sumatra, Java, Celebes, and Borneo, and occasionally to the Philippines. In Burma, Smythies (1953, pp. 326-327) considered it a local migrant, but its movements there have not yet been worked out in detail or with any accuracy. Similarly, the seasonal movements of this cuckoo in southeastern China are yet to be defined with precision. Thus the Caldwells (1931, p. 240) considered it only as a migrant in southern Kwangtung, but in the northern portions of that Province they found it a not uncommon resident.

Clamator glandarius

Both the northern and the southern extreme populations of this species are highly and regularly migratory; the individuals breeding in equatorial portions of Africa are assumed (but not proved) to be nonmigratory. In South Africa and South-West Africa, north to Southern Rhodesia, Nyasaland, and southern Mozambique, the species is present only from September to March. In its Mediterranean breeding ground, where the seasons are reversed, the great-spotted cuckoo arrives at about the time the southern birds go north. Thus, Stresemann (1928, p. 703) noted that this cuckoo arrives from its tropical African winter quarters as early as the beginning of February in upper Egypt and Morocco, in early April in Gibraltar, and that it leaves again for the south in July and early August, and, in Egypt, even as early as June. He pointed out that there was an obvious correlation between its migration dates and its host requirements. It had to establish itself on its breeding grounds before the prospective hosts began to lay. In northwestern Africa, where the hosts are magpies, whose early egg dates are from late March to early April, and in upper Egypt as soon as there are no new nests of its corvine hosts (the crows are all beyond this stage in June), the cuckoo begins to leave for equatorial Africa. This seems to imply a more hurried departure than is characteristic of the birds breeding south of the Zambezi River. Thus, in Southern Rhodesia, Smithers, *et al.* (1957, p. 67) record it as breeding from October to January, but not leaving for the north until April. Meinertzhagen (1930, pp. 345-347) found it was absent from August to December in Egypt (not merely upper Egypt); he noted a marked northward passage at Wadi Halfa, Aswan, and Luxor in early February, when groups of from 10 to 20 individuals were seen passing slowly down the Nile Valley. The same author (1954, pp. 306-307) found this cuckoo to be a regular but infrequent migrant in Arabia, considerable numbers going through in late March and April—a rather late date compared with the earlier passages farther west.

In Eritrea, K. D. Smith (1957, p. 308) recorded a definite influx of birds in the coastal plain between December and March. The birds were common in summer (July and August) below 3,000 feet, and were absent from Eritrea in the winter.

· Cave and Macdonald (1955, p. 174) considered this cuckoo both a resident and a nonbreeding (wintering) visitor in Sudan, but were unable to say to which of these categories most of the individuals belong. In the Darfur Province, Lynes (1925, pp. 353-354) worked out the local situation in greater detail. He concluded that there were two distinct groups of cuckoos, one composed of individuals that bred farther to the south in equatorial or in southern Africa, and which spent their off-season farther north than Darfur, and merely passed through the area twice a year, and another group of Mediterranean breeding birds that migrated through Darfur in smaller numbers than the southern breeders. The southern breeders passed through Darfur from May until August, reaching their greatest numbers in June and July. Lynes found that these included adults, immature birds, and birds of the year, the last varying from 3 to 6 months in age, but not in molt, while the adult and subadult birds were molting. He further noted that in its middle period the passage was rapid, the birds arriving chiefly very early in the morning after some amount of nocturnal travel, and moving on during the day, lingering only to feed. The migration ended in late July, and no more were seen for 3 months, except for one stray young bird about 4 months old collected on August 20. The Palaearctic breeding migrants passed through Darfur in November and December. Lynes found no resident breeding great-spotted cuckoos in Darfur, but it would seem that further observations may demonstrate that the species breeds there regularly, although perhaps not abundantly. It may be recalled that some years after Lynes did his field studies, Madden (1934 pp. 94-95) saw a young fledgling of this cuckoo being attended by its foster-parents, a pair of the starling, *Lamprotornis caudatus,* at Khuwei, southern Darfur. Farther to the east, at Dembo, near the

Bahr-el-Ghazal, the cuckoo has been reported breeding as well, and also to the west of Darfur, in Mali, where Malzy (1962, p. 34) reported some migrants and some "sedentaires."

Madden's notes from southern Darfur included a very marked northward migration through El Fasher in May and June, apparently of birds that had finished breeding somewhere to the south, and also migrants at Ngala in late June, also apparently of southern birds passing through to spend the off-season somewhere to the north of Darfur.

Farther to the south, in the Kagera Park, in the Republic of the Congo, Curry-Lindahl (1961, p. 270) recorded a migratory influx of these cuckoos January 27 and 28. In Uganda and in Kenya, van Someren and others have put on record observations that add up to a somewhat obscured picture because of the obvious difficulty of differentiating in the field resident from migrant birds. There is an influx of nonbreeding (wintering) visitors from the north, and it is possible that southern breeding birds also reach those areas in the southern winter. Van Someren (1931, p. 24) found that he could distinguish migrants from resident birds, from post-mortems of collected specimens, the migrants usually being very fat, the local residents not so. Birds seen in Kenya after May were mostly resident, which suggests that relatively few individuals from south of the Zambezi River reach Kenya. Jackson (1938, pp. 493-495) was inclined to doubt some of van Someren's statements, but he overlooked the fact that the latter had specifically mentioned fledged juvenal birds in May in Kenya, which must have been locally raised.

A similar situation also appears to occur in Tanganyika, but the total evidence is much scarcer. There is definite evidence of breeding, hence of resident birds, in December at Unyanganyi, and in March at Iringa. In Nyasaland the species occurs from mid-September to mid-March, with the greatest number of birds noted between September and November.

SUMMARY AND CONCLUSIONS

The genus *Clamator* originated in southeastern Africa in Pliocene or pre-Pliocene time, from a primordial stock that appears to have its least changed, current representative in the southern race of *C. jacobinus* (*serratus*). From its original locus it expanded its range over most of sub-Saharan Africa and spread to India and southeast Asia, and thence to the Mediterranean basin as well. In its early northward progression in Africa the original *jacobinus* stock gave rise to a larger, pectorally heavily striped derivative that became *levaillantii,* and, somewhat later, in southern Asia, to an equally large, red-winged form, the present stock of which is *coromandus.* This last-named group, in turn, gave rise to what developed into *glandarius,* which emigrated westward from northern India to the Near East, Egypt, and to the western portion of the Mediterranean, the Iberian Peninsula, Morocco, and Algeria. Much later this form suddenly expanded its range southward to encompass much of Africa south as far as Cape Province.

The genus evolved very early from a primordial Cuculine stock that was already parasitic in its breeding, but that had not yet developed the evicting behavior in the young or the tendency to host-adaptive variable egg morphism with the concomitant development of host-specific gentes. In the course of its subsequent history *Clamator* never developed either of these features as did the more specialized genus *Cuculus.* Its original eggshell coloration was plain, unmarked white as in *C. jacobinus serratus,* and in this form there is no sign of host selection with species reference to egg similarity. From this was developed a plain bluish or blue-green egg coloration, as still present in the two northern races of *jacobinus, pica* and the nominate subspecies, as well as in *levaillantii* and in *coromandus.* In these segments of the genus the choice of fosterers has been arrived at with definite correlation to general egg similarity. Finally, in the most advanced species, *glandarius,* we have a patterned, speckled or blotched, egg coloration superimposed on a pale greenish ground color, and in this case the inference to be derived from the evidence is that it developed together with an early fixation upon magpies as hosts.

In the case of *glandarius,* with its unusually fine egg adaptation toward this host choice, we find evidence that this restriction, both in fosterer and in geographic range, became disadvantageous for the species as a whole, and that a large segment of its population underwent a great geographic emigration, in a way comparable to what in morphological evolution has been termed an "escape from specialization."

The start of this escape from host restriction on a fosterer of very limited sympatry had already begun in eastern Egypt where *Corvus* was utilized in the absence of *Pica.* The *glandarius* population that expanded over much of sub-Saharan Africa was apparently the less perfectly adapted portion of its species in its old Mediterranean homeland, as is still evidenced by the great disparity in host-parasite egg ratios shown in its uncorrelated multiple parasitism in its newer breeding range. In the course of its rapid spread over this vast *Pica*-allopatric area, it has not altered its eggshell pattern although it has broadened greatly its range of acceptance of host nest types, enabling it to parasitize such divergent fosterers as arboreal, open-nesting corvids and earth-tunnel nesting sturnids. As is pointed out in the present paper, the fact that *glandarius* was parasitic largely on birds of greater size, capable of rearing multiple parasites as well as some of their own young, gave the cuckoo an immunity from selective pressure, but as it increases its use of smaller, sturnid hosts the parasite may find itself affected by this pressure, from which it is relatively protected as yet.

A factor that appears to have been of considerable importance in the advent of the geographic spread that consummated in the emigration to sub-Saharan Africa of the less perfectly adapted portion of the original circum-Mediterranean population of *glandarius* was the shift in the main stress of selective pressures when that original population became numerically high. Until that demographic saturation had been reached, and especially while the species was developing through its adaptive evolution with regard to its primary host, the chief focus of natural selection was between *glandarius* and its environment (including in the latter, its magpie fixation). Once *glandarius* had become successful and numerous, the primary selective pressure was between members of its own kind, and it is this change that seems to have been involved in its geographic "shedding" of those segments that were less able to stand the new orientation of natural selection. This left only the better adapted individuals in the original homeland, which is the reason for the difference still apparent between them and their sub-Saharan emigres.

Another evolutionary trend found in some other groups of brood parasites, a gradual shortening of the incubation period, is absent in *Clamator*. In fact, the meager data available suggest just the opposite, although the more advanced species of the genus, with longer incubation periods, tend to make use of hosts with still longer ones.

To summarize, brood parasitism in *Clamator* has achieved a high degree of adaptive excellence by virtue of a restriction of host choice to birds of generally similar eggs (northern races of *jacobinus,* and *levaillantii, coromandus,* and *glandarius*), and only relatively recently has this smoothly functioning correlation been upset by a portion of the membership of the most advanced, most "perfectly" adapted species, *glandarius*. Traces of incipient tendencies toward egg morphism may be detected in *levaillantii,* but they have not developed very far.

The original *Clamator* stock, as represented by *C. jacobinus serratus* had a tendency toward plumage polymorphism, a trend that could, potentially, enhance the process of subsequent differentiation into discrete taxonomic entities. This polymorphism remained localized in the ancestral home—southeastern Africa—although traces of the tendency still occasionally crop up elsewhere in African *jacobinus* and, strangely enough, in a very limited portion of its range, in *levaillantii*. No trace of polymorphism has been found in Asiatic *jacobinus,* in *coromandus,* or in *glandarius.* The lack of evolutionary consequences of this early polymorphism is due to the fact of its neutral nature.

The variations in "normal" plumages show clearly that *levaillantii* was derived from *jacobinus;* the phylogenetically conservative tendency of juvenal plumage characters indicates that *glandarius* arose from a *coromandus*-like stock. The fact that *Clamator,* during its very long existence, has produced only 4 species, as against 12 in the younger *Cuculus,* or 12 in *Chrysococcyx* (including *"Chalcites"*), coupled with the evolutionarily inert nature of its polymorphic trends, suggests that the genus is one that has been relatively less affected by evolutionary change.

Similarly, migratory behavior has remained less completely formulated and less rigid in its manifestations in many sections of the genus, even varying markedly in different segments of individual species. We have noted the entire range of behavior from absence of migration to local migration, to partial migration, to total and regular seasonal mass movements of great geographic extent.

We must remember that, like other organisms, birds, their structures and their habits, do not evolve; they are evolved. The creatures are merely the material on which evolutionary processes exert their influence and on which they leave their marks and it is from a study of these marks that we reconstruct their past history and experience.

Clamator has existed in a less active, more "secluded," evolutionary arena than some other genera of its family. Nonetheless, it has had a long, continuous, and successful history, and in the course of this great duration it has shown an early adaptation in egg coloration to a then new and fairly definite set of host species, and much later, in its climax form, a partial escape from the overly restrictive results of this rigid host specificity. In between these two important incidents in its development, it has pursued a fairly even and relatively uneventful existence, although involving differentiation into four species, each with considerable geographic shifting of stock. This brings out the fact that, in studying a group of organisms, the concept of their evolution is not completely the same as that of their history. The former should, technically, be limited to the chronology, and, wherever possible, the explanation, of the changes that transpired in the creatures during their history, but should not be considered as the whole of their story, even though it may involve its most salient features. An organism may, and often does, survive environmental changes without undergoing change in itself, as we have seen in the case of *Clamator glandarius.* This is certainly a part of its history, but is hardly something that ordinarily would be considered in an account of its evolution.

APPENDIX

ADDITIONAL HOST DATA

A. DATA ON THE HOSTS OF CLAMATOR GLANDARIUS

So many new species have been added to my original (1949a, pp. 10-15) host catalog and so much additional information has been amassed on some of the others, and so many changes in nomenclature have come about that it seems better to present a new catalog than to attempt to present only the new material with the multitude of cross-references needed to collate them with what was known before. Where the present data suggest no alteration in the earlier statements, they are given very briefly.

Two birds, not in the subjoined catalog, have been mentioned in the literature as hosts, but there is no evidence to support these statements. The North African little owl, *Athene noctua glaux,* has been mentioned as a victim, based on a very indefinite statement by Canon Tristram (1859, p. 77), which may best be ignored. A year later Des Murs (1860, p. 218) wrote that the great-spotted cuckoo laid "without doubt" in the nests of the thrush, *Turdus merula,* but in the more than a century since then no one has reported an actual instance. This statement should also be ignored.

The data on documented hosts are given below.

Falco tinnunculus Linnaeus **Kestrel**

Jourdain's single record (1920, p. 72; Friedmann, 1949a, p. 10) has remained unique. The fact that the kestrels were using an old magpie's nest probably was a contributing factor in attracting the attentions of the cuckoo, but it should be mentioned that all the eggs were fresh; in other words, the kestrels were already in occupancy when the cuckoo came there. It suggests that it is the nest itself, rather than the actual appearance of its owners, that is of first importance to the parasite. The record involves the nominate race of the kestrel.

Upupa epops Linnaeus **Hoopoe**

Two records of the South African race (*africana*) of this bird as a host of the great-spotted cuckoo have come to my attention. Miss M. Courtenay-Latimer (*in litt.*) found a hoopoe's nest at Bailey Station, eastern Cape Province, on September 9, 1931, containing four eggs of the hoopoe and one of the cuckoo. One of the hoopoe eggs and the cuckoo egg hatched on September 17; two more of the host eggs hatched the next day and the last one on the following day. The young hoopoes remained in the nest for 3 days, when they were found dead and partly devoured by ants nearby. Their actual removal from the nest was not observed, so it is not possible to state whether they were evicted by the young parasite or had died and were removed by their parents. The cuckoo chick remained in the nest for 4 weeks, and the foster-parents were seen feeding it after it fledged, until it flew strongly.

A few years later, near Tregarthens Folly, Cape Province, Miss Courtenay-Latimer saw a hoopoe feeding a fledgling great-spotted cuckoo on November 7, 12, 15, and 20, 1934. The fact that this parent-young relationship was observed on numerous days shows it was not a casual, temporary interest of a food-laden adult in a clamorous fledgling from another bird's nest, and also indicates a duration of postfledging feeding of at least 2 weeks. The first record, entailing an egg of the parasite on September 9, must be one of the earliest egg dates for this cuckoo in South Africa.

The hoopoe has never been found to be parasitized in Europe, but Meinertzhagen (1948, p. 563) noted a single cuckoo apparently closely associated with a hoopoe in Ushant, Brittany, on April 16, 1947. Meinertzhagen did not imply parasitism or any other reason for the observed association and did not even state if the cuckoo was a young bird. If not for Miss Courtenay-Latimer's observation on the South African race of the hoopoe, no one would have suspected any host-parasite situation in Meinertzhagen's terse report. Indeed, as written, it affords no basis for any such interpretation, but the question does arise.

Geocolaptes olivaceus (Gmelin) **Ground Woodpecker**

At Waverly Haasfontein, eastern Cape Province, on October 5, 1952, Miss M. Courtenay-Latimer (*in litt.*) observed a ground woodpecker feeding a fledgling great-spotted cuckoo about a week out of the nest. This is the only record known to me of this woodpecker as a host.

Corvus corone Linnaeus **Hooded Crow**

Two races of this crow have been found to be victimized by the great-spotted cuckoo, the nominate form in southern Spain (one record, now in the British Museum) and the race *sardonius* in Israel and in Egypt. In the last-named country the hooded crow is the chief, if not the invariable, host, and, in all, over 50 Egyptian instances have come to my attention. The numerical relations between host and parasite eggs there are shown in our graph (fig. 10, p. 43), which gives a picture quite different from that of other crows south of the Sahara.

Corvus ruficollis Lesson **Brown-necked Raven**

According to Archer (in Archer and Godman, 1961, vol. 3, pp. 649-659) the local race (*edithae*) of this bird is the chief host of the great-spotted cuckoo in former British Somaliland (now part of the Somali Republic). He gave data on five instances from his fieldwork in that area, the actual localities being Arori Plain, Burao, Baraad, and Oadweina. Two other parasitized nests were collected by M. E. W. North, at Brava, former Italian Somaliland (now part of the Somali Republic), and sent to the Coryndon Museum. I am indebted to J. G. Williams for information about them. Belcher (1949, p. 37) reported another parasitized nest near Gabredarre, Ogaden, former Italian Somaliland (now a part of the Somali Republic). In this case, the nest contained a nestling of the host in addition to eggs of its own and of the parasite.

Corvus corax Linnaeus **Raven**

Hartert (1912, p. 956) recorded this bird (typical race) as a host of the great-spotted cuckoo in Spain, but the basis for this statement is not given; Valverde (1953, p. 294) notes it as found by Lord Lilford at Aranjuez. It remains a unique record. The only parasitized set of eggs of any species of *Corvus* from Spain that I know of is a set of *Corvus corone* in the British Museum.

Corvus albus Müller **Pied Crow**

The number of records of this crow as a victim of the great-spotted cuckoo has been more than doubled since my first (1949a, pp. 11-12) account. I have data on 18 such cases, from South Africa, Southern Rhodesia, Nyasaland, Tanganyika, and Nigeria. The number of cuckoo eggs per nest varied from 1 to 13, the majority of nests having from 1 to 5 of the parasitic eggs.

Corvus capensis Lichtenstein **Cape Rook**

This rook, unique among crows in that it lays pinkish, and not greenish, eggs, with which the eggs of the cuckoo contrast markedly in coloration, is known to be imposed upon in South Africa and Southern Rhodesia (nominate race) and in former British Somaliland (race *kordofanicus*). Of the southern race, there are 13 records in my files; of *kordofanicus,* 2 records (both *ex* Archer and Godman, 1961, vol. 3, p. 657). Five of the southern records are given in my earlier reports (1949a, p. 12; 1949b, p. 514). The additional eight are as follows: five are from Southern Rhodesia (Beatrice, Banket, Salisbury, and Selukwe) and three from eastern Cape Province, South Africa. The number of cuckoo eggs in these sets varies from one to four; in six instances there was a single egg of the parasite with from one to four eggs of the host; in seven nests each had two eggs of the cuckoo with from one to three of the host; one nest had three cuckoo and five rook eggs, and one nest contained four eggs of the parasite and five of the host.

Since the above was written, Pitman (1962, p. 23) has recorded that as many as nine eggs of the cuckoo have been found in a single nest of a Cape rook in South Africa. The exact data on this nest were not presented.

Corvus rhipidurus Hartert **Fan-tailed Raven**

As I mentioned in my first account (1949a, pp. 12-13), Lort Phillips and his party found in 1885 that in northern former Italian Somaliland (now a part of the Somali Republic) nearly all of the examined nests of this bird contained eggs of the great-spotted cuckoo, and that in one nest there were no fewer than eight eggs of the parasite with four of the raven. Archer (*in* Archer and Godman, 1961, p. 657) recorded two parasitized nests found in former British Somaliland (now a part of the Somali Republic), one at Sheikh and one at Ariarleh, the former with three eggs of the raven and two of the cuckoo, the latter with one of the host and four of the parasite.

Archer found the brown-necked raven, *Corvus ruficollis edithae,* to be the most frequently used host in the Somali Republic, and in his discussion he appears to include Lort Phillips's data as pertaining to that species and not to *rhipidurus*. In this he was in error. The Phillips party was in the field from the end of December until the beginning of April, so all the cases of parasitism they observed must have come between these dates. Archer's dates for parasitism on *edithae* were all later, April 29 to June 9, as stated in our discussion of that bird.

Corvultur albicollis (Latham) **White-necked Raven**

This species was added to the known hosts of the great-spotted cuckoo by McLachlan and Liversidge, in their revision of Roberts' "Birds of South Africa" (1957). No details were given; it was merely listed as a host.

Cyanopica cyanus Pallas **Azure-winged Magpie**

The subspecies *cooki* of this magpie is a frequent victim of the great-spotted cuckoo in Portugal and Spain. All in all, I have learned of some 11 instances of parasitism on this bird, an increase of 4 over those listed in my earlier account (1949a, pp. 13-14).

Pica pica (Linnaeus) **Magpie**

The magpie is the primary, almost the exclusive, host of the great-spotted cuckoo in the limited portions of the ranges of the two species where they are sympatric. It is also the one host to which the egg coloration of the parasite is unusually finely adapted. All in all, counting nests with eggs, nests with young, and cases of magpies attendant upon fledgling cuckoos, over 80 instances of parasitism on this host have come to my attention. Geographically they range from Spain, southern France (Arles), northwestern Africa (Morocco, Tunis, Algeria), and Cyprus, to Turkey (Ankara), and Asia Minor.

Five subspecies of the magpie are involved in these records: *melanotos* in the Iberian Peninsula, *pica* in Asia Minor, *bactriana* in Iraq, *galliae* in southern France, and *mauritanica* in northwest Africa. The graph (fig. 12, p. 45) illustrating our present account of "intensity of parasitism" shows the frequency of multiple eggs of the cuckoo in nests of the magpie. This is based on egg records only and does not include cases involving nestlings or fledglings.

The most recent study of the host-parasite relations of the magpie is that of Mountfort (1958, pp. 54-56), whose fieldwork was done in Spain. He found both birds were very common, and that in spite of heavy parasitism the magpies seemed to be thriving. He and his party found some 50 occupied nests in 1956. That there is some variation in the demographic relations of the two species is suggested by Wadley's notes (1951, p. 75) made in central Anatolia, in Asiatic Turkey. He found that the great-spotted cuckoo was well distributed there, but the total population was quite small, although the magpie was numerous throughout.

Mountfort's experience seemed to indicate that parasitism was generally fatal to the magpie eggs and young, as he wrote that ". . . in only one nest did we ever find the young of both species together, and this was only a very brief period. The nest in question at one time contained three eggs of each species, two of those of the Magpie being dented. The remaining Magpie egg hatched three days after those of the Great-Spotted Cuckoo. Two days later the nestling Magpie had disappeared, presumably having been either smothered or starved. Herein lay the crux of the matter, for the incubation period of the Great-Spotted Cuckoo is only fourteen days whereas that of the much larger Magpie is seventeen to eighteen days. Unless therefore the young Magpies can hatch out from eggs laid well in advance of those of the parasite, they can have no hope of survival . . ."

Garrulus glandarius (Linnaeus) Common Jay

In my earlier account (1949a, p. 15) I mentioned that Tristram (1866, p. 282) considered it probable that this jay was parasitized in Palestine, but he listed no actual records. Yet, on this basis, several authors have repeatedly referred to this jay as a fosterer of the cuckoo. Since then, Makatsch (1955, p. 152) definitely reported two parasitized nests of the jay in Asia Minor, of the subspecies, *G. g. krynicki,* collected by Krüper, one on May 9, 1882, and the other on May 6, 1901. Each had an egg of the great-spotted cuckoo. I am not aware of any other instances of parasitism on this jay.

Ptilostomus afer (Linnaeus) Piapiac

Recorded without data, as a victim of the great-spotted cuckoo, by Mackworth-Praed and Grant (1952, p. 505).

Acridotheres tristis tristis (Linnaeus) Common Mynah

This mynah, introduced into South Africa, has recently been found to be parasitized by the great-spotted cuckoo at Estcourt, Natal, where Godfrey Symons (1962, p. 343) observed a parasitized nest, containing four eggs of the mynah and one of the parasite.

Onychognathus morio (Linnaeus) **Red-winged Starling**

In my first account (1949a, p. 14) I listed three records; since then I have learned of six more. The additional cases make it clear that the red-winged starling must be looked upon as a regular victim of the great-spotted cuckoo in eastern South Africa. Elsewhere in its range this starling has not yet been found to be parasitized.

Spreo bicolor (Gmelin) **Pied Starling**

The statement in my earlier account (1949a, p. 14) may be amplified as I now have data on many more instances of parasitism on this starling. It is the most frequently reported fosterer in eastern South Africa, and is the only earth-tunnel nester regularly and frequently used by the parasite. As many as six cuckoo eggs have been taken from one nest of this bird. The graph (fig. 13, p. 46) illustrating the discussion of "intensity of parasitism" shows the relationship in egg numbers of starling and cuckoo in 14 instances.

Spreo albicapillus Blyth **White-capped Starling**

This starling was added to the known hosts of the cuckoo by Archer (*in* Archer and Godman, 1961, p. 657), who found, at Sheikh, in former British Somaliland (now a part of the Somali Republic), on May 14, a nest of this bird containing two eggs of the parasite in addition to five of the host.

Lamprotornis nitens (Linnaeus) **Red-shouldered Glossy Starling**

Three additional cases have been forthcoming from Natal since the four (not three as erroneously recorded) cases mentioned in my earlier account (1949a, p. 14). All refer to the host race *L. n. phoenicopterus.*

Lamprotornis caudatus (St. Müll.) **Long-tailed Glossy Starling**

At El Obeid, Kordofan, Sudan, in November 1932, Madden (1934, p. 94) noted a pair of long-tailed starlings feeding a recently fledged great-spotted cuckoo. This is still the only record for this host. When I first commented on this case (1956, p. 378) it was the only instance of a hole-nesting bird being parasitized by this cuckoo north of South Africa. Since then, a similar case, involving another, but allied, species of starling, has been reported from former British Somaliland (now a part of the Somali Republic), and still another from Southern Rhodesia.

Lamprotornis chalybeus (Hemprich and Ehrenberg)
Blue-eared Glossy Starling

Two races of this starling have been recorded as victims of the great-spotted cuckoo, *cyaniventris* in the Somali Republic, and *sycobius* in Southern Rhodesia. In former British Somaliland (now a part of the Somali Republic), Archer (*in* Archer and Godman, vol. 3, 1961, p. 657) found a nest at Sheikh, on May 26, containing one egg of the starling and two of the parasite. It is the only record that has come to my notice for the race *cyaniventris.*

The southern race, *sycobius,* was added to the known fosterers of the great-spotted cuckoo by Meyer (1959, p. 85), who found a nest near Que Que, Southern Rhodesia, on November 15, 1958, which contained a young cuckoo, still devoid of feathers, but with the quills just appearing on the tail and wings, a young starling, fully feathered, about 10 to 14 days old, a dead young starling, and a broken, unhatched starling egg. Three days later the two nestlings were still there, but on the following day the young cuckoo was the sole occupant and remained there for another week, when it fledged and was seen attended by its foster-parents.

B. DATA ON ADDITIONAL HOSTS OF CLAMATOR JACOBINUS

Since my first host catalog, a number of additions have been sent to me or have appeared in print. These records, with their pertinent documentation, are here reported. While these species are additions to the earlier catalog they are all infrequently used fosterers, as might be assumed from the fact that they have only recently been so recorded. They all come from Africa, where the chief hosts, bulbuls of the genus *Pycnonotus* and shrikes of the genus *Lanius,* have been reported in this capacity so many times since the last (Friedmann, 1949a) catalog as to leave no doubt as to their primary role in the economy of the pied crested cuckoo.

Centropus grillii Hartlaub **Black-bellied Coucal**

A coucal is an unusual host as it builds a fairly domed-over nest on the ground, a site not usually favored by the pied cuckoo. The one known record comes to me from Dr. Johan Ottow (*in litt.*), who has in his collection a parasitized set of the present coucal species, taken at Baviaans Krantz, near Rustenberg, Transvaal, November 30, 1952. The set contained one egg of the host and one of the parasite. The record refers to the race *wahlbergi* of the coucal and *serratus* of the jacobin cuckoo.

Dicrurus adsimilis (Bechstein) **Glossy-backed Drongo**

In my earlier account (1949a, p. 35) I knew of only one old record of Bowker's, quoted by Layard (1877), which was considered questionable. This record remained unique until 1962, when Skead (1962, pp. 72-73) found a parasitized nest in which the drongos successfully reared a jacobin cuckoo. The nominate race of the drongo, and the race *serratus* of the parasite are here involved.

Turdoides jardinei (Smith) **Arrow-marked Babbler**

This babbler, a very frequent fosterer of the stripe-breasted cuckoo, *Clamator levaillantii,* has been listed as a host of the jacobin as well in Northern Rhodesia, by Benson and White (1957, p. 43). On geographic grounds this would involve the host race *T. j. natalensis.*

Terpsiphone viridis (St. Müll.) **Paradise Flycatcher**

Skead (1955, p. 46) found a nest of the paradise flycatcher with an egg of *C. jacobinus* at Fleet Dutch Kloof, King William's Town, eastern Cape Province, December 18, 1954. This is the only instance known to me of the pied cuckoo laying in the nest of this species. This flycatcher is one of the smallest victims yet recorded. The record refers to the race *perspicillata* of the host, and the race *serratus* of the parasite.

Sphenoeacus afer (Gmelin) **Grass Bird**

In my 1956 discussion (p. 379) I mentioned that I saw a parasitized set of eggs of this bird, taken at Inyanga, Southern Rhodesia, by E. F. Allen, in the Victoria Memorial Museum, Salisbury. This is still the only real record, but I have been informed of one other indefinite one since then, also in the general region of Salisbury. The record refers to the race *transvaalensis* of the host and *serratus* of the parasite. This is one of the few birds nesting on, or close to, the ground that are occasionally parasitized.

Motacilla aguimp Dumont **Pied Wagtail**

The African pied wagtail was added to the known hosts of the pied crested cuckoo by van Someren (1956, p. 236) who found it to be imposed upon by no less than three species of cuckoos in the Ngong area, near Nairobi, Kenya; the present one, the solitary cuckoo, and the didric cuckoo. The lone record involving the jacobin cuckoo refers to the race *vidua* of the host, and *pica* of the parasite.

Telophorus zeylonus (Linnaeus) **Bakbakiri**

Additional instances of parasitism on this shrike by the jacobin cuckoo bring the total number of cases known to me up to seven, and make it clear that this bird is a fairly frequent and regular host choice. Of the seven records, six refer to the nominate race of the host, one of the grayish, western race *phanus*.

C. DATA ON ADDITIONAL HOSTS OF CLAMATOR LEVAILLANTII

· The stripe-breasted cuckoo is still less often observed, and hence less completely known, than *jacobinus* or *glandarius*. Observations since my 1949 host catalog have served chiefly to emphasize the fact that babblers of the genus *Turdoides* form the main reliance of this cuckoo. Not only have numerous attitional instances of parasitism on the arrow-marked babbler, *T. jardinei*, come to hand, but also two more species of the same genus have been found to be parasitized. A single record of parasitism on a coly has also come to my attention, but this bird is at best only an irregular or a very occasional victim.

On the whole, *C. levaillantii*, in its host choice resembles the Asiatic population of *C. jacobinus*, but, as far as present data indicate, is more generally restricted to species of *Turdoides*.

One observation on the chief host, *Turdoides jardinei*, calls for mention here. Jubb (1952, p. 162) watched a fledgling stripe-breasted cuckoo with a family group of arrow-marked babblers and wrote that the young parasite ". . . was able to imitate the chatter so characteristic of babblers on the wing . . ." This would imply some vocal adaptation to a host species, such as Nicolai (1961) has suggested in some of the parasitic *Viduinae*. In both cases the suggestion needs further support before it may be appraised.

Colius striatus Gmelin **Speckled Coly**

One record of this coly as a fosterer of the stripe-breasted cuckoo has been reported. White and Winterbottom (1949) noted that an egg of this cuckoo was found in a coly nest at Ndola, Northern Rhodesia, in December, by Hudson. This coly has also been found to be victimized very occasionally by the jacobin cuckoo, but it is not a regular host to either species. The typical race of the coly is involved in the present record.

Turdoides plebeja (Cretzschmar) **Brown Babbler**

In Gambia, Ross A. J. Walton collected two parasitized nests of the brown babbler (local race *T. p. platycircus*) at Kambo, North Bank Division; one on April 30, 1945, with one egg each of the babbler and the cuckoo, and the other on July 4, 1945, with three eggs of the host and one of the parasite. The Adamawa race of this babbler, *T. p. gularis,* had been known earlier to be parasitized in Nigeria. Both sets of eggs were acquired for his collection by R. Kreuger of Helsinki, to whom I am indebted for the data. The set taken on April 30 has since gone to the collection of Dr. Johan Ottow, who informed me (*in litt.*) that the locality on his set was given as Churchill Town, St. Mary, Gambia.

Turdoides reinwardii (Swainson) **Blackcap Babbler**

R. Kreuger of Helsinki (*in litt.*) informed me that he received from Ross A. G. Walton, a set of one egg of this babbler with one of the stripe-breasted cuckoo, taken at Kambo, North Bank Division, Gambia, on May 1, 1944. This is the only instance I know of this babbler as a host. The record refers to the nominate race.

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