Smithsonian Institution
United States National Museum

Bulletin 223

The Parasitic Weaverbirds

By **HERBERT FRIEDMANN**
Head Curator, Department of Zoology
United States National Museum

WASHINGTON, D.C. • 1960

SMITHSONIAN INSTITUTION

UNITED STATES NATIONAL MUSEUM

BULLETIN 223

WASHINGTON, D.C.

1960

The Parasitic Weaverbirds

By HERBERT FRIEDMANN

Head Curator, Department of Zoology
United States National Museum

Publications of the United States National Museum

The scientific publications of the United States National Museum include two series, *Proceedings of the United States National Museum* and *United States National Museum Bulletin*.

In these series are published original articles and monographs dealing with the collections and work of the Museum and setting forth newly acquired facts in the fields of Anthropology, Biology, Geology, History, and Technology. Copies of each publication are distributed to libraries and scientific organizations and to specialists and others interested in the different subjects.

The *Proceedings*, begun in 1878, are intended for the publication, in separate form, of shorter papers. These are gathered in volumes, octavo in size, with the publication date of each paper recorded in the table of contents of the volume.

In the *Bulletin* series, the first of which was issued in 1875, appear longer, separate publications consisting of monographs (occasionally in several parts) and volumes in which are collected works on related subjects. *Bulletins* are either octavo or quarto in size, depending on the needs of the presentation. Since 1902 papers relating to the botanical collections of the Museum have been published in the *Bulletin* series under the heading *Contributions from the United States National Herbarium*.

REMINGTON KELLOGG,
Director, United States National Museum

For sale by the Superintendent of Documents, U. S. Government Printing Office, Washington 25, D. C.
Price $1

Contents

Preface

THIS STUDY OF THE PARASITIC WEAVERBIRDS is an entity in itself, complete as far as available data permit. It is also a part of a general survey of the problem of avian brood parasitism, in the course of which, besides many pertinent short papers, monographs dealing with other families of parasitic birds were issued by me on the cowbirds (1929), on the African cuckoos (1946), and on the honey-guides (1955). To complete the series I hope eventually to publish a comprehensive comparative and interpretive summation of the biological aspects of the subject.

For many years I hesitated to write the present portion of the survey because the available information was fragmentary, and there was little reason to expect that the accounts resulting from this information would lend themselves to clarifying comment. Although new information has been exceedingly slow in coming into print and our present knowledge is still obviously fragmentary, now, after 35 years of patiently watching for such items in the literature, and of extensive correspondence with resident observers in the homelands of the birds involved, in addition to personal fieldwork in Africa, I venture to present the picture, incomplete to be sure, but sufficiently filled in to reveal in general outline the nature of brood parasitism in the weaverbirds.

In the first part of this study is presented the evolution of brood parasitism, and in the second the data on which I have based my interpretation. The study should, I hope, stimulate observers to supply further data and at the same time expedite their work by directing them to the gaps that I have not been able to close.

During the course of my studies, many persons and organizations have assisted me in many ways, all of which contributed to the degree of completeness attained in the following pages. Not that I consider the problems fully worked out or the solutions arrived at as definitive, but I would not have been able to come as far as I have without these contributions. My personal field work in southern and eastern Africa was supported first, in 1924–25, by the National Research Council through funds supplied by the Rockefeller Foundation, and later, in 1950–51, by grants from the John Simon Guggenheim Memorial Foundation, the American Philosophical Society, and the Smithsonian Institution. Without the generous support of these sponsoring groups the field work would not have been possible, and the study would not have been undertaken.

It is a pleasure to record my gratitude about the following kind friends, who contributed to the present study either by direct assistance or cooperation in the field, or by sending me items from their own largely unpublished observational data: J. P. Chapin, N. E. Collias, M. P. S. Irwin, C. H. Jerome, D. W. Lamm, H. M. Miles, G. Morel, B. V. Neuby-Varty, R. H. W. Pakenham, D. C. H. Plowes, the late C. D. Priest, G. A. Radtke, the late A. Roberts, M. Rollo, C. J. Skead, R. E. Symons, V. G. L. van Someren, and J. G. Williams. H. Poulsen of the Copenhagen Zoological Park aided me with data on aviary observations on combassous.

For giving me the opportunity to study specimens in their respective museums, I am indebted to officials of the American Museum of Natural History, New York; British Museum (Natural History), London; Chicago Natural History Museum, Chicago; Coryndon Museum, Nairobi; Durban Museum and Art Gallery, Durban; Kaffrarian Museum, King William's Town; Museum of Comparative Zoology, Cambridge, Mass.; Natal Museum, Pietermaritzburg; National Museum of Southern Rhodesia, Bulawayo; Peabody Museum of Yale University, New Haven, Conn.; Transvaal Museum, Pretoria; and Victoria Memorial Museum, Salisbury.

The American Museum of Natural History, the Chicago Natural History Museum, D. C. H. Plowes, and V. G. L. van Someren contributed photographs that add appreciably to the illustrations in this report. The John Simon Guggenheim Memorial Foundation made a special grant to cover the costs of the colored plates.

To Patricia Hogue, formerly staff artist of the U.S. National Museum, are due my thanks for her work, including plates 2, 9, 11, and 15, and to R. E. Hogue for his three paintings, plates 1, 3, and 4.

The Parasitic Weaverbirds

Evolution of Brood Parasitism in Weaverbirds

That parasitic reproduction occurs in the weaverbirds was first made known in 1907 by A. Roberts,[1] writing about the pin-tailed widow bird, *Vidua macroura*, in South Africa. Shortly afterward, Jackson and his native collector, Baraka, made similar observations on this species in East Africa, and subsequently Mörs and V. G. L. van Someren produced still further evidence. Roberts (1917) and van Someren (1918) also reported almost simultaneously that the cuckoo finch, *Anomalospiza imberbis*, was also parasitic. Since then the same habit has been found in other species of *Vidua* and in the paradise widow bird, *Steganura paradisaea*. Of not one of these species is our present knowledge more than partial; of some it is still extremely fragmentary. These birds offer the naturalists resident in Africa a real opportunity for rewarding work.

Phylogenetic Background

In approaching the problem of the evolution of brood parasitism in viduine weavers and in *Anomalospiza*, I must first establish a frame of reference on which to peg pertinent data. I must first show where these birds fit in the overall picture of the family and what their ancestry within that group may have been.

We are fortunate in having two comprehensive discussions of ploceid taxonomy—one by Chapin (1917) and one by Sushkin (1927)—the first based on extensive acquaintance with a large number of the included genera and species in life as well as in the museum, and the second couched in terms of the skeletal anatomy of the group. Chapin was the first to use characters such as the pattern of the mouth markings of the nestlings, the type of nest constructed, and the presence or absence of seasonal plumage changes—all of which have been found to be more revealing of true relationships than such overemphasized "museum" characters as the relative length of the outermost primary. Sushkin's conclusions provided complementary information concern-

---

[1] At this time there was in the literature an unverified belief that the red-billed weaver, *Quelea quelea*, might also be a brood parasite. This belief since disproved, was based upon the fact that although the bird was very abundant, no one had found and described its nest. Since then, large breeding colonies have been located and studied in considerable detail.

ing the degree of similarity or difference in the skeletal structure of many of the genera of the family.

In addition to these two family-wide studies, many of the subsections of the group and even individual genera were reviewed by, among others, Beecher (1953), Delacour (1943), Delacour and Edmond-Blanc (1934), Mainardi (1958), Stallcup (1954), Steiner (1955), and Wolters (1939, 1943, 1949, 1950, and 1957). All these studies yielded data which have been incorporated into the present study.

Chapin (1932, pp. 380, 386–387) pointed out that the geographic dispersal of the different sections of the family may help reveal something of their past history and even of the relative time and place of their original deviation from the ancestral stock. He particularly noted that two of the larger subfamilies of the Ploceidae, the Ploceinae and the Estrildinae, range from the Ethiopian to the Oriental Region, the Estrildinae ranging even to Australia.

Differences in geographic dispersal were looked upon as possibly lending some weight to recent doubts as to the closeness of interrelationship of these two subfamilies. Beecher (1953, pp. 303–304) went so far as to suggest that the two are families and arose in quite separate parts of the world—the Ploceidae from the Promeropinae or Cisticolinae in Africa, and the Estrildinae from the Meliphagidae or Cisticolinae in Australia. This interpretation seems needlessly extreme, but it does reflect the impression made upon its proposer by the structural dissimilarities in the two groups. Chapin, on the other hand, noted that Asiatic Ploceinae are nearest to *Pachyphantes* and *Brachycope* among African genera—the former a savanna dweller and the latter a bird of forested river banks. In this connection he noted that only two ploceine genera, *Foudia* and *Nelicurvius*, and only a single estrildine species, *Spermestes nana*,[2] occur in Madagascar. The estrildine group became differentiated into more genera and species in Malaysia and Australia. Chapin concluded that an earlier, possibly original localization in southern Africa of the Ploceinae may account for the lesser spread of this subfamily eastward to India and Malaya. The age of the subfamily is sufficient to have given time for an infiltration comparable to that achieved by the Estrildinae, but such an infiltration did not occur.

As Chapin stated, the fact that the forest-dwelling Ploceinae of Africa "are obliged to be so largely insectivorous, despite their gramnivorous beaks, may also stamp this as a secondary adaptation to a new habitat. Likewise the Estrildinae now have forest-dwelling genera such as *Nigrita* and *Spermospiza* in Africa, but not in India or New Guinea. It is the grassland weaver-finches that live in all

---

[2] *Pyrhula nana* Pucheran, Rev. Zool., 1845, p. 52 (Madagascar).

three regions." Sushkin's proposed classification of the family supports the contention that the Ploceidae originated in Southern Africa.

Crook (1958) concluded from behavioral and structural data that the Bubalornithinae, comprising the genera *Bubalornis* and *Dinemellia*, should be considered of family status, allied to but separate from the Ploceidae. He admitted that there were then no behavioral data on *Dinemellia* comparable to those that he produced for *Bubalornis*, and it would be surprising if the two prove very dissimilar basically. I am still unconvinced that anything is to be gained by changing a subfamily to a family of "insecure systematic status," especially as the group is certainly a part of the weaver-bird complex. I prefer to follow Sushkin, who considered *Bubalornis* as the oldest, most archaic genus of the whole assemblage, and *Plocepasser* and its allies as among the primitive "typical" weavers. The two subfamilies Bubalornithinae and Plocepasserinae are confined to the open savanna country of Africa, and may represent some of the oldest ploceid stock from which diverged the Ploceinae, some of whose members spread to Asia. The subfamily Passerinae seems also to have arisen in Africa, but managed to spread to Europe and Asia.

Compared to the Ploceinae, the Estrildinae are birds more generally of the savannas, not the forest. As Chapin suggested, the cooler Palearctic climate may have barred their more northward dispersal even though their favored type of terrain was more generally available there than it was for their sylvan relatives, the Ploceinae. This conclusion seems justified inasmuch as the Estrildinae spread eastward in tropical lands all the way to Australia. Among the genera that did not spread beyond the African continent are the birds of immediate interest to us, the viduines. Judging from their habits and especially from their preference for grass seeds in their diet, Chapin concluded that "*Hypochera*, *Vidua* and their relatives have always been savanna birds. Restricted as they are to Africa, one may regard them as a special development of the southern savannas. The distribution of the two species of *Steganura* [considered as one species in this work], however, may be interpreted as showing that one of them early found its way to the northern savanna, though none of the group reached India."

Whether considered as the subfamily Viduinae or as a specialized part of the Estrildinae, the viduines are certainly closely related to the latter group. The similarity in the mouth markings of the nestlings of the species of *Vidua* and of their normal hosts of the genus *Estrilda* and allied genera speak for close phylogenetic relationship rather than for the results of adaptive evolution after the inception of brood parasitism by the former on the latter. While Wolters (1944, p. 29) saw little phylogenetic significance in these markings within the Estrildinae, still the markings actually suggest a degree of relationship between viduines and estrildines. Because of the special interest attached to these markings and the reflection tubercles, a more extended discussion of them is given elsewhere (pp. 22–30).

The position of the Viduinae within the ploceid family tree is, according to Chapin, one of the terminal branches of the Estrildine section. Sushkin, on the contrary, considered them as a rather primitive offshoot from a much more basal portion of the same subfamilial trunk. He stated that "*Vidua* and *Steganura*, which show some unmistakeable features of the Estrildinae, and none of the characters common to the Ploceinae that could not be interpreted as primitive, are in their skeletons the most primitive of all Estrildinae. I see no reason for placing them at the top of the phylogenetic tree . . .; certainly they are strongly modified in their nuptial plumage, but on a very low base. . . . The Estrildinae almost surely are to be split up after further investigation; of the genera known anatomically in the latter subfamily, *Steganura* and *Vidua* are the least advanced in many respects, and least different from the Ploceinae." Sushkin suggested that the viduines are not too far from the common ancestral stock from which both the Estrildinae and the Ploceinae diverged, and gave as evidence a number of structural characters.

Thus, in the structure of the skull, *Vidua* and *Steganura* agree with the Estrildinae in having a vestigial interorbital fontanel, and in having the palatal crests fairly widely separated; they differ from the Estrildinae, however, and agree with the Ploceinae in having a persistent interpalatal suture, and in having the anterior palatal processes less strongly dilated than in typical Estrildinae, the shape and size of the interpalatal space resembling that in the Ploceinae. Other cranial characters of the viduines listed by Sushkin as primitive traits are the fusion of the pterygoids and palatals; the breadth of the vomer, which is bordered with ventrally protruding sharp edges; the wide base of the parasphenoidal rostrum, which is only feebly swollen anteriorly and only slightly keeled posteriorly; and the descending portion of the nasal being narrow.

According to Chapin (1929, pp. 482–483), the late W. De W. Miller discovered that the *Vidua* group differs from the typical Estrildinae, as it does from all the Ploceinae, in possessing one row of well-developed lesser secondary coverts. *Vidua macroura* has a well formed, clearly visible normal row of these little feathers. *V. fischeri* and *Steganura* have five large-sized lesser coverts, the two or three distal ones being absent. *V. chalybeata ultramarina* shows a similar row of six feathers. While this condition may well be a primitive character, it is not present in the Bubalornithinae, the supposedly most archaic section of the whole family complex. This character and the skull never becoming thickly ossified on top; the marked seasonal change of plumage (in the males); the streaky, "sparrowy" plumage of the females, nonbreeding males, and immature birds of both sexes; and the parasitic mode of reproduction justifies our considering the combassous and their long-tailed relatives as a subfamily, Viduinae, distinct from the Estrildinae.

Still another character by which the Viduinae differ from the Estrildinae is the peculiar type of scratching movement used by the former in searching for food. Poulsen (1953, pp. 37–38) recently described this for *Vidua macroura*, *V. regia*, *V. chalybeata*, and *Steganura paradisaea*, which he studied in the zoological park at Copenhagen. These birds—

> when seeking food on the ground, made small hopping movements on both legs. When their spread feet touched the ground some of the earth was spread about and the birds obtained some seeds lying in the loose soil, *i.e.*, a kind of primitive scratching movement. . .. Previously the weaver birds (*Ploceidae*) were divided into two subfamilies: *Ploceinae* and *Estrildinae*. The whydah birds were classed with the latter subfamily. There is, however, no doubt about these birds which are parasites and in addition possess this "scratching movement" form a distinct group. . . . Three genera . . . *Drepanoplectes*, *Diatropura*, and *Coliuspasser* are very much like the whydah birds (*Viduinae* in . . . appearance. . . . They are, however, not parasitic, and . . . do not possess the above mentioned "scratching movement" as the *Viduinae*.

The fact that the viduines are restricted to the open grasslands of Africa is in general agreement with Sushkin's placement of them near the base of the estrildine stem, rather than near the top as Chapin had earlier suggested. The forms that dispersed to more remote areas (remote, that is, from the African savannas) were the later evolutionary offshoots of the Estrildinae, not their more archaic relatives. Beecher (1953), to the contrary, concluded that the "inability (of the viduines) to reach Australia and their poorness in species suggest a relatively late origin from the Ploceidae." Beecher considered the viduines a section of the typical ploceine weavers, and not of the estrildines, and it is only the latter group that occurs in Australia, where Beecher assumed that they originated, and then spread to Africa. Morris (1958), however, concluded that the estrildine group originated in Africa and spread from there across Asia to Australia. "This probably involved ancestral mannikin forms, which gave rise to the grassfinches when they reached Australia. Many of the grassfinches are now extremely convergent with certain African waxbills. The alternative evolutionary scheme . . . is that both ancestoral mannikins and waxbills spread round to Australia and that the grassfinch group is not a natural unit, but that part of it has come from ancestoral mannikin stock and part from ancestoral waxbill stock. The former view is favoured."

The recent studies by Tordoff (1954), Beecher, Mainardi (1958), Wolters (especially 1957), Stallcup (1954), and others, make me wonder whether there is any valid reason for keeping the Ploceidae as a family distinct from the Fringillidae. In view of the general acceptance of the muscicapine-sylviine-turdine assemblage in one family, it appears that a similar amalgamation may be justified here.

Such a consolidation seems more appropriate than the opposite type of proposal, such as Steiner's suggestion that the estrildines be made a family apart from the rest of the weavers. Steiner's argument was based to a large extent on behavioral characters. The differences that he cited are, however, by no means as definite and trenchant as he implied. Thus, he wrote that the young of the estrildines take regurgitated food from the crop of the parent bird, while the nestlings of the ploceines are fed by the parents who offer nonpredigested food by inserting their bills into the open mouths of their offspring. Such genera as *Euplectes*, *Coliuspasser*, and *Drepanoplectes* are considered Ploceine, and yet recently V. D. van Someren (1958, p. 165) recorded that they feed their young by regurgitation in the same way as the estrildine species do. Furthermore, Steiner stated that in the estrildines both parents share in nestbuilding, incubation, and feeding of the young, and in the ploceines most parental duties are done by the female alone. As will be seen from discussion in the next section of the ethological background of the parasitic Viduinae, neither of these groups is at all homogeneous or uniform in their habits.

If we followed Steiner's suggestion and made the waxbills a family, the Viduinae would be a subfamily of the Estrildidae, as Wolters (1957, p. 91) has already indicated. The Viduinae are nearer to the estrildine than to the ploceine weavers, although distinct from both. Placing the Viduinae in the Estrildidae, however, would largely upset the supposed characters of this family, so it seems better to retain both groups in the Ploceidae. This case is one of those where a study of special groups may well suggest family distinctions, but an overall survey of the entire weaverbird assemblage cautions against making such splits.

I also note Stallcup's suggestion to place Estrildinae with the cardueline finches in the family Carduelidae makes no mention of the viduines, and it is impossible to tell from his discussion whether he would include them with the Estrildinae in his new family or retain them in the Ploceidae. He compared his estrildine material with species of Passerinae rather than with species of Ploceinae, and it is generally admitted that the Passerinae are a fairly distinct group. Stallcup emphasized that in such a relatively stable, supposedly phylogentically conservative character as the pelvic musculature, the carduelines agree with the ploceids and not with the fringillids. This statement agrees with Tordoff's suggestion that the cardueline finches are to be looked upon as ploceids, and it seems unnecessary to establish a new family Carduelidae for them and the estrildines. Certainly, passerine families are slightly marked at best, and to increase their number does not help to solve the elucidation of their relationships.

The nearest relatives of the viduines are the estrildines, and then the ploceines. As I have noted above, the viduines are apparently an early offshoot from the estrildine stock, as they also possess a number of characters of the ploceine stem. While this arrangement seems fairly clear, it is difficult to point to any particular existing species or genera in these groups as the most probable ancestor of the viduines.

In his 1917 diagram, Chapin showed the viduine line branching off from near *Clytospiza*. This guess is as good as any that can be made; I know of no other genus that fits the assumed requirements of a possible ancestor any better than does this one. *Clytospiza* is a fairly generalized, smallish weaver with no specialized feathers or peculiar habits. In the pattern of the mouth markings of the nestlings, in the pure white color of its eggs, and in that it makes no nest of its own but uses abandoned nests of other birds, such as coucals and weaver finches, *Clytospiza* fits into the picture that one might imagine as an ancestral stock for the present parasitic widow birds.

The present distribution of *Clytospiza* is perhaps more strictly tropical, and does not extend as far to the south as might be expected of the ancestral stock, which in the southern savannas is thought to have given rise to the viduines, but we have no way of knowing if *Clytospiza* was not more extensive meridionally in earlier times than now. Furthermore, I use *Clytospiza* not in the literal sense of the present genus, but as a portion of the phyletic stem of the family from which the viduines diverged.

We are now in a position to attempt a more detailed arrangement of the little branches on the viduine stem. Prior to Chapin's revision of the classification of the family (1917) the long-tailed viduas were grouped together with such unrelated but parallel developments as the euplectine genera *Coliuspasser*, *Diatropura*, and *Drepanoplectes* merely on the basis of the long rectrices in the nuptial plumage of the adult males. As Chapin showed, however, the elongation of the rectrices is a character that has developed independently in different sections of the family, and in ways that are really quite dissimilar. Thus, the patterns of tail growth "in, for example, *Coliuspasser* and *Vidua* have nothing in common but their length and their seasonal molt. In *Vidua* and *Steganura* it is only the two median pairs of rectrices that are elongated. In addition they are often rotated so as to press their lower surfaces together forming a sort of tube in *Vidua*." In contrast, all the rectrices in *Coliuspasser* are elongated, and the median ones less so than the lateral pairs.

Inasmuch as rectricial elongation is something that has developed independently in two of the main groups of ploceids, it would seem that within each of these groups the short-tailed species are probably nearer the basal stock from which they deviated than are their long-tailed relatives. As far as the Viduinae are concerned, this arrangement would mean that the combassous, *Hypochera* (herein considered a subgenus), are more primitive than the species of *Vidua* proper. This arrangement is further borne out by R. Neunzig's (1931, p. 545) experimentally induced elongation of the median rectrices of combassous. Chapin correctly stated that these species are merely short-tailed viduas, and in his phylogenetic diagram of the whole family he showed them (there called the genus *Hypochera*) as the stock leading eventually to *Steganura*. *Vidua* is not shown in his diagram, but is ostensibly between these two. Hence, apparently Chapin also believed that the combassous are the most "primitive" of the existing Viduinae.

Too little is known of the biology of the three species of combassous even to suggest which is more primitive, and which is less so. Apparently subgenus *Hypochera* spread northward through the savannas, and in eastern and southeastern Africa eventually gave rise to what has become the blue widow bird, *Vidua hypocherina*. Inasmuch as *V. hypocherina* has brown rather than blackish remiges, its origin would seem to lie with either of the two brown-winged combassous (*V. funerea* or *V. amauropteryx*). On the whole, the gloss of its plumage suggests *V. amauropteryx* more than *V. funerea*, and indeed, von Boetticher (1952, pp. 64-65) suggested that *V. hypocherina* may be only a long-tailed race of *V. amauropteryx*. It is doubtfully profitable, however, to attempt to particularize on this point.

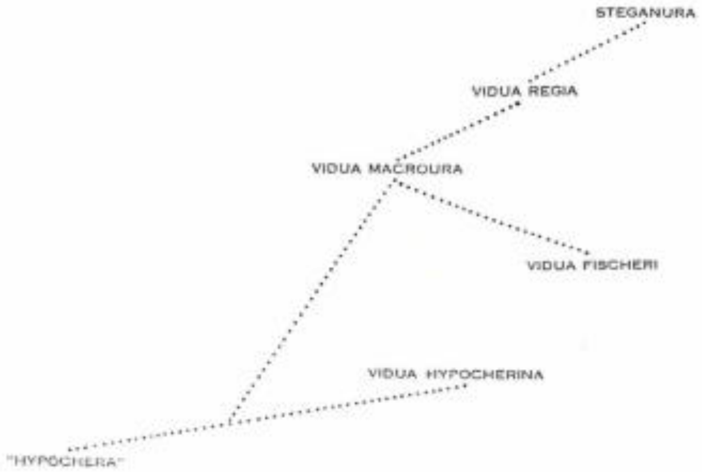
At about the same time or possibly somewhat later, but apparently independently of this offshoot, the pin-tailed widow bird, *Vidua macroura*, evolved and became the most widely distributed member of the group. That *V. hypocherina* has a much more restricted range in northern portions of eastern Africa militates against its being considered the direct link between the combassous and the pintail. From this latter stock, in turn, subsequently arose the other two species of the typical viduas—*V. regia* of the western portion of southern Africa, and *V. fischeri* of eastern Africa from central Tanganyika north to Somaliland and Ethiopia.

It is noteworthy that *Vidua fischeri* appears to be almost wholly sympatric with *V. hypocherina*. They are, as sympatric species should be, completely distinct and show no tendency to cross. I think that they were not originally wholly synchronic as well as sympatric, but that the blue widow bird, *V. hypocherina* probably antedated the evolution of *V. fischeri*. *V. macroura* was probably next in the line of viduine differentiation. The conclusion rests upon the fact that its juvenal plumage resembles that of the combassous and of *V. hypocherina*, and upon its wide distribution, which allowed for geographic contact with these forms. *V. macroura* or the stock of which it is the living representative later gave rise to *V. regia* in the southwestern part of Africa and to *V. fischeri* in the northeastern part. All are of sufficient antiquity to have allowed intermediate stages to disappear long ago. Thus we have the peculiar situation where the archaic, ancestral stock, subgenus *Hypochera*, comprises three closely similar species in which the degree of differentiation (to human eyes at least) is hardly more than what is found in sibling species, while the derivative line, subgenus *Vidua* proper, comprises four species that are very distinct and dissimilar in the adult male nuptial plumage but are much less dissimilar in all other stages.

In his discussion of the problem of sibling species Mayr (1948, p. 231) noted two seemingly feasible explanations. One was that such species are of such recent origin as to preclude the acquisition of pronounced morphological differences, an explanation assuming that reproductive isolation is acquired through very few steps and that, consequently, such species are still genetically very similar. According to the other explanation, the slight morphological characters involved are genetically firmly integrated so as not to become visibly affected by the mutational steps that have produced the ecological and reproductive isolating mechanisms. The combassous seem to be accounted for more adequately by the second of these two explanations. The combassous are old enough to be the ancestors of the long-tailed widow birds, but there is no direct or even implied evidence that causes me to consider the evolutionary history of the combassous as of relatively short duration when compared with that of the long-tailed members of the genus *Vidua*.

Of all the long-tailed species of *Vidua*, the shafttail, *V. regia*, seems most likely to be closest to the stock from which evolved the paradise widow bird, *Steganura paradisaea*. This conclusion is based on the fact that the shafttail shows greater similarity in coloration and also has the tendency for the elongated rectrices to broaden; while admittedly not the most convincing evidence, it is more than may be seen in any of the other existing species of *Vidua*. While *Steganura* would thus seem to be a relatively recent development in the Viduinae, the fact that it has become differentiated into a numer of geographic races indicates a considerable antiquity for the genus. Recently Delacour and a few other workers reduced *Steganura* to a subgenus of *Vidua*, but *Steganura* appears to merit generic status by itself on the basis of its highly peculiar rectricial growth, the arrangement of the mouth markings in the nestling, the marked discontinuity in size between it and the other viduines, and its different, almost larklike aerial display (for further details of its very different rectricial structure, see the discussion of the genus on pp. 137–139).

Insofar as it is possible with present incomplete knowledge of every member of the group to attempt a phylogenetic scheme within the Viduinae, the arrangement would be: 1, Subgenus *Hypochera;* 2, *Vidua* proper; and 3, *Steganura*. The diagram below represents the apparent phyletic relations of the included forms. In considering this diagram, one should keep in mind that the names of existing species are used in a broad sense. They imply not merely the species as it is today but also the stock from which it developed.



Less may be said with certainty as to the systematic position of the other parasitic weaverbird, the cuckoo finch, *Anomalospiza imberbis*. It is clearly not closely related to the Viduinae. In his most recent treatment Chapin (1954, p. 407) placed the cuckoo finch next to *Quelea* because its young are not known to have any mouth spots (which if present would suggest a relationship with the Estrildinae), and because its outermost primary is greatly reduced. Actually, we do not know that its young do not have any mouth markings, as no one has recorded anything about them. In life the cuckoo finch looks and acts much like the species of *Euplectes* or *Coliuspasser* in "off season" plumage, and on present knowledge it seems that it may fit into the picture not far from them. Its choice of brood hosts, all grass warblers, gives no clue in this regard, but the fact that its juvenal plumage is streaky, quite "sparrowy," agrees with the *Euplectes* group fairly well. The curious presence of a spina interna on the sternum suggests that the cuckoo finch is not a typical ploceid, but I cannot imagine where else to place it. In the character of its sternal spine it recalls such genera as *Bubalornis* and *Dinemellia*, but in no other respects does it seem related especially to them.

Boetticher (1952, p. 8) placed the cuckoo finch in a separate subfamily, the Anomalospizinae, but there seems to be no need for this arrangement, and in fact no reasons were given. He placed this subfamily in a linear list between the Amblyospizinae and the Estrildinae.

Ethological Background

Behavior as well as systematic relations must be studied from the same general approach of phyletic descent. Concerning the behavior of brood parasites, it is important to survey variational trends particularly in breeding behavior in the various sections of the whole family to which the parasites belong and especially in the groups most closely related and most probably antecedent to the parasites. We must understand what may be termed the psychobiological background from which the parasitic mode of reproduction developed. Without such an understanding it is difficult to formulate the phyletic homologies in behavior essential for a better understanding of the results now visible in the life histories of the brood parasities.

I made a start on such a survey some years ago (Friedmann, 1950), and to avoid needless duplication, I want to start here with some of the conclusions arrived at in the earlier study. As we saw in the previous section, the Viduinae are somewhat intermediate between the typical weavers, Ploceinae, and the waxbills, Estrildinae, but are more closely allied to the latter group. In many species of ploceines and also in many of the estrildines:

> The hens breed in nests, the actual construction of which has been foreign to their experience and their efforts; in many forms of the latter group, and at least some members of the former subfamily, the care of the eggs is taken over, at least in part, by the cocks.
>
> The parasitic mode of reproduction occurs . . . in five widely separated and quite unrelated families of birds . . . and it is not without . . . suggestive value that this highly aberrant reproduction pattern has developed among the small passerine birds . . . in those two families some of whose members have carried the habit of nest-building to its highest and most complex development. It is all the more noteworthy that in the weaverbirds . . . the parasitic habit has developed in two subfamilies, apparently independently—the cuckoo finch, *Anomalospiza imberbis*, in the Ploceinae, and in the members of the Viduinae. . . . Many more details have still to be learned of the annual cycle of behavior patterns in these

birds before it may be possible to attempt to determine the precise causes and the subsequent evolutionary paths that twice in the history of the weaverbirds have led from nesting and incubation and caring for the young to a state of brood parasitism.

Since the loss of "normal," ancestral reproductive patterns and their replacement by brood parasitism may involve antecedent weakenings and trends in some of the components of the original picture—territorialism, mating relations, nest building, incubation, and caring for the young—these components will now be reviewed as far as available data permit.

TERRITORIAL AND MATING RELATIONS: We find much variability within the weaverbird family in their territorial and mating relations. Noting these variations gives us a clearer picture of the ethological background of parasitic species and also helps us narrow the search for factors contributive to brood parasitism, especially as our knowledge of this portion of the life history of the several parasitic species becomes more definite.

As will be seen in the species accounts described below (beginning on p. 39), some observers described individual species of viduines as polygamous, while others described them as monogamous, but the total evidence is not yet completely convincing about either interpretation.

Both monogamy and polygamy were noted in other sections of the weaverbird family. In his recent study of buffalo weavers, *Bubalornis a. albirostris*,[3] Crook (1958) found that they are polygamous and territorial. The territory may consist of a group of connected nests comprising a "lodge," or a portion of a large and complicated "lodge," but usually contains from three to six nest holes, with a hen installed in each. Of the ploceine weavers, Moreau and Moreau (1939, pp. 317–318) reported that *Ploceus aureoflavus*,[4] and *jacksoni* are polygamous, while other species of the genus—*bicolor*,[5] *reichenowi*, and *ocularius*—are monogamous. Of *bicolor* and *ocularius*, Skead (1953, p. 103) wrote that they appear to mate for life. The Moreaus concluded that the distinction between monogamy and polygamy may follow subgeneric lines. They found that—

> in the monogamous species mentioned above both members of the pair share the building at all stages and share the care of the young, while in the polygamous species all but the final stages of nest-building are done by the male, and the female alone incubates and feeds the young.

Jackson (1938) gives some indication of the function of the sexes for six of the numerous *Ploceus* spp. mentioned by him. In *Icteropsis pelzelni*,[6] both male and

---

[3] *Coccothraustes albirostris* Vieillot, Nouveau dictionnaire d'histoire naturelle, vol. 13, 1817, p. 535 (Senegambia).

[4] *Ploceus aureoflavus* A. Smith, Illustrations of the zoology of South Africa . . ., vol. 2, Aves, 1839, text to pl. 30, fig. 1 (West Africa, probably Zanzibar).

[5] *Ploceus bicolor* Vieillot, Nouveau dictionnaire d'histoire naturelle, vol. 34, 1819, p. 127 (South Africa).

[6] *Sitagra pelzelni* Hartlaub, Zool. Jahrb., vol. 2, 1887. p. 343, pl. 14, figs. 9, 10 (Magungo, Upper Nile).

female feed the young; in four *Sitagra* spp., namely, *vitellina*,[7] *cucullata*, *spekei*, and *jacksoni*, there is evidence that only the males build, while in *S. rubiginosa* only the females feed the young. Thus the indications are that polygamy is a character of the subgenus *Sitagra*, as it may be of the subgenus *Xanthophilus* also.

In the Asiatic weaver, *Ploceus philippinus*, studied by Ali (1958):

> The nests are built entirely by the males. The females appear at the colonies, singly or in small parties, to prospect for laying sites, only after the nests have reached a fairly advanced stage of construction. If a female approves of a certain half-built nest she appropriates it, whereupon the cock accepts her as his mate and proceeds to complete the structure for her. As soon as she has settled down to incubation of the eggs, the cock commences to build another nest on a neighboring branch. In due course this nest is similarly taken up by a second female. Thus cocks are "progressively polygamous"; each may have 2 or 3—exceptionally even 4—nests, more or less concurrently, during a normal breeding season which lasts about three months.

In their compiled data on all the East African species of weavers, Mackworth-Praed and Grant (1955) recorded polygamy in *Ploceus subaureus* (p. 923), *Anaplectes melanotis* (pp. 942–944), several species of *Euplectes* (pp. 949–958)—*orix*, *nigroventris*, *hordeacea*, *capensis*, and *afra*—and also in *Coliuspasser albonotatus*[8] (p. 965), and *Drepanoplectes jacksoni*[9] (p. 973). To these may be added *Ploceus velatus* and *nigerrimus*. There is inconclusive evidence that the species of *Coliuspasser* and of *Drepanoplectes* may be monogamous (Friedmann, 1950, p. 297).

Of the bishop birds (*Euplectes*), Lack's study (1935) of *E. hordeacea* showed that each male has a territory with well-defined limits, which it rarely leaves, and which it defends against other males and strange females. Each cock has a succession of hens, each of which it courts and for each of which it builds a nest, one at a time. As many as three hens, each with a nest, were recorded simultaneously in the territory of a single male bird. Lack found that the so-called courtship display of the male was actually correlated with the territory and not with courtship of the female.

Lack's findings call to mind Emlen's recent report (1956) on a number of species of *Euplectes*, whose territorial behavior may be summed up as follows: Several related species may nest close together in a single area. Within the area males of the several species establish discrete territories on which they display indiscriminately to females of any of the species, and from which they drive away males of their own kind or other kinds. "These trans-specific behavioral responses suggest that in these birds the distinctive features of the males'

---

[7] *Fringilla vitellina* Lichtenstein, Verzeichniss der Doubletten des Zoologischen Museums . . ., 1823, p. 23 (Senegambia).

[8] *Vidua albonotata* Cassin, Proc. Acad. Nat. Sci. Philadelphia, vol. 4, 1848, p. 65 (Durban).

[9] *Drepanoplectes jacksoni* Sharpe, Ibis, ser. 6, vol. 3, 89, p. 246, pl. 5 (Masailand near Nakuru).

plumage and display although used in territorial defense have been evolved primarily with respect to species recognition in mate selection."[10]

Moreau and Moreau (1938, pp. 314–327) found, in *Euplectes nigroventris* and *E. hordeacea*, that the size or position of the territory bears no relation to the availability of food for adults or young. In the latter species the territory is apparently always fairly large in size, from 600 to 1,200 square yards, and the size of the area appears not to be affected by the abundance of breeding males. On the other hand, in *E. nigroventris* the territory is seemingly indefinitely compressible. Sometimes fully functional territories measure less than 10 square yards. "Irrespective of the size of his territory a male *E. nigroventris* has up to five breeding females active in it at once, and may raise eight families in it during the season. In a territory of *E. hordeacea* not more than three breeding females have been found at once. In the breeding population of both species females outnumber males by quite four to one."

In the red-billed weaver, *Quelea quelea*, Morel and Bourliere (1955 and 1956) described an interesting picture of territorial and mating relations. The species is colonial and nests in large groups, and the males outnumber the females three to one. Ten colonies, destroyed with explosives in order to kill all the birds without allowing any to escape, revealed 2,749 males and 946 females. In defense of the use of this technique, it should be noted that the studies of Morel and Bourliere were part of a campaign to control this species, which had become a very serious agricultural pest in the grain growing areas of Senegal.

This uneven sex ratio seems to be a result of differential postnestling mortality, as extensive examination of newly hatched or nearly fledged young show nearly equal numbers of males and females. In one colony with 525 nestlings 1 to 2 days old, 279 were males and 246 were females. Another colony with 323 nestlings, had 159 males and 154 females. Another colony with 182 nestlings about 8 days old showed 86 males and 96 females. Another colony with 136 nestlings had 71 males and 65 females.

The males build the nests, and pairing takes place after the nests are built, but the females may occasionally visit the nests even before they are completed. The courtship behavior is of a mutual type, which may possibly help in the social coordination in the colony. Since the birds appear to be strictly monogamous, the fate of the surplus males remains a mystery.

---

[10] That this sort of arrangement is not necessarily restricted to species with highly distinct male and closely similar female plumages is indicated by Lanyon's (1957) findings in the two extremely similar species of *Sturnella*.

Territorial behavior is reduced to the defense of the nest by both members of the pair. The territory is limited to the nest and its immediate approach. A strange individual is mobbed if it comes close to the nest, but it is not pursued once it leaves. Territorial defense and aggressiveness are at a maximum during the period of pair formation and incubation.

Both sexes incubate for short periods at a time during the day, but only the hens stay on the eggs at night. Throughout the duration of incubation and the rearing of the nestlings, the males continue to add straws to the nest.

To all these rather unusual aspects of the reproductive picture as it exists in this species, one more aspect must be added. Not infrequently whole colonies are abandoned simultaneously by the breeding birds, as if at a signal. The abandonment may happen just after the construction of the nests, or even during the time when nestlings are being reared. In one such abandoned colony three-quarters of the nests contained unincubated eggs.

The reports of the red-billed weaver and of species of bishop birds may be considered as evidence of the unusual ethological background more particularly of the cuckoo finch, *Anomalospiza imberbis*, than of viduine species.

About the territorial and mating relations of the nearest relatives of the viduines, the estrildines, most of the observations indicate monogamy as the usual condition. V. G. L. van Someren (1956, p. 478) placed on record dissenting data. He noted two females of *Euodice cantans* simultaneously involved in the same nest, which held what appeared to be two sets of eggs—one fresh and the other well incubated. Of the partridge finch, *Ortygospiza atricollis*, he (p. 481) "often found nests within about six yards of each other. There were two hens, but only one cock. Is the little finch polygamous?" Obviously, more observations are needed to answer this question.

In looking back over the data, I can assume only that mating relations may effectively influence territorial behavior or may be influenced by it, but that neither of these activities seems to have contributed immediately to the advent of brood parasitism.

Nest building: This component is the most conspicuous and important one of the series. In related, but selfbreeding, nonparasitic members of the family, diminution or loss of nest building is expressed in the incidence or frequency of adoption of available nests built by other birds. This occupation is usually peacefully made in old and abandoned nests, and does not involve seizing them forcibly from their builders, but at times it may involve aggressive action against the builders. At least under conditions of captivity such action may take place. Thus, Parker (1931) wrote that in an aviary, *Amadina* *erythrocephala* [11] always drove off other weavers from their nests and then occupied them. In the wild state, this species usually uses old nests of other birds, and has not been recorded as taking them by force from their rightful owners. The lack of information to this effect may result from insufficient field observation, or it may indicate that such behavior is not necessary in a wild state.

In nest building as contrasted with nest adoption, there is a striking difference between the ploceine weavers and the estrildine group. Many ploceine species carry nest building to excessive proportions by building in and out of season as though driven by a mania for such activity, even though they may make little or no use of these out-of-season nests. Apparently nest building has become a displacement activity. Courtship in these birds is performed at the nests prepared by the unmated males. Extra nest building or building out-of-season nests may prove to result from overly sustained appetence in this regard.

In the estrildines, on the other hand, we find many species that often use old abandoned nests of other kinds of birds, although they sometimes make their own nests. Among these species are *Amadina fasciata*, *Amadina erythrocephala*, *Clytospiza monteiri*,[12] *Estrilda subflava*, *Euodice cantans*, *Estrilda perreini*,[13] *Lonchura cucullata*, *Sorella eminibey*,[14] *Estrilda bengalus*,[15] and *Estrilda cyanocephala*.[16] Manuel (1930) reported that in *Lonchura jagori*, both sexes are involved in building the nest.

Even in the ploceine species that indulge in excessive nest building the activity is largely restricted to cock birds. Among these species may be mentioned *Euplectes hordeacea*, *Amblyospiza albifrons*, *Anaplectes melanotis*,[17] *Quelea quelea* and *Quelea erythrops*, *Malimbus scutatus*,[18] and a large number of species of *Ploceus* (*capensis*,[19] *jacksoni*,[20] *nigerrimus*,[21] *ocularius*,[22] *philippinus*,[23] *reichenowi*,[24] *spilonotus*,[25]

---

[11] *Loxia erythrocephala* Linnaeus, Systema naturae, ed. 10, vol. 1, 1758, p. 172 (Africa; Angola).

[12] *Pytilia monteiri* Hartlaub, Proc. Zool. Soc. London, 1860, p. 111, pl. 161.

[13] *Fringilla perreini* Vieillot, Nouveau dictionnaire d'histoire naturelle, vol. 12, 1817, p. 179. (Malimbe, Portuguese Congo).

[14] *Sorella eminibey* Hartlaub, Journ. Ornith., vol. 28, 1880, p. 211, 325 (Lado, Upper Nile).

[15] *Fringilla bengala* Linnaeus, Systema naturae, ed. 12, vol. 1, 1766, p. 323 (Bengal=Senegal).

[16] *Estrilda cyanocephala* Richmond, Auk, vol. 14, 1897, p. 157 (Useri, near Kilimanjaro).

[17] *Ploceus melanotis* Lafresnaye, Rev. Zool., 1839, p. 20 (Senegal).

[18] *Sycobius scutatus* Cassin, Proc. Acad. Nat. Sci. Philadelphia, vol. 4, 1849, p. 157 (Seirra Leone).

[19] *Oriolus capensis* Linnaeus, Systema naturae, ed. 12, vol. 1, 1766, p. 163 (Cape of Good Hope).

[20] *Ploceus jacksoni* Shelly, Ibis, ser. 5, vol. 6, 1888, p. 293, pl. 7 (Kilimanjaro, probably Lake Jipe, near Taveta).

[21] *Ploceus nigerrimus* Vieillot, Nouveau dictionnaire d'histoire naturelle, vol, 34, 1819, p. 130 (Portuguese Congo).

[22] *Ploceus ocularius* A. Smith, Illustrations of the zoology of South Africa . . . , vol. 2, Aves, 1839, pl. 30, fig. ½ (southeastern coast of South Africa).

[23] *Loxia philippina* Linnaeus, Systema naturae, ed. 12, vol. 1, 1766, p. 305 (Philippines=Ceylon).

[24] *Sycobrotus reichenowi* Fischer, Journ. Ornith., vol. 32, 1884, p. 180 (Great Arusha).

[25] *Ploceus spilonotus* Vigors, Proc. Zool. Soc. London for 1831, p. 92 (Algoa Bay).

subaureus,[26] and *velatus*[27]). While *P. spilonotus* is here listed on the basis of published observations, it was recently shown to be conspecific with *P. cucullatus*, which is listed below as a species with both sexes taking part in nest construction. Either our available data on *P. spilonotus* are incomplete or we have here a case of racial difference in so far as nesting activities are concerned.

How compulsive nest building may become is illustrated by an instance (recorded by Bannerman, 1949, p. 146) of two males of *Malimbus scutatus* actually working on the same nest at the same time. Usually, these weavers make them alone.

In most of these birds, the females may do some work on the nest lining, but apparently not more than this much is the rule. On the other hand, both sexes take part in nest construction in *Quelea cardinalis*, *Ploceus brachypterus*[28] and *Ploceus cucullatus*.[29] In the estrildines, both sexes help build in *Estrilda cyanocephala* if and when they cannot find a deserted ready-made nest of another species.

The instance cited above of two *Malimbus* males building the same nest is duplicated by examples in the Estrildinae. Thus, what appears to be communal nest building sometimes takes place in *Spermestes nigriceps*[30] (Moreau and Moreau, 1939, pp. 318–319), although there is no evidence that a nest constructed by more than one bird is ever finished or used.

> In one striking example seven birds of different ages, two adults, one bird with mottled head, and four juveniles, all helped to build one nest, while a few yards away another was being built by a single adult. . . . Several times an adult arrived followed by three juveniles, all carrying the grass. Often the adult took the grass a young bird brought and built it in, but at other times the young placed theirs themselves after the adult had done so, and apparently in imitation of its action. . . . The birds were working so energetically that at one time the adult was arriving every twenty seconds with material. . . . Forty visits with material were made in thirteen minutes, and at one time five birds were all on the half-made nest at once.

In captivity many weavers that have not actually bred there nevertheless weave straws and raffia to such an extent as to fill all available sites with untidy masses of woven matter. I have seen this activity repeatedly with such birds as *Quelea quelea* and *Ploceus rubiginosus*.[31] The mere sight of one bird carrying nesting materials or weaving them into place seems to be a sufficient stimulus to activate the other individuals present to similar effort.

---

[26] *Ploceus subaureus* A. Smith, Illustrations of the zoology of South Africa . . . , vol. 2, Aves, 1839, pl. 30, fig. 1 (Algoa Bay).

[27] *Ploceus velatus* Vieillot, Nouveau dictionnaire d'historie naturelle, vol. 34, 1819, p. 132 (Namaqualand).

[28] *Ploceus brachypterus* Swainson, Birds of western Africa, vol. 1, 1837, p. 168, pl. 10 (Senegal).

[29] *Oriolus cucullatus* P. L. S. Müller, Des Ritters Carl von Linné . . . vollständige's Natursystem . . . , Supplement, 1776, p. 87 (Senegal).

[30] *Spermestes nigriceps* Cassin, Proc. Acad. Nat. Sci. Philadelphia, for 1852, p. 185 (Zanzibar).

[31] *Ploceus rubiginosus* Rüppel, Neue Wirbelthiere zu der Fauna von Abyssinien gehörig, entdeckt und beschrieben. Vögel, 1840, p. 93, pl. 33, fig. 1 (Abyssinia).

In Liberia according to Allen (1930), if a male *Ploceus cucullatus* came to its nest and began to weave in a strip of straw or leaf that it had just brought, two or three neighboring males would immediately seize the hanging strip and try to pull it out and fly off with it. At times he saw several birds hanging on to the same straw. In the Cameroons, Bates (in Bannerman, 1949, pp. 89–91) noted this species as having a "perfect mania for building, and when not building new nests are all the time repairing the old ones."

This inordinate interest of males of some species of weavers in nest building, together with their habit of using the completed or partial structures as courtship sites, suggests that nest construction has gone far beyond its "normal" function, and has come to include a type of behavior not wholly unlike the bower-building habits of some ptilonorhynchids, without the specialized differentiation between courtship-site-construction and actual nest building found in the latter group. We not only find extreme activity in building prior to reproductive use of the nests, but we also note apparently aimless duration of it after the nests are in use. Thus, of the little grenadier weaver, *Granatina ianthinogaster*, and of the red-billed weaver, *Quelea quelea*, the cock bird is said to continue to bring feathers, twigs, and other lining materials to the nest all through the incubation period.

It is apparent from the various items discussed above that as far as antecedent distortions, extensions, and even eliminations of the nest-building habit contribute to the ethological background, the stage was set for the advent of brood parasitism in the weavers. In comparison with the icterids and the cuckoos, the weavers were more predisposed to develop this type of behavior.

INCUBATION: Incubation is recorded as done solely by the hen in *Euplectes orix*, *franciscana*,[32] and *hordeacea*, in *Ploceus capensis*, *chrysaeus*,[33] *nigerrimus*, *philippinus*, and *velatus*, in *Amadina fasciata* and in *Quelea erythrops*; and by both sexes in *Ploceus luteolus*[34] and *ocularius*, in *Quelea quelea*, *Anaplectes melanotis*, *Lonchura fringilloides*,[35] in *Estrilda perreini subflava*, and in *Pytilia melba*. In the last two incubation is said to be done largely by the male. In *Quelea quelea*, the females do all the nocturnal incubation, but both sexes share this activity during the day.

Occasionally waxbills that normally take care of their eggs and young may act in a way suggestive of brood parasitism. Thus, at Chatsworth, Fort Victoria, Southern Rhodesia, M. P. S. Irwin (in litt.) found on March 16, 1956, a nest of *Spermestes cucullatus scutatus*

---

[32] *Loria franciscana* Isert, Schrift. Ges. Naturf. Freunde, Berlin, vol. 9, 1789, p. 332, pl. 9 (Accra).

[33] *Ploceus chrysaeus* Hume, Stray feathers . . ., vol. 6, 1878, p. 399 (Tenasserim).

[34] *Fringilla luteola* Lichtenstein, Verzeichniss der Doubletten des zoologischen Museums . . ., 1823, p. 23 (Senegal).

[35] *Ploceus fringilloides* Lafresnaye, Mag. Zool., 1835, pl. 48 ("India"; Liberia).

PLATE 1. STRAW-TAILED WIDOW-BIRD

Male (top), female (bottom), and young (middle).

PLATE 2. SHAFT-TAILED WIDOW-BIRD

Male (top), female (middle), and young (bottom).

PLATE 3. CUCKOO FINCH

Male (left) and young (right).

PLATE 4. MELBA FINCH FEEDING YOUNG OF PARADISE WIDOW-BIRD

Melba finch male (top right), female (top left), and young (lower left), with young of paradise widow-bird (lower right).

containing five eggs of the builder and two larger eggs that were similarly unmarked white in color but that obviously belonged to another species. No species of viduines occurred in the area, which was under close and prolonged observation by the collector. Judging from his notes, and from the elimination of unlikely species (on the basis of local ecological notes), I assume that the larger eggs were those of either *Granatina* or *Estrilda*.

Another case was reported by Chapin (1954, p. 535), who wrote that in Natal, J. Vincent found four eggs of *Estrilda subflava clarkei* in a nest with two eggs of *Coliuspasser ardens*. V. G. L. van Someren informed me (in litt.) that in *Euodice cantans* occasionally more than one female may lay in the same nest. He has records of three simultaneous clutches in the same nest, represented by nestling birds, well-advanced embryos, and nearly fresh eggs. He also has similar records for the cut-throat finch, *Amadina fasciata*.

As in nest building, we find much variability in incubation, the sort of variability that if not necessarily conducive to, at least imposed no obstacles in the way of, complete elimination of incubation as is characteristic of brood parasitism.

The tendency to incubate and to brood is hormonally controlled in doves and in poultry, and probably this condition is also true of other birds. Of species of weavers that often breed in adopted nests built by other birds, variability in broodiness and incubation behavior may also be associated with an underlying endocrine imbalance. If found to be true, the occurrence of an endocrine imbalance would be a "critical point" in the antecedent reproductive pattern—the point at which the parasitic mode of breeding began.

Care and feeding of nestlings: We have here essentially the same picture as we found in the survey of incubation. Both parents are known to feed the young in the nest in *Quelea quelea* and in many species of *Ploceus—bicolor, capensis, cucullatus, nigerrimus, ocularius, pelzelni, philippinus*, and *reichenowi*. The female alone feeds the nestlings in species of *Euplectes—orix* and *hordeacea*—and in several species of *Ploceus—aureoflavus, bojeri, jacksoni, rubiginosus*, and *velatus*.

Greater variability probably exists in nestling feeding than in egg incubation since nestling birds, which are capable of movement and vocalization, are more effective stimuli on the behavior of the adults than are such quiescent objects as eggs. I note that in captivity even such an habitual parasite (in the wild state) as a combassou, was known to indulge in attentive behavior, even to the point of raising a brood of young.

Because of its variable nature, nestling care offers less of a clue about the advent of brood parasitism that do nest building and incubation. Nestling care is of value in that it provides opportunities for observing atavistic behavior of parasitic species, and such behavior is an indication of an ancestral mode of life.

Adaptive Features

Because attempts were made by R. Neunzig (1929a) and others to see highly adaptive, mimetic evolution in the remarkable similarities in the color of eggs, in the pattern of nestling mouth markings, and in the nestling plumage of viduines and of their usual foster nest mates, I must discuss these matters in some detail. It should be stated at the outset that these similarities are more probably due to community of descent rather than to any convergence developed after the advent of brood parasitism. I find that I was anticipated by Hoesch (1939) and by Chapin (1954, p. 547) in most of my arguments given below. With regard to the mouth markings, Chapin stated that "the Estrildinae and Viduinae are closely allied and that the latter have retained such markings and papillae ever since the two groups diverged. Natural selection, of course, may aid in keeping them so closely alike."

Possibly Neunzig was unduly influenced by the older classification of Reichenow and others, who placed the viduines with *Euplectes*, *Coliuspasser*, and their allies. This arrangement would cause him to wonder at the convergence of egg coloration, buccal decorations, and juvenal plumage of the parasites, and those of their estrildine hosts.

EGG COLORATION: As far as is known, all viduines lay unmarked white eggs, very similar to those of their usual estrildine hosts. As might be expected, there are some hosts that lay spotted or mottled eggs, which bear little resemblance to those of the parasite, but such instances are in the minority. Neunzig assumed that the white color of the eggs of the parasites was an adaptation possibly originated by mutation and acted upon by selection through the response of the hosts (he apparently implied only estrildine hosts). Actually, we ought to attribute this similarity to the close relationship of the two groups. It seems highly dubious for such resemblance to have come about in birds using domed nests because in the dark interiors, of the nests, differences in the eggs would be scarcely discernible to the hosts.

MOUTH MARKINGS AND REFLECTION GLOBULES OF NESTLINGS: These structures are of two kinds—spots of dark color on the inside of the mouth and on the tongue that form a symmetrical, geometric pattern sharply delineated from the very differently colored mouth lining; and globular, apparently luminescent, but actually merely highly reflective tubercles at the corners of the gape immediately outside the mouth. The colored marks inside the mouth are assumed to function, as in other birds with comparable structures, as directive indices to guide the food-laden adult to place the food directly in the mouth of the nestling and not to one side or the other. The tubercles have a similar usefulness, as the birds involved are all species that make or use more or less spherical, domed-over nests with only submarginal interior illumination. The tubercles glow with reflected light in this semidarkness and indicate by their presence the limits of the mouth of each nestling. They may help to illuminate the pattern of the mouth itself, but this possibility has not yet been established. Thus we have a pair of directive structures—one functioning best in good light and the other in poor light.

When one considers that many birds manage adequately without such aids, one wonders at the apparently prodigal equipment here. The estrildines supposedly have become so attuned to these recognition devices that they cannot carry on as well without them. It would be worthwhile to insert very young nestlings of species not so equipped into nests of some of these birds to see if they would receive enough food and care for normal growth, even though the experiment would not explain the evolution of these structures.

Swynnerton (1916, pp. 279, 284) did attempt such experiments. He placed a nestling *Ploceus ocularius* in a nest of a flycatcher, *Chloropeta natalensis*,[36] a species whose young have a very differently colored mouth lining. He recorded that the "parent flycatchers seemed to experience no inconvenience whatever from the different mouth-colour and the absence of twin spots, or even from the rapid vibration of the head." He also placed a young *Ploceus ocularius* in a nest of a rock thrush, *Monticola angolensis*,[37] and the nestling was adopted "in spite of its different external appearance, its very different mouth, its extraordinary manner, and its different call-note."

When Neunzig first described the very close approximation of the buccal pattern of the viduines and of selected species of estrildines, he assumed that each parasitic species restricted its attentions to a single kind of host, or at least tended to do so. We now know that this assumption is false. The best known of the viduines, the pin-tailed widow bird, *Vidua macroura*, is known to parasitize at least 18 species, not all of them estrildines, and other species of *Vidua* are similarly free of rigid, obligate host specificity. True, the hosts most frequently selected are few in number, but they are still too numerous to account for the degree of parasite-host resemblance postulated by Neunzig, as the various species of estrildines differ from each other

---

[36] *Chloropeta natalensis* A. Smith, Illustrations of the zoology of South Africa . . ., vol. 2, Aves, 1847, pl. 112, fig. 2 (Durban).

[37] *Monticola angolensis* Sousa, Jorn. Sci. Math. Fysicas e Naturaes, Lisbon, vol. 12, 1888, pp. 225, 233 (Caconda).

in their buccal patterns. As Hoesch pointed out (1939), if the Viduine species were as specifically adapted in this character as was implied, this adaptation would have come about only if each species of *Vidua* were confined to a single host species, to which the pattern adaptively evolved. In addition to pointing out the improbability of such a development, Hoesch indicated that localities are known where viduines occur and maintain themselves without their supposed correspondingly patterned host species. Hoesch also reported that the paradise widow bird, which is parasitic chiefly on pytilias, does not show any close correspondence with its host in the character of nestling mouth markings.

If the buccal decorations were acquired as an adaptation to brood parasitism, they would have selective value, but for this consequence there is as yet no real evidence. The resemblance in the mouth markings of the young viduines and of their frequent estrildine hosts might be of some advantage to the parasites. Striking differences in this respect might be enough to interfere with the necessary attentive behavior of the fosterers.

According to Lorenz (1935), the buccal colors and patterns of young parasitic cuckoos of those species that usually evict their nest mates and thus get the undivided attention of the foster parents are not very similar to the mouths of the hosts' young, whereas in those species of cuckoos that grow up together with their nest mates (e.g., *Clamator glandarius*[38]) there is general similarity in pattern and coloration revealed by the gaping mouths of the two kinds of nestlings. Even in these species, however, it is possible and indeed has been recorded that the young parasite can grow up with a nest mate of quite divergent mouth pattern without evoking any critically different parental care. Furthermore, in the viduines, if one considers the semidarkness in which the young of the parasite and of the host grow up together, it is diffiult to see the need for a close correspondence.

Recently in discussing the mouth pattern of one of the estrildines, the bronze mannikin, *Lonchura cucullata*,[39] Morris (1957, p. 199) rightly concluded that "taxonomically these markings are conservative characters and are valuble aids to understanding the evolution of the group." Delacour (1943, pp. 70–72) considered the mouth markings to be of considerable taxonomic significance at the group, or tribal level. He based his conclusion on the observation that all waxbills and grassfinches have spots while all mannikins have semicircular, horseshoe-shaped lines. As Morris (1958, pp. 397–398) pointed out,

---

[38] *Cuculus glandarius* Linnaeus, Systema naturae, ed. 10, vol. 1, 1758, p. 111 (north Africa and southern Europe).

[39] *Spermestes cucullatus* Swainson, Birds of western Africa, vol. 1, 1873, p. 201 (Senegal).

however, at least five species of grassfinches have lines but no spots, and so even this character is not a rigidly unvarying one.

The reflection globules or tubercles at the corners of the mouth, which are found only in viduines and estrildines, seem to be more directly useful and hence seem more apt to have selective value. Even here it is simpler and far more probable to look upon this character as a common ancestral one and not as an adaptive one. The success of an adaptation is a subsequent matter, and not a formative factor. Thus, Hoesch rightly concluded that the presence of these structures may be looked upon as one of the presupposed conditions under which brood parasitism in these birds can succeed.

In a semidark nest interior, young birds without any beak papillae, or as they have been termed "light bulbs," might conceivably be overlooked by the adults returning to the nest with food, especially if the latter are accustomed to placing the food only between such directive markings. Hoesch pointed out that the nestlings exhibit reflex actions, which may be correlated with these organs or at least may supplement them in getting the attention of the food-laden adults. Thus, he observed that nestling grenadiers (*Granatina*) and pytilias when about to be fed engage in very definite twisting motions of the neck and head, but do not move their wings. Other estrildines bend their necks with a downward and lateral slanting motion. The young of *Estrilda melanotis* tend to crouch down and sway the head and body in rapid fashion from side to side (Moreau in Sclater and Moreau, 1933, p. 415), while nestlings of *E. subflava* move one or sometimes both wings forward in a jerking, spasmodic gesture.

As Hoesch suggested, these peculiar food-begging movements may well have more of a selective value for the parents than do the mouth or bill markings. Viduine hosts that are not estrildines and that do not possess buccal marks or light reflectors act as if the presence or absence of these structures plays little part in their tending to parasites and their own nestlings.

Hoesch went so far as to say that he considered impossible the evolution "de novo" of such complex structures as the reflection globules through chance occurrence and the subsequent fixation through natural selection. Very likely the presence of these structures is the result of common phylogeny with the host species. Since viduines are largely parasitic on estrildines and since the two groups are closely related, most probably these characteristics are ancestral to both.

There is no need to discuss further whether parasite-host buccal similarities are due to adaptive convergence or to community of descent; I shall now briefly describe these buccal patterns. In the Estrildinae Delacour (1943, pp. 72–73) found that the waxbills have from seven marks (in *Poephila phaeton*[40]) to one mark (in *Pytilia melba*) on the palate, and even none in two species (*Pytilia phoenicoptera* and *Estrilda melanotis*). Usually there are also black marks on the tongue. The mannikins (*Amadina, Padda,* and *Lonchura*) have a special pattern involving a horseshoe-shaped dark line or series of blotches on the palate, but lack the reflection tubercles.

R. Neunzig (1929b) diagrammatically pictured the mouth patterns of several of the viduines, and it is from his paper that the following figures and descriptions derive. *Vidua macroura* and its commonest host, *Estrilda astrild* (fig. 1, no. 1) have five black spots on the pinkish roof of the mouth. The three more distal ones are larger than the two medioproximal ones. The middle one of the distal three is somewhat bigger than the lateral ones. On the floor of the mouth are two small black spots, one on either side far back near the gape, and a crescentic black mark near the front of the mandible. On the tongue are two small black spots. The pearly colored reflecting tubercles are shaped somewhat like a horseshoe.

In *Vidua fischeri* (fig. 1, no. 2), Neunzig reported a similar pattern, except that on the floor of the mouth the crescentic black mark is extended greatly posterolaterally to form a striking border to the entire lower part of the mouth. The reflection globules are said to be "cornflower" blue with a violet membrane. A similar condition is said to be found in *Granatina ianthinogaster*, the presumed favorite host species. Neunzig did not state the source of his knowledge of the mouth pattern of the nestling straw-tailed widow bird. As far as I have been able to discover, no one has yet found a nestling of this bird in a nest of any host species, and I cannot find any statement in Neunzig's account to indicate that he had any special data. I can only assume that he must have had a specimen, but in the absence of corroborative data, I think that his description needs to be verified.

In *Vidua hypocherina* Neunzig's description was based upon a specimen still partly in juvenal plumage, in the Erlanger collection in the Senckenberg Museum, a not too satisfactory "source specimen" as it may have been old enough to have lost some of its pristine pattern. Possibly his specimen may have been preserved in alcohol as a study skin would not reveal any mouth markings. Neunzig stated that in its buccal pattern, it agreed well with that found in *Estrilda erythronotos delamerei* (fig. 1, no. 3). As may be seen from the diagram, this pattern is similar to that of *E. astrild*, but lacks the posterolateral spots on the floor of the mouth, has the anteroventral crescent slightly longer, but not nearly as long as in *V. fischeri*, and has the mandibular reflection tubercle larger.

---

[40] *Fringilla phaeton* Hombron and Jacquimot, Ann. Sci. Nat. Paris, ser. 2, vol. 16, 1841 (Raffles Bay Northern Territory, Australia).

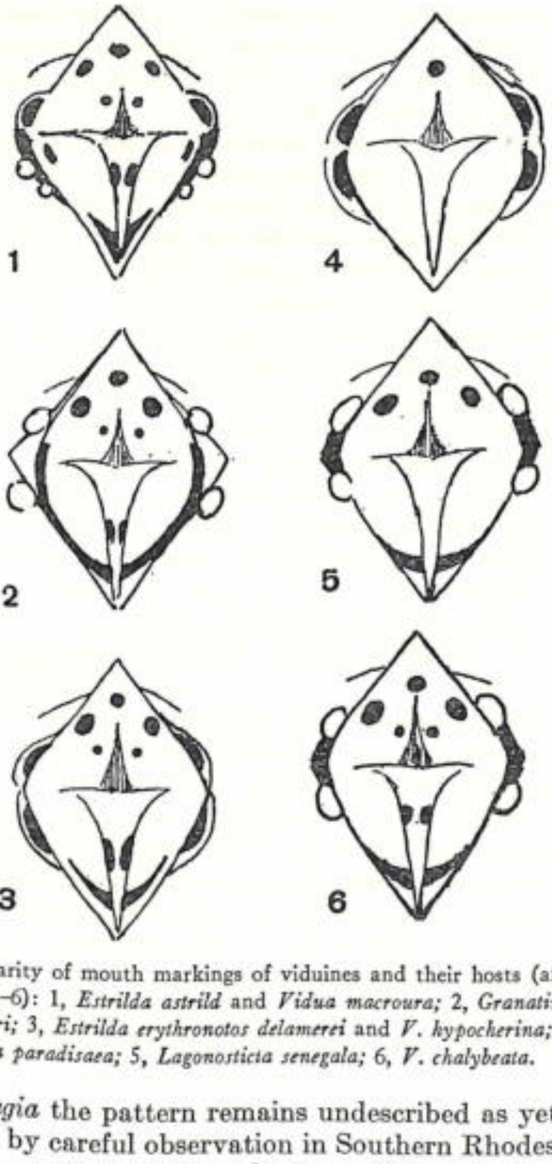


FIGURE 1.—Similarity of mouth markings of viduines and their hosts (after R. Neunzig, 1929b, figs. 1–6): 1, *Estrilda astrild* and *Vidua macroura;* 2, *Granatina ianthinogaster* and *V. fischeri;* 3, *Estrilda erythronotos delamerei* and *V. hypocherina;* 4, *Pytilia melba and Steganura paradisaea;* 5, *Lagonosticta senegala;* 6, *V. chalybeata.*

In *Vidua regia* the pattern remains undescribed as yet, a gap that could be filled by careful observation in Southern Rhodesia or Bechuanaland or the western Transvaal. Because this species is supposed to parasitize chiefly grenadier weavers (*Granatina*), the same host used by the straw-tailed widow bird, *V. fischeri*, it would be well to know if the buccal patterns of these parasites are alike.

In *Vidua chalybeata* (fig. 1, no. 6), Neunzig showed a condition similar to that in *V. hypocherina*, another indication that the latter is of all the long-tailed widow birds the nearest to the combassous. The only difference is in the size and shape of the reflection tubercles.

In this case, the correlation between the parasite and its presumed common host, *Estrilda senegala*, is not as close as in the others mentioned. The latter (fig. 1, no. 5) has no tongue spots and only the three large, anterior spots on the palate.

Chapin (in litt.) examined a nestling *Estrilda senegala* at Richard Toll, Senegal, and found that the three palatal spots showed a tendency to fuse into a band, not shown in Neunzig's figure. What material Neunzig may have used for his figure of *V. chalybeata* is not known. I am not aware that anyone had a nestling of this bird for examination at the time of his paper.

In *Steganura* and its frequent host, *Pytilia melba* (fig. 1, no. 4), the correlation is also given as close. The throat (not shown in the diagram) is said to be pale rose pink with a fairly large pale-reddish-violet spot on either side. In the middle of the palate is a single round black spot. The margins of the bill are bluish white and are said to be provided on the inner side with a small round black spot (which does not show in figure 1). In *P. afra* the black palatal spot is absent, but there is reason to think that it too serves as a host for the paradise widow bird. As has been mentioned, Hoesch (1939, p. 208) failed to find in his material from South-West Africa, the close agreement that Neunzig described in mouth markings of *Steganura* and *Pytilia*.

While we may consider the problem of adaptive convergence as one that existed more in the minds of its describers than in the material that they were studying, the reflection tubercles are so peculiar that a few words about them seem in order. They are found only in the nestlings of the Viduinae and Estrildinae, and were investigated primarily in one of the Australian estrildines, the Gouldian finch, *Poephila gouldiae*,[41] by A. G. Butler (1898), Lewek (1901), Rey (1901), and Brandes (1901), and especially by Chun (1902, 1903), and in *Erythrura* by Sarasin (1913). The structures were also reviewed by Marshall (1913), McAtee (1947) and Auber (1957). Lewek stated that these structures glow in the dark, but he was unable to determine whether this glow was due to an innate phosphorescence or was merely a concentrated reflection of light coming from external sources.

Chun's first studies, based only on examination of preserved material, suggested that the tubercles might be true luminous organs, but his later study of living nestling birds demonstrated otherwise. Birds about 6 days old, with well developed gape tubercles were placed in a photographic darkroom with only a little light entering the room, and these organs definitely glowed, much as do the eyes of

---

[41] *Amadina gouldiae* Gould, The birds of Australia, pt. 15, 1844, vol. 3, pl. 88 (Victoria River, Northern Territory, Australia).

some sphinx moths or some deep sea crustaceans. In total darkness when the room was tightly shut, however, they produced no visible gleam. On letting a little light into the room the glow was again visible. Thus, the "light organs" of the young birds appeared to be not true luminescent structures, but merely highly effective reflecting devices.

Chun then proceeded to study the microstructure of these tubercles, and found them to be essentially hemispheres filled with two layers of cellular padding, but ringed basally with black pigment, deep in the epidermis, which itself becomes relatively thin in the area of the curved edges of the tubercles. The pigment underlying the tapetallike configuration of the tubercles acts much as the amalgam or metallic backing of a mirror and enables the tubercles, which have a finely reticulated surface, as was first described by Butler, to act as a combination of a mirror and a diffraction prism.

The above description is based on one of the Australian estrildine species, *Poephila gouldiae*, and my illustration (fig. 2) is of a New Caledonian species, *Erythrura psittacea*.[42] The two agree very closely, and this agreement suggests that there is a general basic pattern common to the various estrildines. A similar study should be made of a species of *Vidua* to determine whether the structure is actually essentially the same in the two groups, or if it is to some extent a matter of superficial convergence. The former alternative certainly seems far more probable than the latter, but until such a study is made, the question remains unanswered.

NESTLING PLUMAGE: The similarity in juvenal plumage of the viduines to that of their most frequent hosts might seem to be critically significant, as the young of these parasites grow up together with those of the hosts, whereas in other parasitic birds the young of the foster parents frequently are eliminated before the development of plumage. Here again, as is true of mouth markings, community of descent is sufficient to account for the similarities in plumage. Rather than assume adaptive evolution of such resemblances, all that needs to be invoked is moderate selective reaction by the host birds. This reaction could serve to restrict the successful parasitism of individual species of *Vidua* normally to only a few species of hosts.

Hoesch (1939) pointed out that of all the supposed adaptations of the young viduines, the least satisfactory case may be made out for the mimetic resemblance of the juvenal plumage because it runs counter to the general picture of the breeding biology of birds. In most other parasitic birds, we find no such approximation to the

---

[42] *Fringilla psittacea* Gmelin, Caroli a **Linné** . . . systema naturae, ed. 13, vol. 1, 1879, p. 903 (New Caledonia).

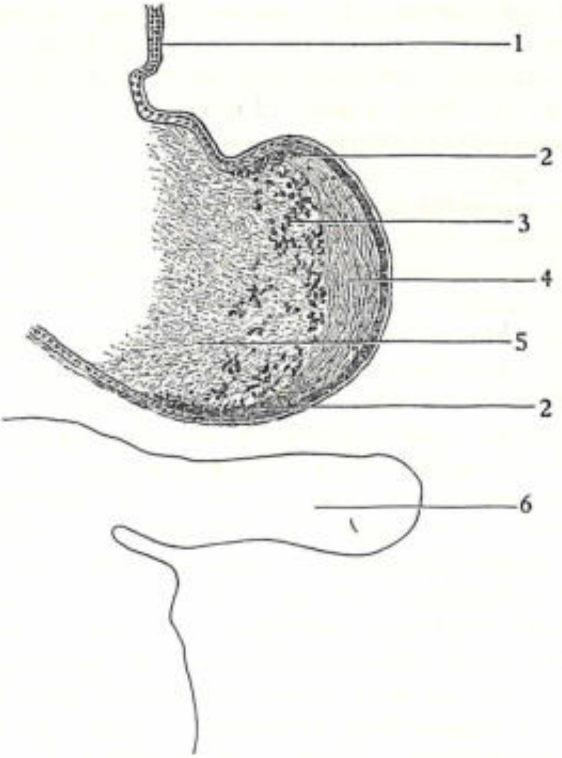


FIGURE 2.—Cross section of reflection globule of *Erythrura psittacea* (after Sarasin, 1913): 1, Epidermis thinned out, with a pelucid layer; 2, ring of densely massed pigment cells; 3, pigment cells in cellular "padding"; 4, densely massed light-refractive fibers; 5, inner cellular "padding" containing stellate pigment cells (three); 6, transverse section of mandible.

foster nest mate, even in cases where the two kinds of young grow up together. The one outstanding exception is the case of the screaming cowbird, *Molothrus rufoaxillaris*,[43] which is parasitic on the bay-winged cowbird, *Molothrus badius*.[44] It is almost impossible to distinguish the young of these species until the advent of the postjuvenal molt. Here we are dealing with two extremely closely related species, and it seems quite obvious that the close resemblance is merely a reflection of a degree of relationship, which happens to work out well in a host-parasite situation (Friedmann, 1929, p. 53). The phyletic proximity is much greater in these two cowbirds than in the viduine-estrildine picture, but the resulting nestling-plumage condition is comparable in the two.

---

[43] *Molothrus rufoaxillaris* Cassin, Proc. Acad. Nat. Sci. Philadelphia, 1866, p. 23 (Buenos Aires, Argentina).

[44] *Agelaius badius* Vieillot, Nouveau dictionnaire d'histoire naturelle, 1819, p. 535 (Paraguay and La Plata River).

The viduines and the estrildines have, on the whole, largely monochromatic, unadorned juvenal plumages, predominantly of shades of brown and gray—other colors being chiefly confined to the rump and lower back, where they are less noticeable in a nest crowded with young birds reaching up toward the feeding adult. There is little evidence that such plumage similarity could elicit effective selective responses from the hosts, especially in the semidarkness of these domed nests. Furthermore, as Hoesch pointed out about the paradise widow bird, *Steganura paradisaea*, and its common hosts of the genus *Pytilia*, the similarity in the nestling plumage is greatest on the underside of the body, which is largely hidden from view in the nest. In other words, the similarity is most pronounced on those parts of the body that are of least significance for adaptation.

I note that the juvenal plumage of *Pytilia* is more like that of *Steganura* than it is like the adult feathering of its own species. This similarity suggests that the juvenal plumage may be a phylogenetic character lost in the more highly developed adult plumage of the host—a further indication of relationship between the estrildine and the viduine stocks.

NONAGGRESSIVE BEHAVIOR OF NESTLINGS: Unlike most other avian brood parasites, such as cowbirds, cuckoos, and honey-guides, young viduine parasites exhibit no hostile or aggressive behavior toward their nest mates. They grow up together with no more jostling or individual struggling than would normally take place within a brood of the host's young. In his general discussion of aggressive behavior in vertebrate animals, Collias (1944, pp. 114–115) pointed out that in birds, the young usually remain dependent on their parents for a longer time than in reptiles, amphibians, or fishes, and that this dependence is correlated with the decrease in precocity of the young with respect to the first appearance of aggressive behavior. While this picture is not true of most brood parasites, it is true of viduines.

It is also true that egg removal by the laying parasite sometimes eases the ensuing crowding and competition, but only to the extent of obviating what would otherwise be excessive crowding. In this connection, we cannot assume such a "goal" as the original cause of the development of the egg removing habit, which merely seems to have been favored by natural selection by virtue of the result. The fact that egg removal operates in this manner bears on the general problems of clutch size and brood size.

According to Lack, in his recent (1954) book on the natural regulation of animal numbers, parasitic birds support his contention that in birds generally clutch size is limited by the amount of food available for the young. He wrote that those parasites that are much larger than their usual victims ordinarily either remove an egg of the latter when laying their own, or damage the eggs in the nest at the time. Also the young parasite may, within the first few days after hatching, by aggressive competition or actual eviction, take the place of the normal brood of the host, which one young parasite roughly equals in size and weight. In those parasitic species that are approximately the same size as their hosts, the implication is that the host should be able to raise more than just the young interloper.

Lack cited the example of the great-spotted cuckoo, *Clamator glandarius*, the young of which do not "eject the nestling corvids. However, on the argument developed here, the full clutch of the corvid should correspond to its most efficient family-size, so that the addition of even one nestling should upset the balance. It is, therefore, pleasing to find that the parent Great Spotted Cuckoo removes one egg of the host species when inserting its own."

The viduines are fairly similar in size and weight to their commonly imposed upon estrildine victims, and they act much like the great-spotted cuckoo. The evidence is still divided as to how consistently egg removal is practised by the laying viduine hen, but that it is frequently done is clear. The case is not, however, as definite as Lack's theory made it out to be. Certainly other parasites, which are hardly larger than their frequently used fosterers, such as the honey-guides (parasitic on barbets of the genera *Lybius* and *Pogoniulus* and the smaller bee eaters of the genus *Melittophagus*), and the didric cuckoo (parasitic on various species of *Ploceus*) usually replace the entire brood of the host with one individual of their own kind.

Morris (1957, p. 198) found that the parental behavior of the estrildines is fairly uniform, there being no marked differences in the various species that he studied. The incubation period is about 2 weeks and is followed by a nestling period of about equal duration, which, in turn, is followed by a period of fledgling dependence on the parents lasting as much as 4 weeks. While we still lack accurate data on these periods for the viduines, it would be strange indeed if they differed greatly from their favored hosts in these respects.

Antiquity

The data pertaining to the age of the brood parasitic habit in the weavers has led some writers to a conclusion diametrically opposed to the one presented below. It is only proper to make this point clear at the outset as it shows either that the data are inconclusive as evidence, or that interpretation may influence the appraisal of the known facts.

While it is generally unwise to carry over evidence and argument from one group of birds and apply them to another, it is necessary to compare the various groups of parasitic birds. Brood parasitism is newer, relatively more recently acquired in the weavers than in the cuckoos and the honey-guides, and possibly even newer than in the cowbirds. The one known parasitic duck is still too imperfectly studied to enable us to estimate the antiquity of its brood parasitism here, although what is known of it gives the impression of relative newness.

The absence of any structures or habits directly inimical to the young of the host, such as we find in the cuckoos and honey-guides, is an indication of the relative recency of the parasitic mode of breeding in the weavers. Furthermore, in captivity one of the most primitive of the parasitic viduines, the black-winged combassou, may occasionally exhibit considerable "attentive behavior" (caring for young) although at other times it shows the usual parasitical behavior, which alone has been recorded for it in the wild state. To a lesser extent, bits of similar attentive behavior have also been recorded for individuals of two of the more advanced species, the pin-tailed and the paradise widow birds, living in similar conditions of captivity. These data suggest a relative ease of regression into a forsaken ancestral behavior pattern, which, in turn, indicates relative newness of the parasitic mode. Furthermore, that the nestlings of weavers grow up together with, but not at the expense of, the young of the host species suggests less adaptation for a parasitic existence than in the cowbirds. The cowbirds have a slightly shorter incubation period and a somewhat faster growth rate than many of their foster nest mates, a large percentage of which do not survive the nestling stage. This relatively less stringently "adapted" parasitism of the weavers presupposes a shorter time for its evolution than the more host-aggressive features of the cowbirds' reproductive pattern seems to presuppose.

In arriving at this estimate of the recency of brood parasitism in the weavers, I am discounting the argument advanced by R. Neunzig (1929b), who assumed that the similarity in the nestling plumage and especially the mouth markings of the nestling viduines and of their chief estrildine hosts was an adaptive resemblance developed in the evolution of the parasitic habit. This concept was accepted by Southern (1954, p. 229), who considered the parasitic weavers as the most specialized of all avian brood parasites, "for in these each parasitic species has its own host species to which it is permanently attached and a very complicated form of mimicry has arisen involving the recognition pattern of the chick's mouth markings." If this view were accepted it would presuppose a much greater antiquity for the habit, but, as was indicated in the previous section, these similarities are far more probably due to community of descent than to subsequent adaptive convergence. Furthermore, we now know that the extreme host specificity assumed by Neunzig and accepted by Southern is not correct.

While the lack of specialized adaptive features makes the parasitic habit appear less highly developed here than in other avian groups, it may be questioned whether any further adaptation would add to the success of the parasitic species. In a conversational discussion on parasitism in social insects, the late W. M. Wheeler once suggested that in one respect the most perfect parasites are those that do not kill off their fosterers, as in this way they practice parasitism without decreasing the supply of their normal hosts. They live successfully in the present without in the least mortgaging the future. To put the matter in a different way, we may say that in contrast to the other groups of avian brood parasites, the parasitic weavers possess no known special structures, habits, or functional gradients that give them particular advantages over their nest mates, but this condition does not mean that they are not adequately equipped for competing with them on equal terms. The parasitic habit here often involves no discomfort to the hosts other than the need for gathering more food to nourish their enlarged broods of nestlings.

The viduines are parasitic chiefly on not too distantly related estrildine species, of essentially similar body and egg size and food requirements, and of supposedly comparable incubation and nestling periods. In this respect they resemble the most primitive of the parasitic cowbirds, *Molothrus rufoaxillaris*, which is parasitic chiefly on its nonparasitic ancestral relative *Molothrus badius* (Friedmann, 1929). The cuckoo finch, *Anomalospiza imberbis*, which is parasitic chiefly on grass warblers of the genus *Cisticola*, has, it is true, gone farther afield taxonomically in its host fixation, but without encountering any essential differences in adaptive requirements, as far as may be learned from present data and understanding.

Contributive Factors

Precise causes of brood parasitism are not definable in the sense of pin-pointing critical spots of antecedent ethological variations or weaknesses; however, the problem itself requires no great stretch of the imagination for a superficial solution. By superficial solution, I mean a logical, historical statement couched in terms of the observable habits of the parasites and of their relatives.

That the cuckoo finch is more nearly allied to the ploceine weavers and that the viduines are related to the estrildines clearly indicate that we have two separate, independent but parallel developments of brood parasitism. Thus, brood parasitism has happened twice in the history of the weavers. Apparently, antecedent variations in breeding habits within the group were such that at more than one point occurred the necessary combination of loss of nest building and reduction of broodiness. Since loss of nest building, as expressed by habitual use of adopted, deserted, or usurped nests built by other birds, frequently occurs among ancestors of both parasitic lines, probably this state of affairs was the underlying one, and the decrease or total loss of broodiness was superimposed on it. I have noted evidence suggestive of this condition in individual cases of several species that still ordinarily take care of their eggs. Fortunately, we can complement these data with others pertaining to the occasional occurrence of bits of atavistic selfbreeding behavior in the most primitive of the parasitic viduines, the combassous, and also in two of the more advanced viduine species, the pin-tailed and paradise widow birds, even if only under the artificial conditions of aviary living. The data pertaining to the ethological variations in the nature of the ancestral stock of selfbreeding weavers show that there was a fertile ground for the development of brood parasitism within the group. The atavistic glimpses afforded by the most primitive of the parasites reveals the past from which they developed.

An essentially comparable situation in parasitic invertebrates was reported by Baer (1951, p. 211), who found that many organisms give evidence of having been "predisposed to becoming parasitic, and that they were preadjusted to a different mode of life that has enabled them to establish themselves successfully in a new biological niche."

The diverse antecedent ethological variations that we have reviewed constitute essentially some grade or degree of preadaptation toward brood parasitism. In this connection I note that in his study of recent views of evolutionary processes, Carter (1951, p. 275) summed up the matter of preadaptation as follows: "In its most general sense preadaptation implies merely the possession of characters suitable for use in some situation, and the possession of these characters before the situation arises, before there is any opportunity for the use to which they are preadapted. In all adaptation the animal must to some extent be preadapted in this sense; it must always possess characters that can be modified to give the adapted character."

In his general discussion of avian brood parasitism, Miller (1946, p. 246) came to generally similar conclusions. "Resort to parasitism under several sets of circumstances has not presented great evolutionary difficulties, although its appearance seemingly has depended on the presence of some essential preadaptations that chanced to be available. Having once taken the decisive step and become dependent, the parasitic species may have added refinements, such as rapid delivery of eggs, killing of competing young, and mimicry of egg pattern. In these respects cuckoos are vastly greater specialists than cowbirds, but they probably have been practicing parasitism for a much longer time." To this statement I add that the weavers are as new if not newer than the cowbirds as brood parasites.

That it is not possible to point with any certainty to discrete, immediate causes need not, in itself, be disturbing. Such information would indeed be most welcome, but the improbability of obtaining it is also significant. Brood parasitism is not necessarily an advantageous mode of reproduction toward which, as an ultimate goal, we might expect to find traces of antecedent trends in varying stages of development.

To make this point clear, I must digress briefly. When we examine the life history of a parasitic bird, we find that it seems to flourish at the expense of its hosts. In other words, it appears to have a relatively "easier" or more advantageous way of life. These advantages we as humans read into nature and are not actually present in it. No evidence supports the view that self breeding makes life more difficult for other birds and that any tendency to "get away" from these portions of their behavior would necessarily become an evolutionary asset. Brood parasitism is merely another way of breeding. It has been established in a number of groups of birds but this fact does not imply that it is a better or more efficient way.

In their recent book Rothschild and Clay (1957, p. 38) discussed the insecurity attendant on a parasitic existence, and pointed out that egg or larval mortality is vastly higher in most parasites than in their hosts. While this fact is true especially of arthropod and nemathelminth parasites, these authors extended their generalization to include even avian brood parasites like the European cuckoo, which they claimed lays four or five times as many eggs as do its hosts. This generalization is only partially applicable to avian brood parasites, e.g., the great egg mortality in one of the South American parasitic cowbirds, *Molothrus bonariensis*.[45]

In parasitic birds generally, such "advantages" as have been read into their lives by their describers are not, in themselves, biological goals toward which we may expect directive evolution, more successfully attained in one group or species and less completely in another. These "advantages" are merely the particular features of a habit that have given it survival value. Their status as "advantageous" elements is something determined by the operation of natural selection after the advent, and not something toward which the particular species involved was "striving." Thus, if "striving" were present, it would be expected to leave observable traces, and we might well be

---

[45] *Tanagra bonariensis* Gmelin, Caroli a Linné . . . systema naturae, ed. 13, vol. 2, 1789, p. 898 (Buenos Aires).

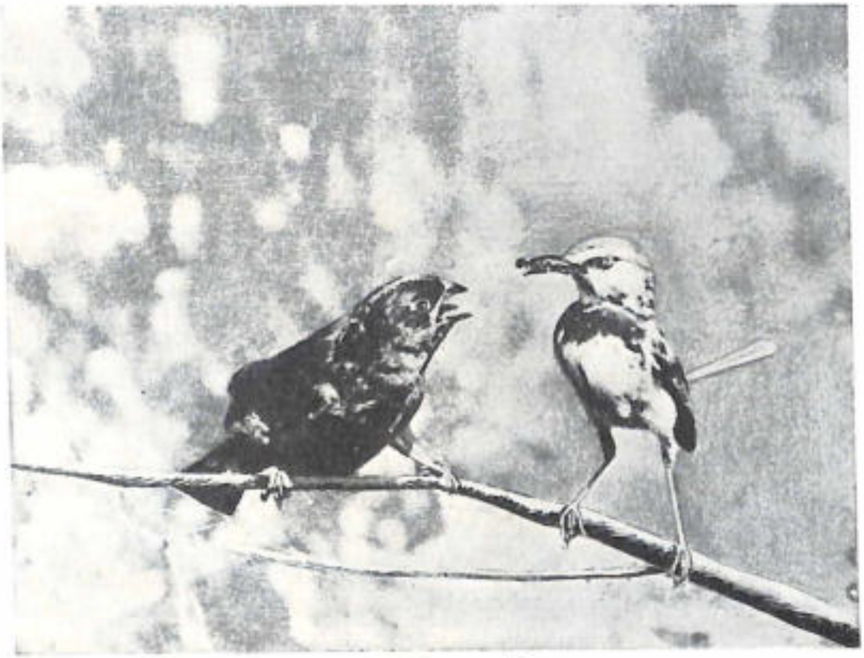


PLATE 5. CUCKOO FINCH

Upper: Fledgling cuckoo finch from nest of grass warbler, *Cisticola cisticola victoria*, Kisumu, Kenya, July 1912; photo by V. G. L. van Someren. Lower: Fledgling being fed by black-chested longtail, *Prinia flavicans*, Transvaal; photo by A. Roberts, 1917.

PLATE 6. FIRE FINCH, BLACK-WINGED COMBASSOU, AND ORANGE-BREASTED WAXBILL

Upper: Nestling fire finch, *Estrilda senegala* (left), and black-winged combassou (right), from nest of fire finch, Richard Toll, Senegal, November 1955; photo by G. Morel. Lower: Orange-breasted waxbill, *Estrilda subflava*, at an adopted and relined nest of a red bishop bird, *Euplectes orix*—a step toward the parasitic habit, Matopos Mountains, Southern Rhodesia; photo by D. C. H. Plowes.

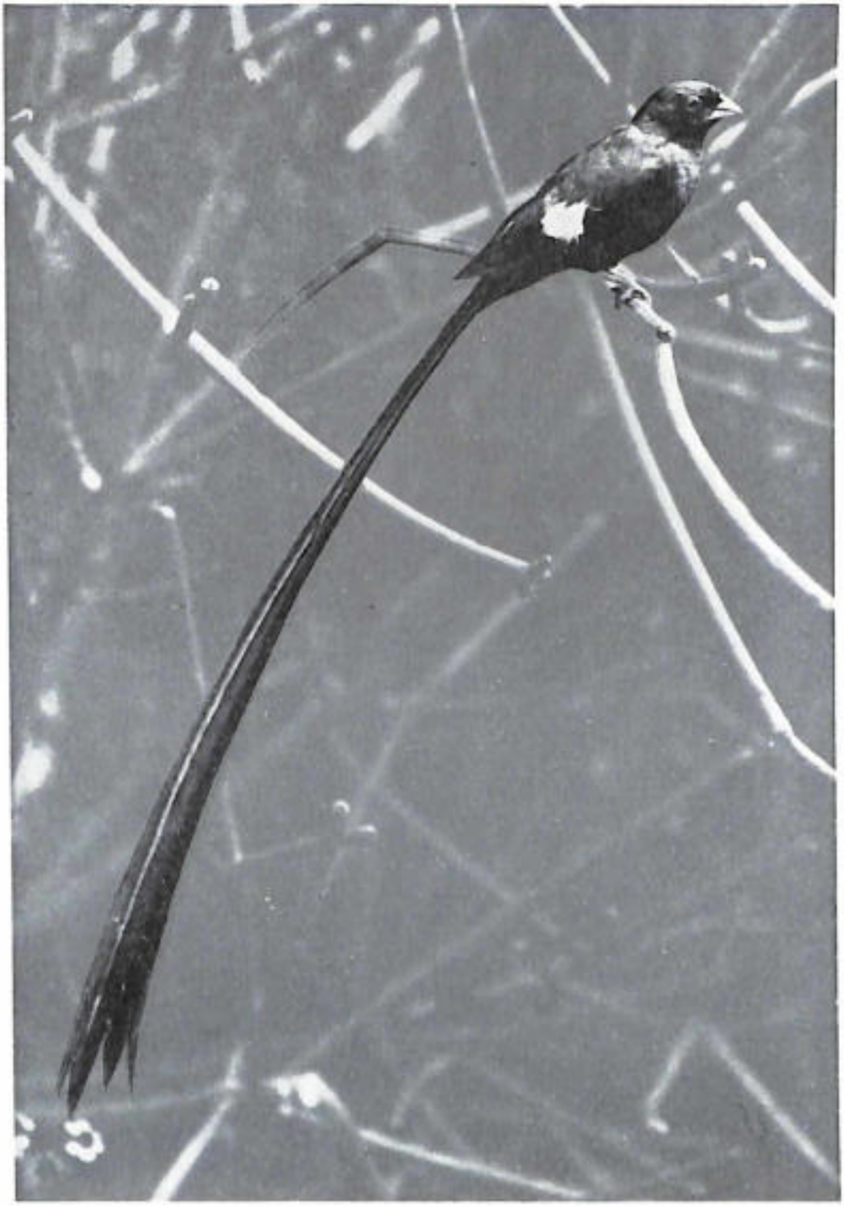


PLATE 7. BLUE WIDOW BIRD

Male blue widow bird; photo by V. G. L. van Someren (1956, p. 504). courtesy of Chicago Natural History Museum.

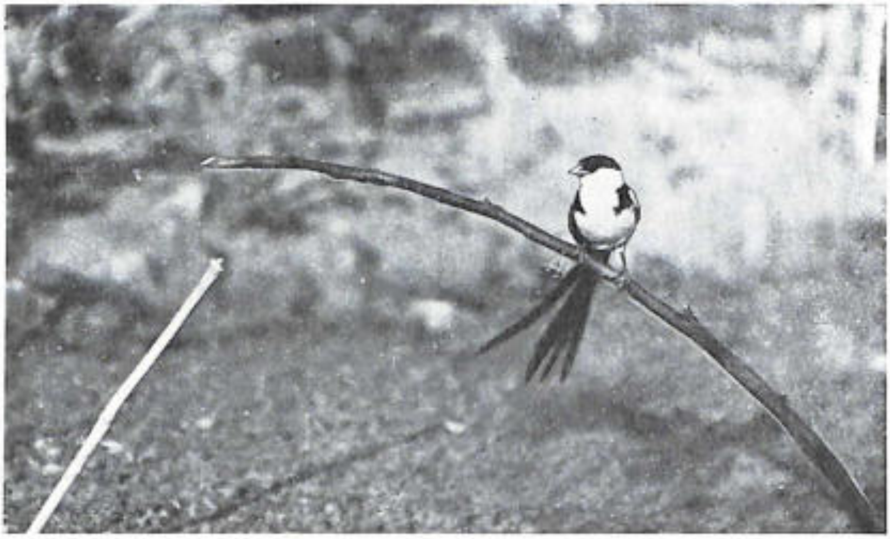


PLATE 8. PIN-TAILED WIDOW BIRD

Upper: Photo by V. G. L. van Someren (1956, p. 502), Kenya, courtesy of Chicago Natural History Museum. Lower: Photo by Chapin (1954, pl. 25, fig. 1), courtesy American Museum of Natural History.

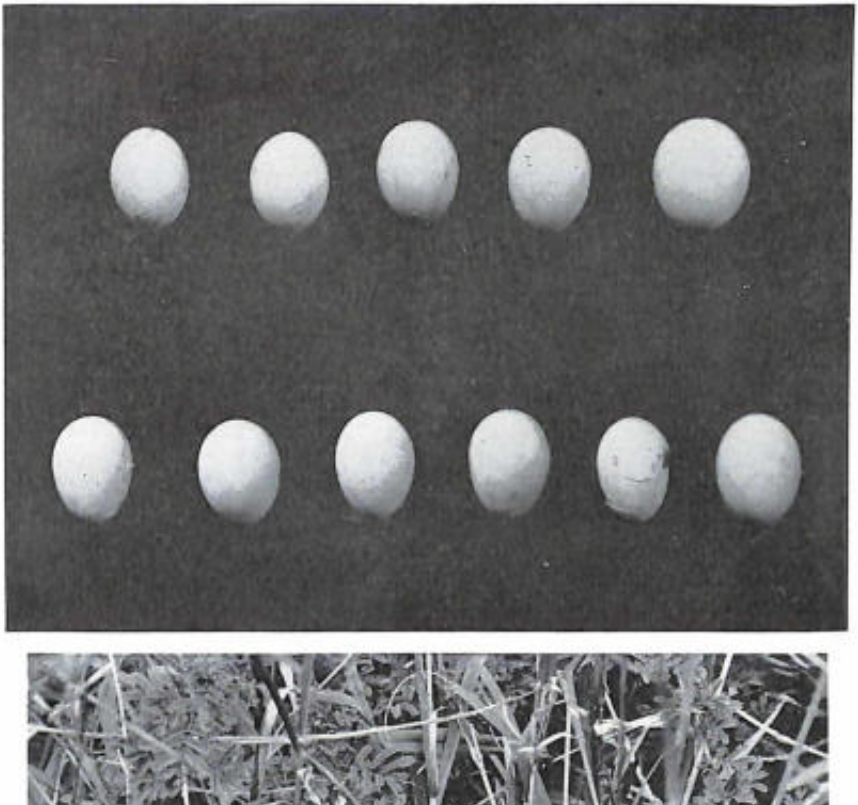


PLATE 9. EGGS OF PIN-TAILED AND SHAFT-TAILED WIDOW BIRD

Upper: (Top) Set of four eggs of the common waxbill, *Estrilda astrild*, with one of the pin-tailed widow bird; (bottom) set of five eggs of the bronze mannikin, *Spermestes cucullatus*, with one of the pin-tailed widow bird; all in U.S. National Museum. Lower: Nest of longtail, *Prinia flavicans*, with three eggs of its own and one of the shaft-tailed widow bird, Moordrift, Transvaal, January 1, 1925; photo by author.

PLATE 10. SHAFT-TAILED AND PARADISE WIDOW BIRDS

Upper: Male shaft-tailed widow bird in partial molt, April 1954. Lower: Male paradise widow bird in molt. Both photos by D. C. H. Plowes at Nyamandhlovu, Southern Rhodesia.

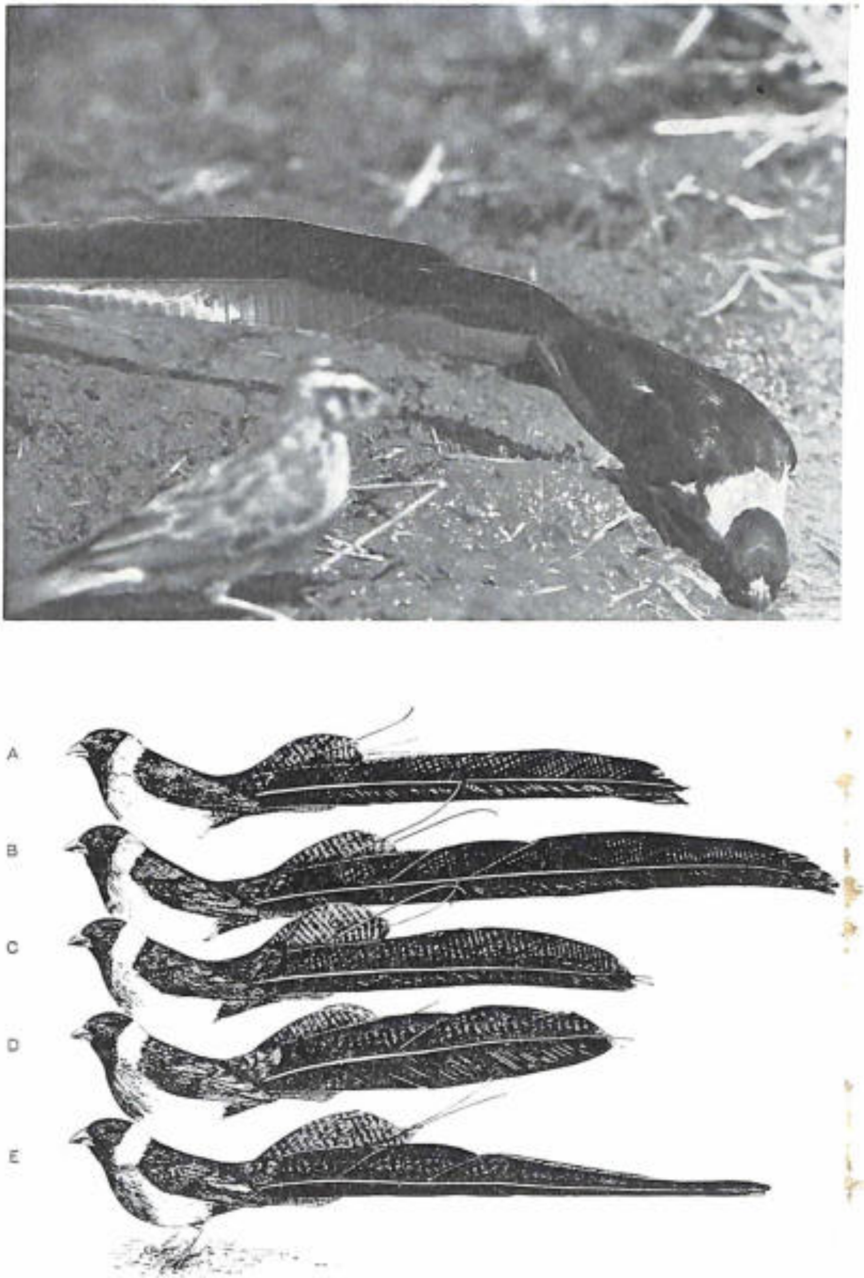


PLATE 11. PARADISE WIDOW BIRD

Upper: Male and female feeding on ground, photo by D. C. H. Plowes, at Nyamandhlovu, Southern Rhodesia. Lower: Subspecific variations in tail form (after Chapin, 1922): A, *Steganura paradisaea aucupum;* B, *S. p. interjecta;* C, *S. p. orientalis;* D, *S. p. obtusa;* E, *S. p. paradisaea.*

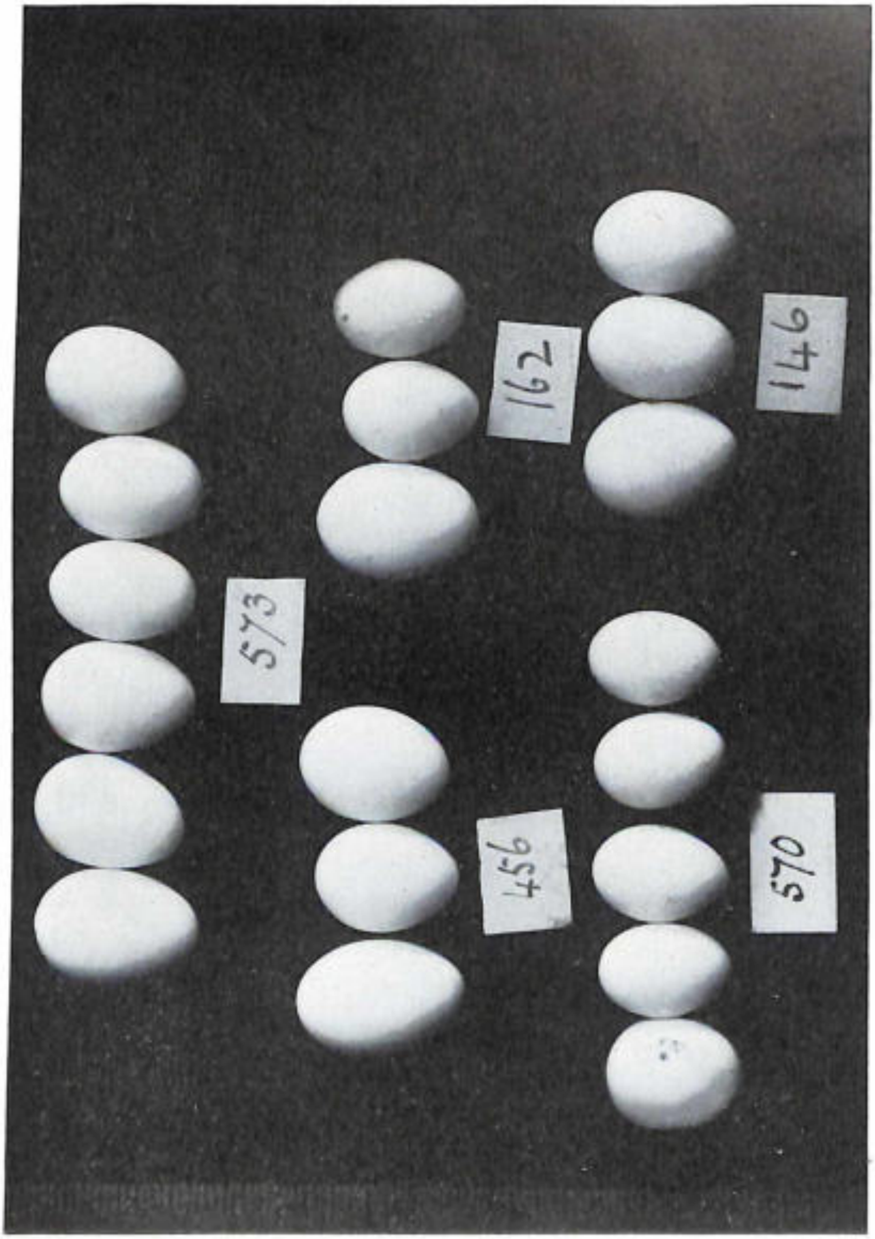


PLATE 12. EGGS

Set 573: Two eggs of *Pytilia afra* with four of *Steganura* (three at left and one at right end), Nyambadwe, Nyasaland, June 25. Set 456: Two eggs of *Pytilia afra* with one of *Steganura* (at left), Blantyre, Nyasaland, June 30. Set 146: Two eggs of *Pytilia* sp. with one of *Steganura* (at left), Mpindi, Nyasaland, February 13. Set 570: Four eggs of *Pytilia* sp. with one attributed to a combassou (at left), Nyambadwe, Nyasaland, April 2. Set 162: Two eggs of *Pytilia afra* with one of *Steganura* (at left). Photo by Belcher (1930, pl. 3).

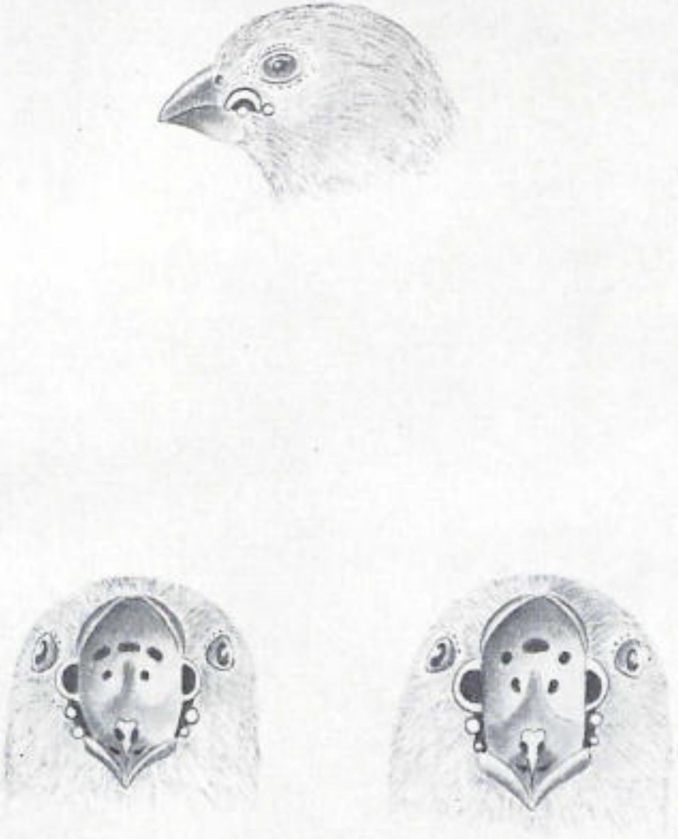


PLATE 13. MOUTH MARKINGS

Mouth markings of a nestling pin-tailed widow bird and of its chief host, the common waxbill, *Estrilda astrild*, after a field sketch by Chapin.

PLATE 14. USUAL HOVERING COURTSHIP FLIGHT OF PIN-TAILED WIDOW BIRD

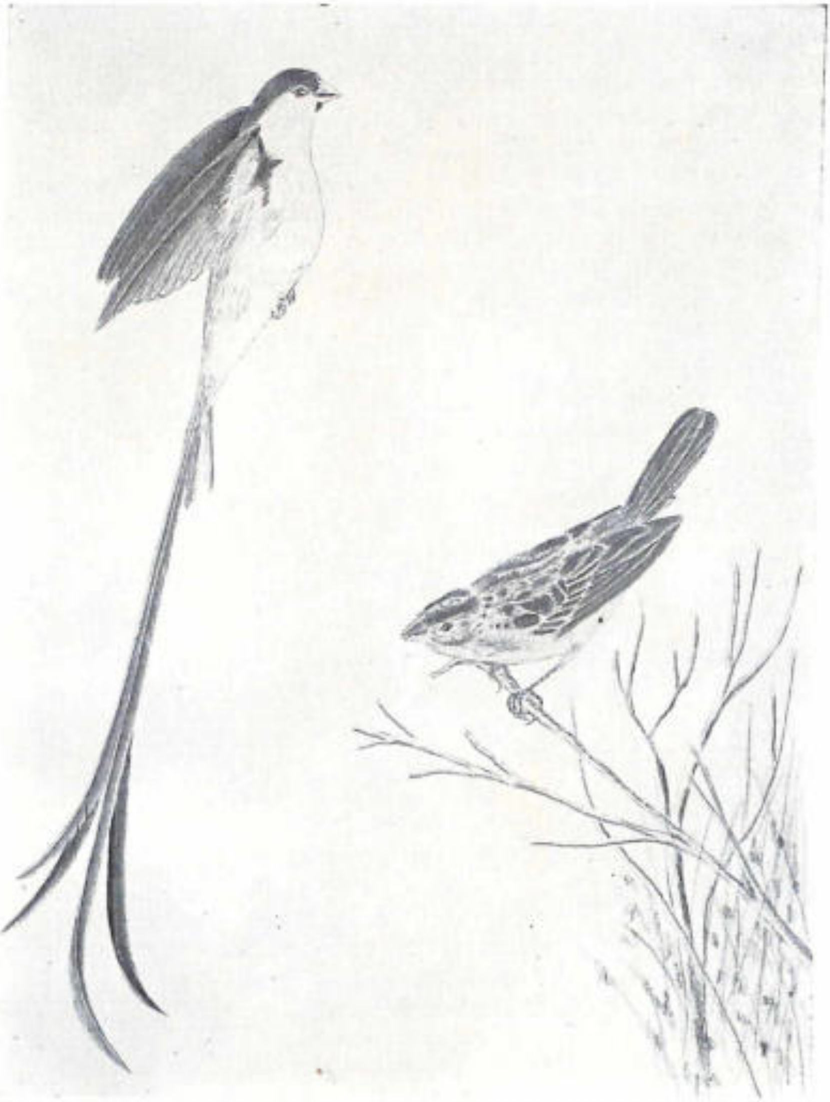


PLATE 15. VERTICAL HOVERING COURTSHIP FLIGHT OF PIN-TAILED WIDOW BIRD

PLATE 16. COURTSHIP FLIGHT OF PARADISE WIDOW BIRD

disturbed at not being able to find them. The absence of "striving" can hardly be expected to leave ethological "footprints" for the present day investigator to uncover. All that we may reasonably hope for and that we have now found are the antecedent variations that could conceivably produce a situation conducive to the development of brood parasitism, and some glimpses of atavistic behavior in the species that have become parasitic. While there is great need for fuller information on every one of the parasitic species of weaverbirds, it seems unlikely that a more complete, more detailed picture will yield presently unsuspected clues or indices to the origin of their mode of breeding.

The lack of intermediate stages of parasitism may be explained by the simple fact that such intermediates would not be able to survive as they would be unable to reproduce effectively. In a behavioral way this observation corresponds to the frequently noted, but less readily explained, discontinuities in structural evolution. As Nissen (1951, p. 347) remarked, the evolutionary evidence often is exasperatingly fragmentary at the critical points of transition from one entity to another. Yet these discontinuities do not invalidate the concepts involved. As has already been intimated in the foregoing discussion, the evidence enables us to conclude only that in the weavers the parasitic habit arose among stocks which already had the habit of breeding in old nests of other birds, and among which occasional loss in incubation broodiness occurred.

A further indication that loss of nest building and occasional loss of incubation broodiness occurred in the phylogenetic source stock of the viduines may be sensed from the fact that the courtship patterns of these birds have, as yet, revealed no suggestion of ritualized derivatives of nest-building actions. Morris (1954,a,b; 1958) found such derivatives in a large number of estrildine species, especially grass-finches and mannikins. He found that a considerable number of their actions involved in sexual displays appeared to derive from nest-building motions, such as straw holding, bowing with a straw in the bill, looping straw, and movements suggestive of cavity scooping. The lack of any such behavior in the viduines is suggestive of an absence of nest-building activities in their direct ancestry.

The preceding remarks outline a superficial solution of the problem of brood parasitism in the weaver birds. The deeper, biological explanation is one that cannot be made with present information. Endocrine imbalance or change, may have brought about the loss of broodiness and ushered in the parasitic mode of reproduction. Possibly the endocrine change was brought about genetically rather than physiologically, but this possibility can only be determined by investigating the latter possibility. The postulated endocrine change need not have been attuned directly to any external factors, either of obvious selective value or not. Aside from the loss of broodiness, the fact that the viduines appear not to breed until their second year, whereas many small birds, including their estrildine relatives, do so in their first year, further suggests an endocrine "lag."

Endocrine changes seem in light of current knowledge to be the most promising approach to the discovery of the underlying mechanism involved in the establishment of conditions that led to the origin of brood parasitism. This approach does not reveal the other factors that may have had their effect in making possible, in an evoluntionary sense, the loss of selfbreeding to survive and to develop as brood parasitism, but the approach seems to be a necessary first step for further investigation, even if it may not be as direct and as simple as one might wish. Beach (1948, p. 77) recently summarized his conclusions by saying that apparently "seasonal correlation of nest building, egg laying, and parental responses with glandular hypertrophy, in many wild birds is in accordance with the thesis that such behavior is affected by endocrine products; but it must be admitted that observations of this type are of little assistance in any attempt to define the responsible hormones." Even in cases where gonadal hormones appear to stimulate parental responses, it is not yet possible to indicate the accuracy of the conclusions, especially since in other cases it was equally apparent that broodiness can be delayed or even inhibited by substances such as androgen.

With current information as a guide, the factors underlying the development of brood parasitism will probably be found to fall in line with Zuckerman's general statement (1955, p. 249) that evolution or change in the endocrine picture often consists of changes of hormonal emphasis rather than of kind, or of the development of a new mode of tissue response to hormones already in existence. Studies of the endocrine situation in brood parasites are being planned, but what results will come of them cannot be previsioned here.

The Species of Parasitic Weaverbirds

Cuckoo Finch: Genus *Anomalospiza*

Anomalospiza imberbis (Cabanis)[46]

PLATES 3, 5

The cuckoo finch is one of the two known isolated brood parasites, i.e., a single parasitic species with no close relatives with similar habits. The other one is the black-headed duck (*Heteronetta atricapilla*[47]) of southern South America.

In the following account all the data are brought together relating to the biology of this well-named, anomalous weaver finch—all the published information together with a very considerable number of unrecorded observations kindly sent to me by the men who made them, the data on museum specimen labels, and the little that I was able to learn of this bird in the field. My field acquaintance with it was limited to a few hours near Nairobi, Kenya, in July 1925, but the birds had finished breeding and had assembled in a sizable flock in a little swamp.

DISTRIBUTION

The cuckoo finch occurs from the Transvaal (Woodbush, Pretoria, Barberton) and Damaraland (?), north through Mozambique (Ile), Southern Rhodesia (near Salisbury, near Marandellas, near Bulawayo), Northern Rhodesia (Ndola, Balovale), Nyasaland (Dowa, Dedza, Nchisi, Mzimba), Angola (Chimporo), southern and eastern Belgian Congo (Katanga, Kasai, Kivu, and Uelle District, north at least to Lake Edward), Tanganyika, including Zanzibar and Pemba Islands (Kilosa, near Mwanza, Ngomeni), Kenya (Mombasa, Thika, Nairobi, Kisumu, Elgon, Moroto, Turkwel, Fort Hall, Ugaia), Uganda (Lango), to the southern Sudan (Kajo Kaji, Lado area), and Ethiopia (where it is known as yet from only two areas, Jiomma in the southwestern part of the country and the Lake Tana area in the northwest), and also west to Cameroons (Tibati), French Guinea (vicinity of the Nimba Mountains), and Sierra Leone (Bo).

---

[46] *Crithagra imberbis* Cabanis, Journ. Ornith., vol. 16, 1868, p. 412, (East Africa, probably on the coast opposite Zanzibar).

[47] *Anas atricapilla* Merrem, in Ersch and Gruber, Allgemeine Encyclopedia, vol. 35, 1841, p. 26 (Buenos Aires).

Throughout its range, it is a bird of open savanna grasslands, both fairly arid and moist. Its altitudinal range is from sea-level up to between 7,000 and 9,000 feet (in northwestern Ethiopia). The cuckoo finch has been generally regarded as scarce in most parts of its range; however, it is often overlooked because of its general superficial similarity to some of the yellowish finches of the genus *Serinus*. The cuckoo finch is not scarce where it occurs in parts of Kenya, Pemba, southern Sudan, and Northern Rhodesia, as sizable flocks have been reported in each of these areas.

No less than seven races have been proposed, but most of them are based on seasonal plumages or on very slight characters. The most recent revision is that of Chapin (1954, pp. 407–410), who recognized three of these subspecies. I would go a little further and recognize only two: The nominate race of southern and eastern Africa from the Transvaal and Damaraland, north to Ethiopia, and west to the eastern savannas of the Belgian Congo; and the race *A.i. butleri*[48] that occurs from southern Sudan (upper Bahr-el-Jebel) and northeastern Belgian Congo (Faradje), and west to the highlands of the northern part of the Cameroons (Tibati) and to Sierra Leone. The race recognized by Chapin but not by me is *A.i. macmillani* of Ethiopia. Of this form Chapin was doubtful himself, as he wrote that it differs very little from typical *imberbis* "except that the beak of the males seems lighter in color, and the female may perhaps be a little darker above. Wings of males measure 69–72 mm. [as against 66–73 mm. in *imberbis*]. If valid, it is supposedly restricted to Abyssinia."

All the life history data on this species, to date, refer to the nominate race.

BREEDING SEASON

Although local seasonal movements, or at least seasonal absences, of the birds have been recorded from Southern Rhodesia, few data suggest that the cuckoo finch is actually migratory. Neuby-Varty informed me that it occurs locally only in the summer on his ranch near Marandellas. Irwin (1952, p. 114) calls it a "wet season visitor to Salisbury area. . . . In 1950 it was first seen on October 26 and in 1951 on November 5." Smithers, Irwin, and Paterson (1957, p. 152) considered the cuckoo finch as apparently migratory in Mashonaland, it having been recorded there from September to March and once in June. Although there may be other areas where the birds are present for only part of the year, the species probably breeds throughout

---

[48] *Anomalospiza butleri* Sclater and Mackworth-Praed, Ibis, ser. 10, vol. 6, 1918, p. 460 (Kajo-Kaji, near southern border of Sudan).

most of its geographic range. The following data give our present information as to the time of breeding:

ETHIOPIA: Northwestern part near Lake Tana, nestlings August to November.

KENYA: Nairobi, eggs May and June. Kisumu, fledglings June and July. Fort Hall, male in breeding condition, March 30.

TANGANYIKA: Nestlings in May. Ngomani, fledgling in August.

PEMBA ISLAND: Breeding September to January.

BELGIAN CONGO: Breeds during the rains when the warblers are nesting. Near Lake Edward May and June. Southeast of Lake Moero, at Kasengo, January.

MOZAMBIQUE: Quilimane Province, February 4–12, males collected with much enlarged testes.

NORTHERN RHODESIA: Mporokoso, recently fledged young collected May 29 (Benson, 1956, p. 45).

SOUTHERN RHODESIA: Umvuma, near Marandellas, and 18 miles from Salisbury, eggs and young late December to March 5.

TRANSVAAL: Pretoria, December 17 to February 3, fledglings.

SONGS AND CALLS

The only note I ever heard from this species was a sparrow-like double *cheet-cheet* note repeated several times as the birds flew into the sedges in a little swamp near Nairobi. This note is apparently the same as the one described by V. G. L. van Someren (1918, pp. 282–283) in Kenya and by Benson (1941, p. 41) in Nyasaland. In Mozambique, J. Vincent (1936, pp. 102–103) recorded what seems to be a slight variant given by a bird perched in a tree top, a nasal chirp, *choop-ee-choo*, much like the chirp of a house sparrow in quality. In Mashonaland, Irwin (1952, p. 114) wrote that the bird gives "a tittering call as it flies and often breaks into a garbled warble especially when coming to rest. The latter call appears to be associated with its coming into breeding condition and probably constitutes its song." In Pemba Pakenham (1939, p. 553) found the song of the male to be a squeaky *tsileu-tsileu-tsileu*, given with an upward stretching of the neck, and the call note to be a thin squeaky monosyllable, usually uttered while in flight.

COURTSHIP, TERRITORIAL BEHAVIOR, AND MATING

No one has described any courtship behavior in wild birds of this species. My own field experience with it was after the breeding season, and so I saw nothing akin to courtship. Neuby-Varty informed me (in litt., December 28, 1950) that in his many years of acquaintance with the cuckoo finch, he has never seen any indication of courtship display; however, according to Chapin (1954, pp. 407–410), a male cuckoo finch in captivity was noted displaying by fanning the wings and uttering "sizzling" notes. Unfortunately we have no indication whether a female was present or not, or how persistent and definite this behavior may have been. The term "sizzling" is not too informative.

The mating and territorial behavior of these finches are still inadequately understood, and the descriptive data do not all point to the same picture. Thus, in Mozambique, J. Vincent (1936, pp. 102–103) found a flock of about 30 cuckoo finches, all of which looked alike. He collected three of them and found all to be males in full breeding condition, like birds that one would expect to find established on individual breeding territories. Similar observations have come to me from Rhodesia (C. J. Vernon, in litt.).

In 1950 Neuby-Varty wrote me of his experience with these finches in Rhodesia. His experience led him to conclude that they did not form pairs, as he saw them in groups of three, four, or five individuals all through the breeding season, and once he found one male with several females. Since these birds were not collected, however, some of the "females" may actually have been immature birds of either sex.

More recently (in litt., June 24, 1956), Neuby-Varty informed me that he found cuckoo finches apparently paired off, with marked territorial behavior and apparent monogamy. He found one pair (A) in a stretch of vlei (grassland) along the river on his ranch; further up the same river was a second pair (B); and about 1½ miles away he discovered a third pair (C) in a vlei on the boundary of his land. He carefully combed other open spaces on his property but found no others. They seemed to confine themselves to a limited stretch of country and definitely to prefer country with wet vleis and shortish grass. He found that they were very pugnacious and that there was only one pair in an area; they would not tolerate any invasion from nearby birds. One day he tried to drive pair A into pair B's territory by slowly walking up the river. They flew nearly up to B, but B chased them down river again. He then tried to get pair B into A's territory with the same result. They could go just so far when the other pair would intercept them and drive them back. They seemed to range over a large bit of country, and so he came to the conclusion that they require an enormous amount of territory. He estimated that A had about 350 acres; B slightly less, about 300; C had about the same as B. However, I think that this excessive spacing is a reflection of low numerical numbers rather than an expression of actual need. In response to further questioning, Neuby-Varty informed me of pair A that the male and female were very easily distinguishable, and that their resting spot of dried reeds was about 30 yards from a road traversed by him every day except Sunday. He used to see this same pair every day.

In keeping with these observations of Neuby-Varty, the fact should also be noted that other writers have commented on the pugnacious disposition of the cuckoo finch. Thus, V. G. L. van Someren (1918, pp. 282–283) had to remove them from an aviary containing other birds because of their quarrelsomeness and general pugnacity.

Pakenham's observations in Pemba (1939, p. 553) bear on the question of individual territoriality. He found a grass warbler's nest with two young cuckoo finches in it, one much more developed than the other. As he stated, the "disparity in age of these two suggests different parentage, and therefore lack of definition (if not total absence) of the system of 'territory' among the adult birds, a state of affairs I can well believe from the numbers I encountered within the comparatively small area of ground where the Cisticolas were nesting." The situation in Pemba was apparently quite different from that on Neuby-Varty's Rhodesian ranch.

Eggs and Egg Laying

The few reliably identified eggs of the cuckoo finch show some variation in their appearance. Thus, one egg found in a nest of *Cisticola juncidis* Neuby-Varty (1950, p. 37) described as having a white shell color, with small spots of pale lavender and dark reddish brown scattered over the entire shell, but more densely spotted at the thick pole, and measuring 18 by 12.75 mm., the egg essentially rather long and pointed. Two fairly similar eggs taken from other nests of the same host species A. W. Vincent (1949, p. 663) described as white, tinged with blue, thinly speckled with fine dots and a few larger, but still small, spots of chocolate brown and shades of light and dark-violet gray, and measuring 17.3 by 13 and 17.1 by 13 mm. On the other hand, Payne (1944, p. 235) described the first known specimen of this egg, from a nest of a *Prinia subflava*, as "pale dull pinkish, clouded at the thick end with faint purplish, with a few reddish brown blotches and rather more spots of brownish red, becoming fewer in the middle and only appearing as tiny markings at the thin end of the egg, and measuring 17×12.5 mm." Recently Neuby-Varty (in litt., June 24, 1956) described another egg from a nest of the desert grass warbler, *Cisticola aridula*, as very light pale blue with small pinpoint spots of russet scattered all over but concentrated around the thick pole so as to form a well defined band. The egg measured 17.5 by 13 mm.

It follows that the eggs are either whitish, pink, or pale bluish, variably flecked or speckled with reddish brown and violet gray, with usually more of these markings at the large pole than at the small one. The eggs vary in size from 17.0 to 18.0 by 12.75 to 13.0 mm.

The descriptions of the eggs enable us to dispose of the eggs attributed to the cuckoo finch by Skinner (1923, a and b) on the identification of their collector, Carlisle, who obtained a "set" of three eggs that he considered to belong to the cuckoo finch at Strathmore Ranch, near Bulawayo, Southern Rhodesia. Aside from the fact that the cuckoo finch does not have a nest and a readily collectable "set" of eggs, Carlisle's specimens are too big (18 to 19.5 by 13 mm.) and are marked with a few very sharp spots of dark umber or black on a pale-blue shell color.

All but one of the eggs found so far have been considerably larger than those of the hosts with which they were associated, the *Cisitcola* eggs varying from 14.5 to 15.5 by 10.5 to 11 mm. The one exception was found in a nest of the striped grass warbler, *Cisticola natalensis*, whose egg measured 2 mm. longer than did that of the parasite.

That there are several records of two eggs or young of this parasite in one nest indicates that either two females may lay in the same nest, or that the same hen may lay more than one egg in the nest. We lack data to determine which is true. In this connection, Pakenham (1939, p. 553) in Pemba noted two young cuckoo finches in one wren grass warbler's nest "of which one was almost ready to leave the nest, and the other had sprouted quills, but not feathering generally. The disparity in age of these two suggests different parentage. . . . An alternative explanation, of course, would be that the layer of the first egg laid again in the same nest after an interval of a few days."

Aside from the mere appearance of the egg shell, and the fact that two eggs may be laid in the same nest, we know nothing as yet of the other important aspects of egg laying in the cuckoo finch. We still need to discover the number of eggs laid in one season by one female, the interval between them, their incubation period, whether each hen shows any sign of host specificity in its choice of nests, and whether it removes or punctures an egg of the host when depositing one of its own. In one instance, described below under the striped grass warbler, *Cisticola natalensis*, there was one broken egg of the host together with a whole one of both the parasite and the host, but there was no evidence as to the cause of the breakage.

The meager data available do not permit any conclusions whether the eggs of the cuckoo finch regularly show any similarity in coloration with those of the host. The described eggs of the species of *Cisticola* and *Prinia* victimized are sufficiently variable so that some of them could approximate the descriptions of cuckoo finch eggs, but in only one of the actual instances did the collector comment on whether the eggs were notably similar or dissimilar. In this instance the observer was impressed by the difference between the egg of the parasite and that of the host (*Cisticola natalensis*), but this difference was chiefly in size, and was not very great at that.

Sich (1926) reported on cuckoo finches nesting in captivity. He wrote that they not only nested and laid four eggs, but brought out three young. There appear, however, to have been numerous other birds in the same large cage, and it is not stated that an adult cuckoo finch was ever seen at the nest or with the young attributed to it. Furthermore, the description given of the nestlings does not agree with the known juvenal plumage of the cuckoo-finch, a fact suggesting that the identification of the birds is open to question. The case is too indefinite to be accepted. R. Neunzig (1926, pp. 547–548) gave additional details of Sich's report, but nothing that really substantiates it. It is particularly unfortunate that his information is so uncertain, as it would otherwise supplement well-substantiated comparable information on one of the combassous (see pp. 64–68).

Hosts

Whereas the parasitic viduine weavers confine their attention largely to related estrildine species, the cuckoo finch, insofar as is known, victimizes grass warblers exclusively. Undoubtedly additional host species will be added with further field studies, but the records available to date clearly point to the sylviine genera *Cisticola* and *Prinia* as the mainstays of the cuckoo finch.

Even within these sylviine genera there may be some selection by the cuckoo finch, as is suggested by Cheesman's data (in Cheesman and Sclater, 1935, p. 615). In northwestern Ethiopia he found three species of *Cisticola* (*galactotes*, *cantans*, and *brunnescens*) parasitized, but noted that a fourth locally breeding form, *eximia*, was not found molested. This result may be due to the peculiar, much moister habitat selected by this species—watery meadows studded with pedestals or clumps of earth about 9 inches high, crowned with a growth of water grasses and sedges, and flooded throughout the whole of the summer rainy season almost up to the tops of the pedestals. *Cisticola eximia* nests in the grasses on the tops of these pedestals along with such typically marsh birds as snipe. Had Cheesman examined a greater number of *eximia* nests, however, he might have found signs of the cuckoo finch in them, as I have seen cuckoo finches in a marshy, sedge-covered area of Kenya not too dissimilar from Cheesman's description of these Abyssinian watery meadows.

Habitat may well play a role in the cuckoo finch's selection, but nest structure apparently does not. The recorded cisticoline host species include forms building each of the various types of nests that Lynes (1930, pl. 19) depicted for the genus. Lynes distinguished three main kinds of nests: The "ball" type, a more or less globular nest with the entrance on the side, near the top; the "soda bottle" type, a vertically more elongated nest with the opening from above; and the "tailor" type, similar to that of a tailor bird, attached or sewn to the underside of large leaves.

Delacour (1943, p. 71) considered that cuckoo finches are in a less advanced stage of parasitism than are the viduine weavers, as the former victimize various small warblers, while the viduines are largely restricted to estrildine species, with whose nestlings viduine nestlings have in common distinctive mouth patterns and plumages. Any attempt to read into the viduines a more highly specialized degree of brood parasitism must be based on the assumption that these remarkable mouth patterns are a highly adaptive feature, but, as was already discussed, this buccal similarity is indicative more of a common ancestry and close relationship between the parasites and their main hosts than of something acquired to expedite their success with their hosts.

On the consideration that the ploceine weavers may have originated from the Cisticolinae, and the further consideration that the cuckoo finch is a ploceine species, Beecher (1953, p. 304) concluded that in its parasitism of grass warblers, the cuckoo finch presents a parallel to the screaming cowbird, which usually parasitizes its close relative, the bay-winged cowbird. The two cases are, however, quite dissimilar, as the two cowbird species are extremely closely related, the baywing being practically the immediate ancestor of its parasite, while no one would think that the cuckoo finch is close to the grass warbler.

All the known victims of the cuckoo finch and the available records of each are given below. All cases refer to the nominate race of the parasite.

Wren grass warbler: *Cisticola juncidis* (Rafinesque)[49]

Two races of wren grass warblers are known to be parasitized—*C. j. perennia* Lynes[50] and *C. j. terrestris* (Smith).[51] Pakenham (1939, p. 553) found *perennia* victimized frequently in Pemba. On one occasion, he noted two nests, the first nest containing one and the other nest two young cuckoo finches. On another occasion, he saw a pair of wren grass warblers feeding two fledgling cuckoo finches already out of the nest. He wrote that in Pemba the cuckoo finch parasitizes this host very intensively from September to January. After the period covered by his publication, Pakenham observed additional cases of recently fledged cuckoo finches being fed and attended by wren grass warblers at Konde, North Pemba Island—one in November and two in February.

The race *C. j. terrestris* was first found to be victimized near Umvuma, Southern Rhodesia, on February 14, 1939, when A. W. Vincent

---

[49] *Sylvia juncidis* Rafinesque-Schmaltz, Carratteri . . . animali . . . Sicilia . . ., 1810, p. 6 (Sicily).

[50] *Cisticola juncidis perennia* Lynes, Ibis, ser. 12, vol. 6, 1930, *Cisticola* supplement, p. 105 (Mokia, near Lake George, i.e., Ruwenzori).

[51] *Drymoica terrestris* A. Smith, Illustrations of the zoology of South Africa . . ., vol. 2, Aves, 1842, pl. 74, fig. 2 (between Latakoo and Kurrichane, Bechuanaland).

(1949, p. 663) found a nest containing two eggs of the cuckoo finch and none of the host. Subsequently, at "Torre," near Marandellas, Southern Rhodesia, Neuby-Varty (1950, p. 37) found a nest on February 14, 1950, with one egg of the host and one of the parasite. In the Selukwe Native Reserve, Southern Rhodesia, C. T. Fisher found three more parasitized nests of this grass warbler (records of which were not published but were sent to me by Harry M. Miles). The first one was on March 19, 1954, a nest containing only a young cuckoo finch with its feathers just sprouted. On March 27 it was well feathered, and on April 4 it left the nest. On March 26, 1954, he discovered a nest containing four eggs of the grass warbler and one of the cuckoo finch, and on March 3, 1955, he found two fledgling cuckoo finches that were still in or near the nest and were attended by wren grass warblers. The fledgling parasites were not yet able to fly well. In 1954 and 1955, two further instances were reported to to me.

These actual cases are the only ones known to me, but a few other incomplete and hence indefinite cases are also in my files. Chapin (1954, pp. 407–410) listed the wren grass warbler as a known victim of the cuckoo finch, probably on the basis of some of the above-mentioned records. J. Vincent (1936, pp. 102–103) noted numbers of cuckoo finches near Ile, Mozambique, in fields where the wren grass warbler was present.

Wren grass warblers are very prone to desert their nest if they are touched by the observers, and Neuby-Varty suggested that this same tendency may also pertain to nests intruded into by the cuckoo finches. As a consequence, a considerable percent of eggs of the latter would be lost.

Desert grass warbler: *Cisticola aridula* Witherby[52]

Neuby-Varty (in litt., June 24, 1956) wrote me that on February 9, 1956, on his ranch "Torre" near Marandellas, Southern Rhodesia, he found a nest of this species with two of its own eggs and one of the cuckoo finch—all about half incubated. The race of the host involved was *C. a. kalahari* Ogilvie-Grant.[53]

Brown-grass warbler: *Cisticola brunnescens* Heuglin[54]

In northwestern Ethiopia, Cheesman (in Cheesman and Sclater, 1935, p. 615; 1936, p. 194) found the nominate race of the brown grass warbler to be parasitized by the cuckoo finch (which he erroneously listed as the pin-tailed widow bird, *Vidua macroura*, but later cor-

---

[52] *Cisticola aridula* Witherby, Bull. British Ornith. Club, vol. 11, 1900, p. 13 (60 miles south of Khartoum, i.e., Gerazi, White Nile).

[53] *Cisticola kalahari* Ogilvie-Grant, Bull. British Ornith. Club, vol. 25, 1910, p. 121 (Molopo River, Bechuanaland).

[54] *Cisticola brunnescens* Heuglin, Journ. Ornith., vol. 10, 1862, p. 289 (Gudofelasi, Serawi, Abyssinia, 6,000 feet).

rected). Although he collected only one nestling cuckoo finch from a nest found on August 9, he probably observed other instances, as he wrote that nearly all the first broods reared by the brown grass warbler there are young cuckoo finches. No young brown grass warblers were noted in nests containing the young parasites. Cheesman considered it likely that the cuckoo finches dispose of the eggs or the young of the host, "whereas with larger species of *Cisticola* they were not always successful in getting rid of them."

Rattler grass warbler: *Cisticola chiniana* Smith[55]

Two races of the rattler grass warbler have been found to serve as hosts for the cuckoo finch—*C. c. victoria*, and *C. c. ukamba.*[56] V. G. L. van Someren (1922, p. 147) found a young cuckoo finch in a nest of the former race (there listed as *C. ruficapilla fischeri*). More recently (in litt., November 23, 1950) he informed me that he found eggs and young of the cuckoo finch in nests of the race *ukamba* in the Nairobi area in May and June. Chapin (1954, pp. 407–410) listed *C. chiniana* as a host of the cuckoo finch, apparently based on van Someren's records.

Singing grass warbler: *Cisticola cantans* (Heuglin)[57]

Cheesman (in Cheesman and Sclater, 1935, p. 617; 1936, p. 194) found the nominate race of the singing grass warbler parasitized in northwestern Ethiopia. He collected a nestling of the parasite from a nest of the host on August 6 and another from another nest on October 9. He noted that in their first nest, a pair of singing warblers had reared a young cuckoo finch. Their second nest was destroyed. Their third nest (October 9) contained one unfledged cuckoo finch. This nest fell and was destroyed a few days later. The Mackworth-Praed and Grant (1955, p. 480) statement that the singing grass warbler is much parasitized by the cuckoo finch (incorrectly called the pin-tailed widow bird) was apparently based on Cheesman's data.

Rufous grass warbler: *Cisticola galactotes* (Temminck)[58]

Cheesman (in Cheesman and Sclater, 1935, p. 619; 1936, p. 194) found a nest containing one young rufous grass warbler and two young cuckoo finches ready to fly in northwestern Ethiopia on November 22.

---

[55] *Drymoica chiniana* A. Smith, Illustrations of the zoology of South Africa . . . , vol. 2, Aves, 1843, pl. 79 (near Kurrichane).

[56] *Cisticola chiniana victoria* Lynes, Ibis, ser. 12, vol. 6, *Cisticola* supplement, 1930, p. 264 (new name for *C. fischeri* van Someren; Victoria Nyanza Basin, type from Kisumu). *Cisticola chiniana ukamba* Lynes, Ibis, ser. 12, vol. 6, *Cisticola* supplement, 1930, p. 267 (Ukamba Province, Kenya).

[57] *Drymoeca cantans* Heuglin, Ibis, ser. 2, vol. 5, 1869, p. 96 (Abyssinia, type from Gondar).

[58] *Malurus galactotes* Temminck, Nouveau recueil de planches colories d'oiseaux, livr. 11, vol. 3, 1823, pl. 65, fig. 1 (New Holland, South Africa, apud Lynes).

Striped grass warbler: *Cisticola natalensis* (A. Smith)[59]

One record, was kindly sent to me by the observer, C. J. Vernon, who flushed what seemed to be a cuckoo finch from a little clump of vegetation along the Marimba River, near Salisbury, Southern Rhodesia, on February 28. Inspection revealed a nest of the striped grass warbler with a whole and a broken egg of its own and a whole one of the cuckoo finch. Since the striped grass warbler is prone to desert its nest very easily, and might well have done so because of the damaged egg, Vernon collected the two whole eggs in the set. Both proved to be fresh, unincubated eggs. Whether the parasite had broken the second egg of the host accidentally or deliberately cannot be determined. The record referred to the nominate subspecies of the host.

Tinkling grass warbler: *Cisticola tinniens* (Lichtenstein)[60]

Two races of the tinkling grass warbler have been reported as victims of the cuckoo finch—the nominate race and the Kenya race, *C. t. oreophila* van Someren.[61] Two definite records are at hand for the southern, nominate race. A. Roberts (1913, p. 37) wrote that many years earlier, his brother shot a young cuckoo finch being fed by a pair of tinkling grass warblers, and that "Mr. Noome" informed him of the type and cotype of *Heliospiza noomei* (i.e., young cuckoo finch) also shot while being fed by some tinkling grass warblers. Roberts' record was the first hint of the cuckoo finch being a parasite. Many years later Roberts (1939, p. 117) collected a fledgling cuckoo finch being fed by a pair of tinkling grass warblers at Potchefstroom, Transvaal, and two others on other occasions also attended by grass warblers (of unidentified species). Neuby-Varty (in litt., December 28, 1950) found a similar fledgling attended by tinkling grass warblers at Torre, near Marandellas, Southern Rhodesia, in either late December 1948 or early January 1949. One unsupported statement referring to the Kenya race *oreophila* suggests that it is also victimized. Chapin (1954, pp. 407–410) listed the tinkling grass warbler as a fosterer of cuckoo finches, probably on the basis of Roberts' Potchefstroom record.

Tawny-flanked longtail: *Prinia subflava* (Gmelin)[62]

Two records refer to race P.s. *affinis* (Smith).[63] O. Payne (1944, p. 235) found a nest with four eggs of the tawny-flanked long-tail and

---

[59] *Drymoica natalensis* A. Smith, Illustrations of the zoology of South Africa . . ., vol. 2, Aves, 1843, pl. 80 (Port Natal, *i.e.*, Durban).

[60] *Malurus tinniens* Lichtenstein, Verzeichniss einer Sammlung von . . . Vögeln aus der Kafferniande . . ., 1842, p. 13 (Kaffirland).

[61] *Cisticola tinniens oreophila* van Someren, Nov. Zool., vol. 29, 1922, p. 214 (Mount Kenya, 7,000 feet).

[62] *Motacilla subflava* Gmelin, Caroli a Linné . . . systema naturae, ed. 13, vol. 2, 1789, p. 982 (Senegal).

[63] *Drymoica affinis* A. Smith, Illustrations of the zoology of South Africa . . ., vol. 2, Aves, 1843, pl. 77 (interior of South Africa, Rustenburg apud Roberts).

one of the cuckoo finch near the Hunyani River about 18 miles from Salisbury, Southern Rhodesia, on March 5, 1944. Neuby-Varty (in litt., December 28, 1950) saw a fledgling cuckoo finch cared for by a pair of tawny-flanked longtails at Umvukwe Ranch, Banket, Southern Rhodesia, in February 1945. Winterbottom (1951, p. 21) noted that the tawny-flanked longtail was a host of the cuckoo finch. Whether he had data additional to the cases listed above, however, is not clear.

Black-chested longtail: ***Prinia flavicans*** **(Vieillot)** [64]

A. Roberts (1917, pp. 259–262) found a nest of the black-chested longtail near Pretoria, Transvaal, on January 24, and it contained one of its own and one young cuckoo finch. This record was the first evidence that the cuckoo finch was a brood parasite, and to date no one has found another of the black-chested longtail serving as host. Chapin's inclusion of the black-chested longtail among the hosts of the cuckoo finch (1954, pp. 407–410) was undoubtedly based on this record.

UNVERIFIED HOST RECORDS: Mackworth-Praed and Grant (1955, pp. 1000–1001) wrote that the cuckoo finch is parasitic on, among other birds, quail finches (*Ortygospiza atricollis*). Unfortunately, they gave no supporting evidence or documentation, and I have not been able to learn of any. The same authors (p. 873) stated, in their account of the Kenya rufous sparrow, *Passer rufocinctus*, that "pale blue eggs with faint spots . . . often in these birds' nests . . . are believed to be those of . . . *Anomalospiza imberbis* . . . but it would be of interest to establish this." To date no proof has been offered. The statement appears to have been originated by Paget-Wilkes (1938, p. 129), who wrote that he twice found such eggs in nests of this sparrow, and that he once saw a cuckoo finch coming out of such a nest; he raised the question whether the strange eggs might be due to this parasite. Inasmuch as Belcher (1949, p. 19) once recorded eggs of Klaas' cuckoo (*Chalcites klaas*) from a nest of the Kenya rufous sparrow, the record, uncertain to begin with, is made quite unusable.

V. G. L. van Someren (1918, pp. 282–283) found a nest at Kisumu, Kenya, June–July 1912, containing young "quite unmistakable" cuckoo finches. "The nest resembled somewhat that of *Quelea cardinalis*, being slung between grass stems and composed of fine grass." This record was made before it was known definitely that the cuckoo finch was a parasite, and it seems that van Someren naturally assumed that the nest belonged to the cuckoo finch. No one has since reported *Quelea cardinalis* as a host, so this record must be left unverified.

---

[64] *Sylvia flavicans* Vieillot, Encyclopédie méthodique . . ., vol. 2, 1820, p. 438 (South Africa, Namaqualand, ex Levaillant).

NESTLING STAGE

The meager data available on the nestling stage indicate that while usually only the young parasite survives to leave the nest, sometimes the young of the host also survive. Cheesman (in Cheesman and Sclater, 1935, pp. 615–619) noted that in nests of the brown grass warbler, *Cisticola brunnescens*, in which he found young cuckoo finches, no young of the host were present, and he inferred that the parasites "seem to entirely dispose of eggs, or more probably the young, whereas with larger species of *Cisticola* they were not always successful in getting rid of them." In one nest of the larger rufous grass warbler, *Cisticola galactotes*, he found a fledgling warbler and two young cuckoo finches, all ready to fly. Similarly A. Roberts (1917, pp. 259–262) found a nest of the black-chested longtail, *Prinia flavicans*, with a young longtail and a young cuckoo finch. In this case the young parasite filled the whole of the bottom of the woven nest, and at first sight the young warbler was not seen, as it was more or less hidden by the larger parasite.

The behavior of the newly hatched cuckoo finch toward other young or eggs in the nest has not been observed. The duration of the nestling stage is also still to be determined. The nestlings of cuckoo finches are not known to have any mouth markings or papillae as do the viduine parasites, but further definite information on this point is urgently needed.

A few writers intimated that the juvenal plumage of the cuckoo finch is very similar to that of grass warblers of the genus *Cisticola* that the cuckoo finch parasitizes very intensively. While the degree of similarity present may seem to be of possible advantage to the cuckoo finch, this buffy, sparrow-like plumage is similar to what we find in many species of ploceine weavers, and it need not be looked upon as an adaptation acquired subsequently to parasitic breeding. The lack of such similarity does not seem to impair the cuckoo finch's success with *Prinia* hosts. For that matter, the frequently great disparity between nestling plumages of parasites (e.g., cuckoos and cowbirds) and of their numerous fosterers does not appear to be a critical disadvantage for the parasites.

YOUNG OUT OF THE NEST

A number of naturalists have seen recently fledged cuckoo finches being fed by their foster parents. These instances are described under the pertinent host species. In the case observed by A. Roberts (1917, pp. 259–262), the young parasite was attended by its fosterers for at least a few days after leaving the nest. It kept up an incessant demand for food and was fed by the longtails on an average of about once a minute. It was tamer, less timid with respect to the human observer, than was the young warbler with which it was reared. Chapin (1954, p. 409) summarized the little that was recorded, as follows: "For a while the fledglings are fed by their fosterers, then they begin to recognize their own kind and gather by dozens into flocks with numbers of adults." Cheesman (in Cheesman and Sclater, 1936, p. 91) once saw an apparently unattended, lone fledgling near Dangila, northwestern Ethiopia.

Food and Feeding Habits

Adult: The adult birds are largely seed eaters. In the gizzards of two specimens collected in Pemba, Pakenham (1939, p. 553) found seeds of bullrushes. Mouritz (1915, p. 558) reported small seeds and remains of insects in an example from Southern Rhodesia. In the same country Irwin (1952, p. 115) describes the birds as feeding on the ground. Chapin (1954, pp. 407–410) found nothing but seeds in the stomach of a bird taken at Faradje, Belgian Congo. He writes that as a rule this species clings to the stalks of grass and feeds on the seeds.

Probably associated with its feeding habits is the peculiar structure of the mouth of this bird. The sides of the mandibles are dilated inward to the extent that they form two horny pads and leave only a narrow medial groove between them in which the small tongue is fitted. A similar medial groove accommodating the tongue occurs on the palate, while on either side of the roof of the mouth, near the gape, is a hard circular hollow into which the horny mandibular pads fit when the bill is closed. The function seems to be to help crush hard seeds used as food. Bannerman (1932, p. 254) sensed this function when he commented that the "powerful bill must enable it to eat some kind of hard seeds which are not available to other birds."

Young: Pakenham (1939, p. 553) watched a pair of grass warblers feeding two fledgling cuckoo finches some green caterpillars and grasshopper-like insects, and the gizzard of one of these young birds contained the top of a small snail shell as well. Two fledglings taken by Lynes near Mwanza, Tanganyika Territory, and now in the British Museum, had bits of the shells of fairly big snails in their gizzards.

Plumages and Molts

Anomalospiza imberbis imberbis

Adult male in fresh plumage: Forehead, lores and anterior part of crown light Aniline Yellow (capitalized colors refer to the nomenclature of Ridgway, 1912). Rest of crown slightly darker and washed with Light Grayish Olive, this color largely on tips and margins of feathers. Hind neck and upper back more pronouncedly grayish olive because of increase in width of these marginal parts. Feathers of back between Pyrite Yellow and Warbler Green with blackish shaft stripes, and tipped with Light Grayish Olive. Rump and upper tail-coverts similar but with dark shaft stripes more reduced and more completely hidden. Upper wing-coverts similar to feathers of the back. Primaries and outer secondaries dark Brownish Olive, externally narrowly edged with Warbler Green, and internally, on the basal two-thirds, broadly edged with Drab Gray to Smoke Gray. Inner secondaries and rectrices Fuscous Black, externally edged with Warbler Green basally and with Light Grayish Olive on their more distal portions. Cheeks, auriculars, chin, and throat Olive-Ocher, slightly duskier and more olivaceous on sides of head than on chin and throat, this darker tone extending down along sides of throat. Breast as sides of neck but clouded with even duskier olivaceous tone. Abdomen Olive-Ocher, darkening slightly on sides and flanks, which are obscurely marked with dusky shaft streaks, and become slightly paler on under tail-coverts. Under wing-coverts pale Olive-Buff becoming yellower on edge of wing. Iris dark brown. Bill dark brown to blackish brown becoming much paler, brownish gray, on basal and gonydeal portion of mandible. Feet grayish brown to brown. Wings 64–71 (68) mm. Tail 40–46 (43.5) mm. Culmen from base 12–13 (12.7) mm. Tarsus 16–18 (17) mm.

ADULT MALE IN WORN PLUMAGE: Remarkably different from the above, but the change is due wholly to abrasion. Grayish or Light Grayish Olive edgings are worn off and cause the bird to appear light Aniline Yellow to Pyrite Yellow, and make blackish shaft streaks of upper parts much more noticeable and striking, less obscured by paler margins of feathers. Feathers of breast have lost their dusky olivaceous tinge, and under wing-coverts are yellower and less grayish in appearance. The more worn the plumage, the more strikingly yellow with black dorsal streaks the bird becomes.[65]

JUVENAL MALE: Very different from adult. Narrow frontal line, superciliary areas, lores, cheeks and auriculars Clay Color. Feathers of crown and occiput with fairly wide black shaft streaks, laterally broadly edged and tipped with Clay Color. Feathers of back, rump,

---

[65] Mackworth-Praed and Grant (1948) describe what they call an "immature" plumage, which is chronologically intermediate between the adult and the juvenal or nestling plumage. It is characterized briefly as similar to the adult male in fresh plumage, but generally darker on the anterior upper parts. The Aniline Yellow on the forehead is restricted to a thin line. The crown and occiput are Orange Citrine to Medal Bronze. The feathers have indistinct dusky shaft streaks. Other parts are as in the freshly plumaged adult (description based on specimens that I assume correspond with what Mackworth-Praed and Grant had in mind). Although the top of the head is darker than in most freshly plumaged adult male birds, I am still doubtful that this condition is a real plumage stage, and not merely the dark extreme of the adult plumage. Chapin (1954, p. 407) found that "even in the fresh feather the shaft of each barb is bright yellow, but the outer part of all the barbules is dusky and tends to mask the yellow color, giving the general effect of olive." While Chapin's comments refer to unquestionably fully adult birds, I have examined forehead feathers from these dark-headed "immatures" microscopically and find exactly what Chapin observed.

upper tail-coverts, and upper wing-coverts similar except that margins are slightly paler, between Cinnamon-Buff and Clay Color, palest on rump and upper tail-coverts. Primaries and outer secondaries Olive-Brown narrowly edged with pale Cinnamon-Buff to Pinkish Buff externally and more broadly with Pale Pinkish Buff internally on their basal two-thirds. Innermost secondaries Fuscous to Fuscous-Black edged with Pinkish Buff. Rectrices Olive-Brown narrowly edged externally with Cinnamon-Buff and internally and terminally with Pale Pinkish Buff. Chin, throat, breast, sides, and flanks between Warm Buff and Ochraceous-Buff. Abdomen paler, especially medially where it becomes Light Buff. Under tail-coverts and under wing-coverts Warm Buff. Iris brown. Bill Dusky Brown on maxilla, brownish white on mandible. Tip of bill dusky like the maxilla. Tarsi and toes grayish brown.

The juvenal plumage fades with wear, and loses some of the bright Clay Color above and becomes almost whitish on the underparts. In Kenya V. G. L. van Someren (1922, p. 147) found the postjuvenal molt to begin in June. One such specimen before me shows the very onset of the molt—a few yellow feathers coming in on the whitish abdomen and breast, while the upper parts are as yet unaffected.

ADULT FEMALE IN FRESH PLUMAGE: Feathers of forehead, crown, occiput, nape, back, rump, upper tail-coverts and upper wing-coverts with broad Fuscous shaft stripes, broadly edged and tipped (less broadly) with Olive-Brown, dark medial streaks averaging heaviest on head and upper back, slightly less pronounced on rump and upper tail-coverts. Remiges and rectrices Olive-Brown to Clove Brown, narrowly edged with pale Olive-Brown. Lores and superciliary line, cheeks, auriculars, and sides of neck light Dresden Brown to Buckthorn Brown to Tawny-Olive. Chin Chamois to Cream-Buff. Feathers of throat, breast, sides and flanks grayish Tawny-Olive to dusky Isabella Color, with narrow darker shaft streaks. Abdomen Cartridge Buff darkening to pale Chamois near the vent and on under tail-coverts. Under wing-coverts pale Tawny-Olive. Iris brown. Bill and feet brown. Size as in male.

ADULT FEMALE IN WORN PLUMAGE: Similar to that in fresh plumage, but paler edges of the feathers of upper parts of head and body narrower (by abrasion) and paler (by fading), Buffy Brown, causing the dark shaft streaks to be more pronounced. Lores, superciliaries, chin, throat, cheeks, auriculars vary from pale Mustard Yellow to Light Buff. Feathers of breast, sides, and flanks pale Buffy Brown, with dusky Buffy Brown medial streaks. Abdomen Light Buff. Under tail-coverts Pinkish Buff. Under wing-coverts pale Tawny-Olive.

JUVENAL FEMALE: Indistinguishable from the corresponding plumage of the male.

Anomalospiza imberbis butleri

Little known. Adult male smaller than nominate form (wings 62–69 mm.; tail 36–39 mm.). Bill lighter brown. Dorsal plumage with narrower streaks.

MISCELLANEOUS DATA

Neuby-Varty (in litt., June 24, 1956) wrote that when resting, the cuckoo finch seemed to have a definite preference for the same spot day after day. The male bird usually perched a little above the female. One pair regularly used a patch of dead reeds; another one used some dead branches that a native had put around his small garden; a third pair used a small, 6-foot tree, the top half of which was dead and leafless, and also a barbed-wire fence next to the tree.

Other writers reported that this species is wary and difficult to approach. It perches only a few feet from the ground and flies off into cover when danger threatens. These reports agree with my own experience with the species near Nairobi. According to Irwin (1952, p. 115), on the ground it assumes an upright position and walks with an awkward gait.

After the breeding season is over, the birds may gather in flocks containing 200 or more individuals. In late July 1925, V. G. L. van Someren and I observed a loose flock of at least 50 birds in a little swamp not far from the city limits of Nairobi.

According to Ohnesorge (1924, p. 579), the cuckoo finch was kept in captivity in Berlin, but nothing was recorded of its habits there.

Short-Tailed Widow Birds: Subgenus *Hypochera*

STATUS OF *Hypochera:* The short-tailed species of widow birds, which are commonly known as indigo finches or combassous (hereinafter called combassous), have generally been treated as a genus distinct from *Vidua* and *Steganura* merely because in breeding plumage the males have none of the rectrices elongated as do the more typical widow birds. Among recent authors, Delacour is the leading advocate for combining *Hypochera* and *Vidua*, although this combination was first suggested as long ago as 1880 by Forbes (1880, p. 475). Bannerman, Bates, Chapin, Grant, Mackworth-Praed, Roberts, Sclater and others used the name *Hypochera* for the short-tailed species. The chief argument advanced by Delacour for including this group in *Vidua* is that aside from its elongated median rectrices, one species of the latter group, *Vidua hypocherina*, is remarkably similar to the species of *Hypochera*.

Bolstering Delacour's argument is the generally overlooked and quite inadequately published note of R. Neunzig (1931, p. 546), the gist of which is as follows: Neunzig took some combassous "of the Senegal form" and treated them with certain glandular extracts ("mit bestimmter Drüsenpräparaten"). Two of his experimental birds developed elongated median rectrices after the molt; one had them about 15 mm. longer than normal, and the other about 40 mm. longer, or about 80 mm. in total length. These short-tailed birds thereby became more similar to the long-tailed *Vidua hypocherina*. Unfortunately, Neunzig did not indicate the glandular preparations used and the dosage, time, and intervals involved; however, his results seem to indicate that the species of *Hypochera* and *Vidua*, especially *Vidua hypocherina*, are very closely related.

Uncertainty has arisen, however, about the kind of birds that Neunzig used. While he refers to them as of "the Senegal form," the taxonomy of the combassous, even now not wholly clear, was certainly poorly understood and much confused in 1931. Possibly his birds came from eastern Africa and were of a species then considered the same as the one occurring in Senegal. There is the annoying fact that in eastern and northeastern Africa, the long-tailed blue widow bird, *Vidua hypocherina*, is found; one cannot, therefore, rule out the possibility that Neunzig may have had some birds of this species mixed up with his combassous, especially if he began his experiments with birds in the brown "off-season" plumage, when it is very difficult to tell them apart. Inasmuch as he reported that the birds developing lengthened retrices did so after the molt, the experiment probably was started before the molt—with birds in the off-season plumage. Against this possibility one must admit that an aviculturist of Neunzig's experience would likely have been alert to the need for knowing exactly the birds that he was studying. Furthermore, in East Africa, the combassous are more generally available for capture for the avicultural trade than the blue widow birds. Neunzig should publish the full details of his work, or the experiment should be repeated under better conditions, and fully recorded.

If further evidence should corroborate Neunzig's undocumented results, the case for reducing *Hypochera* to not more than a subgenus of *Vidua* would be much strengthened. No doubt the two are closely related, and even without further evidence a good case may be made for putting them together. In his recent book Boetticher (1952, p. 60, footnote) referred to the fact that Neunzig once told him of two of his specimens of "*Hypochera chalybeata*" acquiring elongated retrices. This statement probably refers to the same experiment discussed above, but gives a more definite identification of the birds.

Of particular interest in connection with Neunzig's experiments is the following observation: In a live bird dealer's shop in Aachen, Wolters (1943, p. 99) saw a male combassou with elongated middle tail feathers. It was definitely not the blue widow bird, *Vidua hypocherina*, as it had a white bill, whereas *V. hypocherina* has a bright red one. Furthermore, only the median pair of retrices, not this pair and the next pair, were elongated, and they were not as long as in *V. hypocherina*, but merely twice as long as the lateral retrices instead of being several times as long. They were also somewhat unequal, the right one being slightly shorter than its left counterpart. In other words, here was a nonexperimental bird that for some unknown reason had also developed to some extent the trait of excessive median retricial growth. Boetticher (1952, p. 65, footnote), went so far as to suggest that *V. hypocherina* may be only a northern, long-tailed race of the similarly red-billed combassou, *V. amauropteryx*, a "peritype" is the sense used by some authors.

The phylogenetic insignificance of rectricial elongation, which argues against its use as a generic character, is shown in other groups of birds. For example, within a single species of flycatcher of the genus *Terpsiphone* some races have the median tail feathers greatly elongated, while others have them no longer than the lateral ones.

Further evidence of the close relationship of all the viduines is afforded by the fact that the two extremes of the group—the combassous and the paradise widow birds—have been known to hybridize occasionally. One such example, described by A. Roberts (1926, pp. 224–225) as a new bird under the name *Microchera haagneri*, supposedly taken near Bulawayo, Southern Rhodesia, lived in the Pretoria Zoo for three years, and molted each summer from a plain winter plumage to a long-tailed black summer one. Another bird was described as new under the name *Prosteganura haagneri okadai* by Yamashina (1930, p. 11) and was based on a cage bird brought to Japan from an unknown African source. These two instances are not the only ones, as is indicated by Priest (1936, p. 364), who saw specimens corresponding to them at Chipoli, Southern Rhodesia, but was unable to obtain any, and by Alston (1951, p. 92), who reported seeing another in the Umvukwe, not far from the escarpment of the Zambezi valley in Southern Rhodesia, in late December, "a blackish-purplish widow bird with four fluttering tail feathers and brownish edge to the wings. . . . It was just like the bird pictured as the 'purple widow bird' [in Dr. Roberts' book], and in Captain Priest's book as the 'Okada's pintailed widow bird.'" Another specimen received in England in a consignment of cage birds from Basutoland was reported by Yealland (1959, p. 49) and by Everitt (1959, p. 96). Another type of cross was reported by Abrahams (1939, pp. 303–204), who collected a hybrid between the shaft-tailed widow bird and the paradise widow bird.

Aside from the short tail of the nuptial male plumage, the combassous are, it is true, slightly different in parts of their habits from the long-tailed widow birds. The combassous are less aggressive and pugnacious than the species of long-tailed widow birds, and the male combassous are more inclined to use definite singing perches and to bounce from these perches in their courtship antics, whereas the long-tailed widow birds do practically all their singing and courtship in flight. These differences are slight and thus hardly constitute generic characters. For convenience as a name by which to refer to the combassous, *Hypochera* may be retained as a subgenus, but not as a genus distinct from the long-tailed widow birds, *Vidua* proper.

INCLUDED SPECIES AND SUBSPECIES: It is difficult to determine with certainty how many species of combassous are valid, which of the 17 described forms are races of which species, and which names are synonyms. Much of the literature is of no great benefit, for there are as many arrangements as there are arrangers. In recent publications, Mackworth-Praed and Grant (1955) listed seven species from eastern Africa alone; Chapin (1954) considered the forms found in the Belgian Congo to fall into four species, of which he is uncertain of the specific status of one; Delacour and Edmund-Blanc recognized six species in their revision in 1934, but in 1951 Delacour reduced this number to three; and Benson (1953, pp. 80–81) listed four species from Nyasaland but raised the possibility that all may be only a single species with color variants showing in the male nuptial plumage.

On the basis of the material that I have examined, I have concluded that there are only three valid species, one of which appears to have wide variational limits, if not actual color phases, in the breeding plumage of the adult male. I do not, however, in the present state of our knowledge claim any finality for this arrangement. I am aware of no characters or combination of characters by which females, nonbreeding males, or young of the three species can be distinguished.

The disturbing similarity in these critical plumages unfortunately makes it impossible for us to utilize some of the published notes on habits and occurrence. As Chapin (1954, p. 565) put it, we have as yet no way of knowing "whether males of different colors may not associate with the same party of brownish birds. How can they recognize females of their own kind, so a species can preserve its separate existence?" As a matter of fact, recent information kindly given me by Donald W. Lamm makes me wonder if they can, or at least if they do. In Mozambique he saw a female combassou of uncertain species being courted simultaneously by a male glossy combassou, *Vidua amauropteryx*, and a male dusky combassou, *V. funerea* (the red bill of the former and the white bill of the latter plainly noted). Chapin also stated: "The case is very like that of *Steganura paradisaea*, especially in the regions where two forms of paradise whydah occur together. In *Steganura* the form of the tail (in adult breeding males) is evident at a distance; in *Hypochera* the colors of the bill and feet are sometimes distinctive, and they should always be carefully noted."

I strongly urge that collectors make every effort to get apparently paired breeding birds and mark them so that later the female can be identified by the plumage characters of its male companion. The observation of Lamm's cited above suggests that even if the males cannot or do not distinguish between females of their own and closely related species, the females may do so with the males. This possibility would fit in with what Emlen (1956) reported for *Coliuspasser* and *Euplectes*, which have numerous species, and whose females and males in nonbreeding plumage are almost indistinguishable, but whose breeding males are very different. Emlen found that the males establish discrete territories on which they go through their courtship display indiscriminately for females of any of the species and from which they drive away males of their own or other species. According to his conclusion, the distinctive male nuptial plumage and the display, although used for defending the territory, probably evolved primarily with respect to species recognition in mate selection by the females.

That two or more species of combassou were found together in several parts of Africa in breeding condition merely emphasizes the need for elucidation, which can only come from more careful and critical collecting. As it is, few of the identifications made of female and nonbreeding male specimens in museum collections can be looked upon as more than guesses, regardless of how definitely their labels were inscribed with names subsequently used in published reports.

To simplify reference to the following taxonomic discussion, I shall list the names proposed for combassous with a brief statement of their disposition:[66]

aenea: a synonym of *chalybeata*
amauropteryx: a valid species
camerunensis: a synonym of *nigeriae*
centralis: a synonym of *orientalis*
chalybeata: a valid species
codringtoni: a race of *chalybeata*
funerea: a valid species
ignestii: a synonym of *nigeriae*
neumanni: a race of *chalybeata*
nigeriae: a race of *amauropteryx*
nigerrima: a race of *funerea*
nitens: a synonym of *chalybeata*
orientalis: a race of *chalybeata*
purpurascens: a synonym of *nigerrima*
sharii: a synonym of *nigeriae*
ultramarina: a race of *chalybeata*
wilsoni: a race of *funerea*

On the whole, the arrangement arrived at and outlined below is very similar to Delacour's (1951, p. 124). The species recognized are *Vidua amauropteryx*, *V. chalybeata*, and *V. funerea*, with their included races.

Vidua amauropteryx has two races—*amauropteryx* and *nigeriae*. To the race *nigeriae* are relegated a number of names as synonyms—*camerunensis*, *ignestii*, and *sharii*. I have seen no material (apart from the description) of *ignestii*, and follow recent authors in placing this

---

[66] *Hypochaera amauropteryx* Sharpe, Catalogue of the birds in the British Museum, vol. 13, 1890, p. 309 (Rustenburg).

Hypochera aenea Hartlaub, Journ. Ornith., vol. 2, 1854, p. 115 (Senegambia).

Hypochera chalybeata camerunensis Grote, Journ. Ornith., vol. 70, 1922, p. 398 (between Nola and Mbaiki, southeast Cameroons).

Hypochera chalybeata centralis R. Neunzig, Zool. Anz., vol. 78, 1928, p. 113 (Kissenji, Ruanda).

Fringilla chalybeata P. L. S. Müller, Des Ritters Carl von Linné . . . vollständiges Natursystem . . . Supplement, 1776, p. 166 (Senegal).

Hypochera codringtoni Neave, Mem. Manchester Lit. Phil. Soc., vol. 51, 1907 (Molilo's, Loangwa Valley, northeast Rhodesia).

Fringilla funerea de Tarragon, Rev. Zool., 1847, p. 180 (Natal).

Hypochera ignestii Moltoni, Atti Soc. Italiana Sci. Nat., vol. 64, 1925, p. 46 (Dintorni di Gondor, Abissinia).

Hypochera neumanni Alexander, Bull. British Ornith. Club, vol. 23, 1908, p. 33 (Yo, near Lake Chad).

Hypochera nigeriae Alexander, Bull. British Ornith. Club, vol. 23, 1908, p. 33 (Kiri, Gongola River, northern Nigeria).

Hypochaera nigerrima Sharpe, Proc. Zool. Soc. London, 1871, p. 133 (Angola).

Fringilla nitens Gmelin, Caroli a Linné . . . systema naturae, ed. 13, vol. 2, 1789, p. 909 (based on Latham, in Brasilia=Senegal).

Hypochera ultramarina var. *orientalis* Reichenow, Die Vögel, *in* Deutsch-Ost-Afrikas, vol. 3, 1894, p. 188 (Pare Mountains, northeastern Tanganyika).

Hypochera purpurascens Reichenow, Journ. Ornith., vol. 31, 1883, p. 221 (Usequa, i.e., Usegua, Tanganyika).

Hypochera chalybeata sharii Bannerman, Bull. British, Ornith. Club, vol. 43, 1922, p. 29 (Ratu, Gribingui River, French Equatorial Africa).

Hypochera ultramarina Gmelin, Caroli a Linné. . . systema naturae, ed. 13, vol. 2, 1789, p. 927 (Abyssinia.)

Hypochera funerea wilsoni Hartert, Nov. Zool., vol. 8, 1901, p. 342 (Yelwa, Middle Niger).

name here. There is no doubt among recent authors that *sharii* is a synonym of *camerunensis*, but the question meriting some discussion and elaboration is the suggested identity of *camerunensis* and *nigeriae*. The latter has, it is true, a somewhat less bluish, more greenish sheen in the nuptial plumage of the adult male than does *camerunensis*. Specimens fitting the characters of *nigeriae* are all from within the range of *camerunensis*, although the latter, if the two were to be kept distinct, is also known from a little farther east (perhaps to western Ethiopia). Chapin (1954, p. 573) compared *nigeriae* with *camerunensis*, and noted the greener gloss of the former; however, he was not convinced that the difference is enough to validate the specific status of *nigeriae*. The two "forms" are seasonal visitors to northeastern Belgian Congo, with the same dates of occurrence, further suggesting their identity. Delacour and Edmond-Blanc (1934) considered *nigeriae* as "probably" a race of *amauropteryx*, but did not specifically state that *nigeriae* and *camerunensis* are the same. It is not, however, possible to assign discrete ranges to them as one is wholly contained within the other. I therefore conclude that they are identical although this arrangement gives a greater range of color variation (in the adult breeding male) than is found in any of the other combassous.

V. chalybeata has five races—*chalybeata*, *codringtoni*, *neumanni*, *orientalis*, and *ultramarina*. This arrangement is in agreement with Delacour (1951) and Chapin (1954, pp. 567–569) with the exception that Chapin listed *codringtoni* tentatively as a species, although he wrote that "if not a valid species, *codringtoni* may perhaps be a southeastern race of *H. chalybeata*, more greenish than *orientalis* but of similar size."

V. funerea has three races—*funerea*, *nigerrima*, and *wilsoni*. Here the only point at which the present arrangement differs from those of Delacour and Chapin is that *purpurascens* is considered a synonym of *nigerrima*. Delacour may have come to the same conclusion as he did not mention *nigerrima*, but listed *purpurascens*. The name to be used, however, is *nigerrima*, which has 12 years priority over *purpurascens*. Although he kept the two separate, Chapin (1954, pp. 564–565) admitted that he found "it difficult to fix the limits between *nigerrima* and *purpurascens* and can only assume that the former ranges from Angola west to the Lualaba River near Kasongo." He stated of the species *funerea* that "in Angola and the Kasai region it is supposed to be replaced by *nigerrima*, of which the males are blue-black, not very glossy; and in Tanganyika Territory, the Katanga, and the Kivu by *purpurascens*, probably more purplish though not very glossy."

The color of the primaries in the breeding plumage of the adult male is the most stable and useful character by which to distinguish the species of combassous. These feathers are black or dark blackish brown in *Vidua chalybeata* and its races, and are paler brown (earth brown to pale fuscous) in *V. funerea* and *V. amauropteryx* and their included forms. The latter two species may be told apart (in breeding adult males only) by the fact that *funerea* has the entire head and body black with little or only moderate luster, tinged with purple or violet, while *amauropteryx* has a much more pronounced gloss tinged with blue or green, but not with violet. The difference between the black and the paler brown of the remiges is not due to fading or abrasion as might on first sight seem to be the case. As far as is known, the molts and the molting seasons seem similar in all the species.

Aside from the color of the remiges and the degree and hue of the general plumage gloss, the color of the bill and feet is of some diagnostic usefulness. The evidence from this character, however, does not parallel or agree very closely with that of the remigial character, and here again, unfortunately, the potential utility of this character pertains only to breeding adult males. In the nominate race of *V. amauropteryx*, the bill and feet are coral red; in its northern race *nigeriae*, and in both the other species, the bill is said to be white to pinkish white, and the feet are recorded as whitish to pinkish to orange yellow or pale brownish, except in *V. chalybeata neumanni*, in which the feet are said to be red. It is not known with certainty how constant these color characters are, or how significant they are. Wholly on the basis of bill color, *nigeriae* and *amauropteryx* are very different, but they seem to be conspecific otherwise and are so treated here.

The ranges and characters of the races of each species are treated under the respective species accounts.

INTERSPECIFIC RELATIONS IN LIFE: Determining the relations between species of combassous rivals the difficulty posed by the African *Zosterops*, a problem recently elucidated by R. E. Moreau (1957). The combassous have the same problem concerning the allopatry and sympatry of the included forms. It appears that while the geographical ranges of species of combassous overlap extensively over very wide areas, their ecological ranges coincide less completely. In one respect the problem in the combassous is even more difficult to settle. During the nonbreeding season, the combassous form loose flocks, which may contain more than a single species, but in such cases it is impossible to identify component elements because of the similarity in plumage of "off season" males, females, and young birds of several species. Furthermore, if two locally sympatric species were to hybridize, it would be almost impossible to sense the hybridization from subsequent examination of specimens, as the species involved differ only in the breeding plumage of the adult males. Even in this respect they differ only in the degree and hue of sheen, the degree of darkness of the remiges, and the color of the bill and feet. Also the bill and foot color is quickly lost if not recorded on the label by the collector, so that the diagnostic usefulness of this color is frequently quite limited, if not absent.

The obvious similarity in appearance and the equal similarity in habits of the species of combassous makes me wonder how much competition exists between them. While there is as yet not enough information on this point, possibly the combassous are less in conflict interspecifically than mere geographic occurrence records indicate. I was informed by M. P. Stuart Irwin (in litt.) that in his area in Southern Rhodesia, the species *Vidua amauropteryx* and *V. funerea* are ecologically fairly well separated, the former living on the outskirts of human habitations, gardens, and roads, while the latter is largely restricted to the wilder areas. This separation is definite enough to impress the observer in the field as a well marked difference. Irwin found that plotting the positions of singing adult males in the breeding season on a large scale local ecological chart bears out the field impression completely. During the nonbreeding season, these combassous occur in flocks of as many as 30 or 40 individuals, but during these months it is impossible to say whether or not the two species remain apart. When the birds begin to come into breeding condition, the flocks do not seem to "split up" but rather to "fan out" over a suitable area, where the males establish their singing posts. This result is true of both species. Since the local population of both in Irwin's area is rather small for the total amount of space available, in some instances the two species may not come in contact and hence have little or no cause or opportunity to compete.

There apparently is, however, some variation in this matter as Irwin informed me that once when he shot a male *Vidua amauropteryx* from its singing tree, its place was taken quickly by a *V. funerea*, which, in turn, after being collected was replaced rapidly by another of the former species. In Mozambique, Lamm (in litt.) saw the two species in mixed flocks together with pin-tailed widow birds, *V. macroura*.

Ross's recent (1957) study of natural coexistence of very similar species of leaf-hoppers is of comparative interest here. His data suggest that even closely similar species differ slightly physiologically, and hence any two species will have slightly different ecological optimum needs. He also pointed out that every ecological niche is not continuously uniform, but is subject to changing degrees of local and annual variation around ecological means. As a result, each such niche may be inhabited by more than one species concurrently. It seems, in the absence of definite interspecific competition, that the number of similar species temporarily coexistent in a given niche is not subject to a predictable limit, and also that mixing of organisms between niches increases the frequency and the complexity of such natural coexistence.

Perhaps even more pertinent as comparable material, because of its avian nature, is the case of the two species of *Sturnella* that Lanyon (1957) recently studied. The two are very similar morphologically and in their breeding behavior, but where they overlap, they seem, nevertheless, to be effectively isolated reproductively. The slight, differential ecological preference shown by them hardly constitutes more than a partial isolating mechanism, but, similar to the combassous, what else serves to keep them apart is unknown. Lack (1947) discussed a fairly comparable situation in the finches of the genus *Geospiza* in the Galapagos Islands.

In most of Kenya and Uganda, areas from which observational data can be expected, only the black-winged combassou occurs, but in large areas of Africa the situation is otherwise, and it is hoped that, in them, observers will determine the degree and the manner of coexistence of these closely allied species. Coexistence raises the question of the applicability of Gause's principle (see Gause, 1934; Crombie, 1947; and Mayr, 1947), which states that generally two or more closely similar species with similar ecological requirements cannot live sympatrically indefinitely because one of them will probably prove to be more efficient and will eventually outbreed and replace or supplant its competitors.

AVICULTURAL DATA ON LIFE HISTORY: If our knowledge of the life histories of the various combassous were greater, we possibly would sense differences in habits and behavior of species that are not now noticeable. Unfortunately, so little is known of any of the species that the full value of some of the published observations cannot be elicited because they cannot be identified to species with certainty. As all the included forms probably differ only in relatively minor ways, however, a few notes not definitely referrable to particular species are worth recording here as contributing to the general picture of the biology of the combassous.

At this point it is necessary to anticipate the largely unwarranted, but recurrent objections that many field naturalists raise against observations of birds living under the limiting conditions of captivity. Undeniably, the observer must be very much on guard against easy acceptance and uncritical transference of such data into the more arduously pieced-together fabric of the ethology of each species, but the restrictions of captivity enable us to make observations that would be exceedingly difficult to make in the field, and even then only under very favorable conditions. Still more important, captivity affords a good opportunity to view behavioral patterns, or fragments of such patterns, away from the environment to which they are adapted and in which they are apt to seem more purposive than they really are.

In the older literature are descriptions of nests attributed to combassous, but practically all students of African birds consider these descriptions in error. There is general agreement that combassous are brood parasites entirely. I too agree, but feel that in all fairness, the following cases, all based on birds in aviaries, should be presented and discussed here.

According to A. G. Butler (1899, p. 265) Russ, after years of effort to breed combassous in captivity, noticed that—

> a female was continually flying round the nest of a pair of little Red Astrilds [*Lagonosticta* sp.] and now and again slipped into it. The Ornamental Finches did not permit themselves to be at all disturbed thereby. . . . But the female of the latter never proceeded to egg-laying. . . . After a long time the female Steel Finch dragged coarse bents into an already used, and very dirty Zebra Finch nest, upon the compressed structure, and formed upon the latter a semi-domed nest cavity. The laying of five eggs was incubated by the female alone in twelve days, whilst the male defended the nest jealously, and pursued all other birds, even very large ones, with outcry and flapping of wings.

While this account states that the hen combassou built a nest and incubated her eggs, there is no real evidence to prove this most important point. There is too much likelihood of insufficient observation to rule out completely the possibility of the hen zebra finch having been further involved. Unfortunately Russ's original account (1884, pp. 175–176) gave no further data. True, Hopkinson (1926, p. 27) appeared to accept Russ's claim to have bred combassous (here identified (?) as *Vidua chalybeata*), but Hopkinson added that the first aviculturist to do so in Germany was Tittel. K. Neunzig (1921, p. 33) meanwhile had stated that the bird had been bred only once in German aviaries.

A recent case in a Danish aviary reopens for appraisal the question of possible nonparasitic breeding in the combassous. K. Nielsen (1956, pp. 11–13) wrote that in 1951, A. Nielsen succeeded in breeding combassous (*Vidua chalybeata*) as parasites on a pair of fire finches, which hatched and fed the young parasites. Furthermore, in 1955 K. Nielsen had—

> succeeded in breeding the Combasou, but in this case the Combasous themselves constructed the nest, hatched and fed the young.
>
> About the 1st of July I saw the male Combasou gather dry grasses, hemp, and other kinds of nesting materials, but I didn't pay much attention to this, as I had read . . . that the Combasous were parasites. . . . It was only when I

saw just one of the Combasous at a time in the aviary that I became suspicious that something was about to happen.

I didn't dare investigate the nest, which was placed in the wire netting, and was very loosely constructed of grass and hay, with the entrance sloping down. In the middle of July I again saw both of the Combasous in the aviary at the same time, but only for a short visit. Then the female returned to the nest again. I can't say if they took turns in hatching, but I noticed that they were both in the nest at night.

About the feeding, I have learned that both the male and the female are ardent feeders as long as the young are in the nest. It always happens in this way—first the female enters the nest, and directly after her the male. The male is always the first to leave the nest, perhaps the direct feeding is undertaken by the female alone.

On the 3rd August, two fledglings left the nest, and now these two fledglings are fed by the male only. The female has no interest at all in the young, even if they are begging her for food. Now and then I have seen the young begging Zebras and Cordon-bleus for food. Sometimes they succeed, but it also happens that they are pecked at instead of getting something to eat.

The male Combasou guards his young carefully, and will not tolerate their being harmed by any other bird. The female is, as stated above, quite indifferent. In spite of the fact that the fledglings left the nest seven days ago, they spend the nights with their parents in the nest.

This detailed account, surprising and contradictory as it seems to be, cannot be dismissed very easily. I must accept the observations of the adult male combassou feeding the fledged young, even though I still wonder whether the female of a host species remained unobserved in the nest during incubation (K. Nielsen carefully abstained from examining the nest so as to avoid frightening the birds, and he says that there were many other kinds of birds in the cage).

Commenting on this case, Prestwich (1956, p. 13) wrote that he knew of no record of a similar instance in British aviaries. The nearest to it was a case that Boyd (1914, p. 338) described. She had one young combassou reared by cordon bleus. "The hens of the respective pairs (combasous and cordon-bleus) each laid eggs in the same nest, the combasou three and the cordon-bleu four. The cordon-bleus alone incubated. . . . of the seven eggs only three hatched out, one combasou and two cordon-bleus, but the latter were not fed; the young combasou, however did well, and is now fending for itself." This case is more similar to that of A. Nielsen than to the one reported by K. Nielsen. My attempts to get further information from the latter individual have thus far met with no success. Poulsen (1956) redescribed but did not add new data to the two Nielsen cases.

Three more instances of avicultural breeding of combassous should be discussed. Tomlinson (1935, pp. 40–41) reported that in his aviary a pair of combassous laid their eggs in a nesting box in which an Australian shafttail (*Poephila acuticauda*) was incubating. One combassou chick was hatched but was drowned a few weeks later in a heavy rain. No further details are available on this case.

In a recent number of the Avicultural Magazine (vol. 53, 1947, p. 104), it was announced that the Avicultural Society of South Australia had awarded its medal in 1937 to C. C. Cosgrove for breeding black-winged combassous in his aviary. Through the kindness of Phyllis Barclay-Smith and Alan Lendon, I contacted Cosgrove. He informed me that his combassous were raised by a pair of fire finches in the aviary. His first indication of the young combassous came when they were already independent of parental (or foster parental) care. About 5 weeks later he noted a male fire finch feeding a young bird different from its own. He then discovered a pair of fire finches feeding three young birds, which, when they reached maturity turned out to be black-winged combassous.

Olsen (1958) reported what amounts to a dual case. In his aviary in Denmark, a young black-winged combassou was reared in 1956 by a pair of fire finches. The following year this combassou, which turned out to be a hen, mated with its father and layed two eggs in a nest of the same host, together with three eggs of the latter. One young combassou and two fire finches were reared from this nest. Olsen reported that the female fire finch began to incubate on July 20 and that all the eggs hatched on July 31, the period of incubation amounting to 11 days and being the same for both the host and the parasite. The parasite had no accelerated developmental gradient as occurs in some brood parasites. The young of both species left the nest on August 18, the nestling period amounting to 18 days.

We have, then, two reports (Russ and K. Nielsen) that suggest a certain amount of nest building (or at least the picking up and carrying of nesting materials), and of care of the young, (possibly also incubation) by combassous in a state of captivity. One of these (Russ) is less definite than the other. Contrasting with them are at least five reports (Boyd, Cosgrove, A. Nielsen, Olsen, and Tomlinson) of parasitic breeding. These reports agree with what is known of the habits of the various species of combassous in the wild state. The only conclusions that I draw are that these birds are brood parasites and that the two supposedly contrary instances are not as completely established as their reporters seemed to think. True, years ago A. G. Butler (1914b) wrote that combassous in his aviaries built in any of the usual nesting receptacles placed there, but he never reported any details and never succeeded in raising these birds. He attributed his failure to the fact that his hens generally died from egg binding, but his observations were not recorded and therefore do not constitute data. The facts, which seem acceptable, that the adult male combassou feeds the fledged young birds and that the adult male picks up and carries nesting materials, even though observed as yet only in captive aviary birds, give a small but welcome ray of light on the possible habits of the remote, ancestral condition from which these birds have deviated with the advent and development of the parasitic mode of reproduction.

Aside from the question of parasitic versus nonparasitic breeding, avicultural observations have yielded the following more or less disconnected items about these birds:

Plumage changes: Like the long-tailed widow birds, the short-tailed species do not seem to acquire complete nuptial plumage in their first year. A. G. Butler (1899, p. 265) found that in the first year the young males only partly assumed the nuptial black plumage, and became dappled in appearance. Mackworth-Praed and Grant (1955, p. 1041) wrote that *Vidia chalybeata ultramarina* often breeds in immature plumage, but I am not aware of any evidence to support this statement.

Longevity: A glossy combassou lived for 10 years in an aviary, a longevity of considerable duration for so small a passerine bird (Schorkopf, 1937, p. 455). Another glossy combassou of unrecorded age when acquired lived for 5 years in captivity (Reimann, 1937, p. 159). Still another is recorded as surviving for 10 years, 4 months in captivity (Mitchell, 1911, p. 476).

Clutch size: The number of eggs laid in one season (one clutch or more) by one hen is not known, but the following figures of egg laying by captive birds may give something of an indication. Steinmetz (1937, pp. 352–354) recorded four eggs from a combassou in the Berlin Zoo. Russ (1884, pp. 175–176) noted five eggs for his bird. Boyd noted (1914, p. 338) three eggs for her individual.

Brown-Winged Glossy Combassou

Vidua amauropteryx (Sharpe)

DISTRIBUTION

The glossy combassou, here understood as comprising only two races, *V.a. amauropteryx* and *V.a. nigeriae* (of which *camerunensis* is a synonym), ranges from western Transvaal,[67] Bechuanaland, and Damaraland, north to Matabeleland, across eastern and central Northern Rhodesia (from Livingstone to the Kafue River and west to Mapanza) and Nyasaland, north to southern Angola, the Kasai District of the Belgian Congo (Kwamouth to Luluabourg and the Lomami district), Mozambique, Tanganyika, along the coast to

---

[67] Although this combassou has not been collected southeast of western Transvaal, Walker (1932) saw a red-billed combassou as well as the common white-billed combassou, *V. funerea*, in the eastern Cape Province (Queenstown and the Kei Valley). The red-billed combassou was probably *V. amauropteryx*. Further observations are needed to establish the southern limits of its range.

Kenya, and north of the equatorial forest from Gambia, Portuguese Guinea, Sierra Leone, Ghana, Nigeria, northern Cameroons, to the Darfur and Bahr-el-Jebel areas of Sudan, the Uelle District of the extreme northeastern Belgian Congo, and to northern Ethiopia (Gallabat, Machigay, Gondar). The nominate race is the southern portion of the species, and ranges north as far as southern Angola, the Lundazi region of Northern Rhodesia and in eastern Africa north through Mozambique, Nyasaland, and eastern Tanganyika to the coastal belt of Kenya (Malindi). The rest of the range given above for the species is occupied by the subspecies *nigeriae*.

In parts of its range, this species, or at least its northern races, may be locally migratory. Thus, in the Uelle District, northeastern Belgian Congo, Chapin (1954, p. 571) found it present only from September to January, during which time it apparently bred there, He concluded that it probably spends the remaining months to the north in the Sudan. How far north is not known, but in the part of the Sudan immediately north of the Uelle, the Bahr-el-Ghazal, it is as yet unreported. Still farther north, in the Darfur Province, Lynes (1924, p. 670) recorded it as arriving in mid-September to breed, apparently very much like the situation Chapin found a little farther south. Lynes, however, considered the arrival as "merely indicating the cessation of off-season rovings, not an immigration." Elsewhere in its range the glossy combassou has not been recorded as seasonal except in a very loose way, which probably indicates insufficient observation rather than actual movements of the birds. As an example of such inconclusive reporting, I cite Priest (1936, p. 350), who wrote that in Southern Rhodesia, "it seems as if it is a migrant to us in the rains."

Everywhere throughout its range, the glossy combassou is a denizen of the tree-dotted grassy savannas and of bushy growths, but does not occur in forested areas or in very arid regions. It frequents the vicinity of native villages, but does not seem to come into them, and feeds on the ground in small, loose flocks in the patches of cleared and cultivated land immediately adjacent to them. It is often seen along roads in bushy areas, where the sides of the more open spaces of the pathways offer it the edge vegetation that it likes. Its recorded altitudinal range is from close to sea level up to 7,000 feet.

BREEDING SEASON

The following are the pertinent data as to the time of breeding of the glossy combassou in various parts of its range:

SIERRA LEONE: Northern Koinadugu, November, "obviously their breeding season" (Serle, 1949, p. 125), a statement based on the fact that the males were in nuptial plumage and were in full song; however, there are no actual breeding records.

CAMEROONS: Cameroon grasslands, breeding specimens taken in October and January (Bates, 1930, pp. 515–516).

BELGIAN CONGO: Faradje, Uelle District, December 6, fully grown fledgling collected. Adult male in breeding condition collected November 19.

SUDAN: Darfur, breeding in September (Mackworth-Praed and Grant, 1955, pp. 1045–1046), based on Lynes (1924, p. 670), who merely assumed that these combassous arrive to breed there in mid-September.

NORTHERN RHODESIA: "Along the Zambezi River," no date given, female *amauropteryx* with a male in close company seen to enter the nest of a cordon-bleu. Magoya Mazabuki, January 5, male nearly in breeding condition collected.

SOUTHERN RHODESIA: Hunyani River at Sinoia, Mashonaland, January 6, male in breeding plumage in full song (no breeding records however). Insiza District, February 21, eggs attributed to this combassou, but identity must be considered as unproved.

TANGANYIKA: Matengo highlands north of Lake Nyasa, breeding season begins in the dry season, February to June (Meise, 1937, pp. 155–156).

MOZAMBIQUE: Mocuba, February, male with gonads beginning to enlarge. Others April 27, May 28, and June 5 with testes subsiding after recent breeding (J. Vincent, 1936, pp. 111–112). Movene, January 28, "males were definitely approaching breeding." April 19, male collected with testes still somewhat enlarged (Lamm, in litt.).

NYASALAND: Breeds February to June (Mackworth-Praed and Grant, 1955, pp. 1042–1043). Breeds March to July (Belcher, 1930a, pp. 335–336). Males in full breeding plumage with enlarged gonads collected May and June in northern Nyasaland (Benson, 1941, p. 45). Egg "very probably of *Hypochera* sp." April (Benson, 1953, p. 80).

SONGS AND CALLS

When singing the male glossy combassou usually uses an exposed, elevated perch on top of a tree in or near an expanse of grassland. Thus, in Sierra Leone, Serle (1949, p. 125) wrote that in "northern Koinadugu, in the orchard bush, in November, it was no uncommon sight to see a male Indigo-finch perched in the summit of a tree in or near a clearing, singing cheerily. This was obviously their breeding season." In Mashonaland, Southern Rhodesia, Irwin (1952, p. 115) noted a male in full breeding plumage singing from the top of a bush along the Hunyani River at Sinoia, on 6th January. In Nyasaland, Belcher (1930a, pp. 335–336) found the males began to come into the black nuptial plumage toward the end of the rains and to breed from March to July. In the breeding season the flocks tend to break up into pairs, "and the male . . . may be seen perched on a high branch in the scrub, singing at intervals a pleasing little strain." In Mozambique, Lamm noted that adult males in breeding plumage were occupying conspicuous perches on the tops of dead trees, and were in full song in March and April.

The song is quite similar to that of the pintail (*Vidua macroura*), a rapidly repeated series of notes neither rising nor descending in pitch and possessed of little carrying power. The only call note that I ever heard was a somewhat rasping single *tsip* or *dzip* note. Chapin (1954, p. 572) noted that the race *nigeriae* has a call note often given while flying, a harsh *cha-cha-cha-cha*, and a song consisting of thin twittering *chwee* syllables.

Courtship, Territorial Behavior, and Mating

The glossy combassou has a courtship display similar to that of the East African species *Vidua chalybeata*. The male either bobs up and down in a jerky movement of very short distances from its perch, or actually flies up from its perch a short but still considerable distance of about 15 or 20 feet, and then back to it again several times in rapid succession, and gives its song as it flies. I observed this behavior on two occasions in January in Southern Rhodesia. In Sierra Leone, Serle (1949, p. 125) noted that the male "hovered with flapping wings for several seconds before the female who was perched on a small tree. This hovering display flight resembles that of *Vidua macroura*." Chapin (1954, p. 572) observed similar hovering by males near hen birds in the Belgian Congo, where he also once saw a brown-feathered, second-year male behaving the same way. In Mozambique Lamm (in press) once saw a female combassou of uncertain species courted simultaneously by a male glossy combassou and a male dusky combassou, *V. funerea*.

Little is known of the territorial behavior of this species, but the fact that certain exposed perches have been noted being used hour after hour and day after day as singing perches by males (probably the same ones) suggests some degree of territoriality. In Nyasaland, Belcher (1930a, pp. 335–336) noted that with the advent of the breeding season, the "winter" flocks break up into pairs, but he gave no details as to the actual disintegration process.

Eggs and Egg Laying

As was mentioned in our discussion of hosts, Mackworth-Praed and Grant (1955, pp. 1042–1043) described the eggs as white, but gave no indication of where they got their information and of how they identified the eggs. No doubt all combassous lay unmarked white eggs, but proof for each species is still needed. The little that is known of the glossy combassou and its close relatives also suggests that it does not commence to breed until it is 2 years old.

Hosts

Although statements in the literature indicate that the glossy combassou is parasitic on fire finches, I do not know of a single completely authenticated egg or nestling. Thus, the statements are only assumptions, as the records on which they are based are uncertain. The pertinent statements are the following:

Chapin (1954, p. 572) wrote that the glossy combassou (race *nigeriae*) bred in the Uelle District of northeastern Belgian Congo by laying its eggs "in nests of fire-finches or waxbills, although *Lagonosticta senegala* was not available there. It may well be that the choice of fosterers varies with the different species of *Hypochera*." Mackworth-Praed and Grant (1955, pp. 1042–1043) wrote of the glossy combassou: "Parasitic on the Red-billed Fire-Finch and other Waxbills, eggs white, no measurements available." Unfortunately, no supporting information was given, and I have not been successful in learning who found and described the eggs and how their identification was determined.

In 1951 in the Victoria Memorial Museum, Salisbury, Southern Rhodesia, I found an entry in the catalog about a set of four eggs of the glossy combassou taken by T. Collins from a nest of a red bishop (*Euplectes orix*) [68] in the Insiza District, Southern Rhodesia, on February 2, 1939. I was unable to locate the specimens. According to the catalog entry, a pair of glossy combassous were seen near the nest "very agitated in their behaviour." Apparently the collector was under the impression that the combassous had nested in an old nest of a bishop bird, an impression heightened by the excited actions of the pair of combassous; however, in the light of what we know of the parasitic reproduction of combassous in general, there is no reason to accept this inference.

Winterbottom (1951, p. 39) wrote that the cordon bleu (*Estrilda angolensis*) [69] was recorded as a victim of the glossy combassou. This statement seems to be based on two indefinite records: One by Belcher (1930b, p. 74) of an egg tentatively identified as of a combassou, found with a set of eggs attributed to *Estrilda angolensis* in a nest apparently built in an old nest of a *Pytilia;* and one, an incomplete observation by Winterbottom apparently not published until a year after (1952, p. 40) an earlier statement of his. Winterbottom saw a hen glossy combassou with a male close by enter the nest of a cordon bleu, near the top of a high *Acacia* along the bank of the Zambezi River. The nest was inaccessible, and, consequently, he was not able to determine if this activity was actually a case of parasitism. I recall Adlersparre (1922, p. 10) stating that "*Hypochera*" (no specific identification given) is parasitic on the cordon bleu; unfortunately, he gave no supporting data, and at this late date it is impossible to learn what observations he may have had as a basis for his pronouncement.

---

[68] *Emberiza orix* Linnaeus, Systema naturae, ed. 10, vol. 1, 1758, p. 177 (Africa, Angola).

[69] *Fringilla angolensis* Linnaeus, Systema naturae, ed. 10, vol. 1, 1758, p. 182 (Angola).

Benson (1953, p. 80) listed under this species the following very uncertain comment: "Egg, very probably of *Hypochera* sp., April; host probably *Pytilia* sp." As far as I know there is no authentic record of a *Pytilia* as a host of a combassou.

YOUNG OUT OF THE NEST

Chapin (1954, pp. 570–571) described a newly fledged glossy combassou as follows (paraphrased): Bill dull horn color, darker above. Interior of mouth whitish, with five dusky spots on palate, those on sides of the palate larger than more median ones. On back of tongue two dark spots, and black crescent on inside of mandible beneath tongue. Skin at corners of mouth pink, but no longer showing any swelling (which probably existed earlier).

There is an unfortunate dearth of information concerning the nestling and the postnestling stages of this bird. Judging from the other viduine weavers, I assume that the young are reared along with their foster nest mates in apparent amity; however, field observations are sorely needed.

FOOD AND FEEDING HABITS

The food of the glossy combassou seems to be restricted to small seeds of grasses and similar plants. Writing of the race *Vidua amauropteryx nigeriae* in northeastern Belgian Congo, Chapin (1954, pp. 571–572) found only such seeds in the crops of six specimens collected. He noted small flocks of these birds hopping about along paths and cultivated clearings where there were grasses and other potential food sources.

PLUMAGES AND MOLTS

Vidua amauropteryx amauropteryx

ADULT MALE IN BREEDING PLUMAGE: Entire head and body, upper wing-coverts, scapulars, and long innermost secondaries Black with moderately pronounced Bluish Slate-Black gloss. Concealed tuft of white feathers on either side of rump. Remiges Clove Brown to pale Fuscous, internally edged pale Drab, and the narrow outer webs of the primaries narrowly edged with the same, appearing almost like whitish lines. Under wing-coverts whitish to Tilleul Buff. Rectrices uniformly Fuscous. Bill Coral Red. Feet Flesh Ocher to Apricot Orange. Iris Fuscous-Black. Wing 64–70 mm. Tail 38–41 mm. Culmen from base 9.5–11 mm. Tarsus 13–14 mm.

ADULT MALE IN NONBREEDING PLUMAGE: Forehead, middle of crown, lores, and broad superciliary stripe pale Buffy Brown to pale

Tawny Buff. Lateral margins of crown and occiput dusky Saccardo's Umber, each feather with a Fuscous shaft streak. Some of buffy feathers of central portion of occiput also with Fuscous medial streaks. Two lateral coronal bands broadening markedly on occiput. Line from bill through and behind eye Fuscous. Back and upper wing-coverts tawny buff with Fuscous medial portions. Dark inner areas widening on upper wing-coverts to the extent that buffy areas are reduced to fairly broad edgings. Remiges dusky Clove Brown to Fuscous. Long innermost secondaries broadly edged with tawny buff. Feathers of lower back, rump, and upper tail-coverts dull, dusky Tawny-Olive, with centers dusky Olive-Brown. Outer rectrices Clove Brown to Fuscous, narrowly edged, and somewhat more broadly tipped with white or buffy white. Median rectrices somewhat paler, grayish brown. Cheeks, auriculars, sides of throat, entire breast, flanks, sides, and thighs pale Ochraceous-Buff to pale tawny buff. Chin, center of throat, abdomen, and under tail-coverts white. Iris and feet brown. Bill reddish brown.

FEMALE: Indistinguishable in coloration from nonbreeding males. Wings 62–68 mm. Tail 35.5–39 mm. Culmen 9–11.5 mm. Tarsus 12–13 mm.

JUVENAL (SEXES ALIKE): Similar to nonbreeding adult plumage, but with crown and occiput more uniformly Olive-Brown. Lateral areas only faintly darker than median portion. Edges of feathers of upper back, upper wing-coverts and remiges slightly more rufescent, Buffy Brown, of nape almost uniform Buffy Brown. Cheeks, chin, throat, and breast browner, between Avellaneous and somewhat tawny Wood Brown.

Vidua amauropteryx nigeriae

ADULT MALE IN BREEDING PLUMAGE: Similar to corresponding stage of nominate race but with gloss slightly more greenish, Dull Blue-Green Black. Bill whitish. Feet pale, to very pale, brownish. Size slightly smaller, with wings 61–66 mm., tail 40–40.5 mm., culmen 9–10 mm., tarsus 12.5–13 mm.

ADULT MALE IN NONBREEDING PLUMAGE: Like that of the nominate race.

FEMALE: Like that of the nominate race.

JUVENAL: Like that of the nominate race.

NATIVE NAMES

The following are native names reported for the glossy combassou. I doubt that the natives distinguish between the different races of these birds, and suspect that the seemingly definite allocation of the terms to species is open to question.

Native name	*Tribe*	*Locality*
Kadyasila	Tumbuka	Northern Rhodesia
Kaujiri (female)	Nyungwe	Nyasaland
Leng	Baya	French West Africa
Mtundufundo	Kunda	Northern Rhodesia
Nanchecheche (male)	Nyungwe	Nyasaland

MISCELLANEOUS DATA

LONGEVITY: As is noted in my discussion of the genus as a whole, Schorkopf (1937, p. 455) kept a male of the present species in his aviary for 10 years.

Brown-Winged Dusky Combassou

Vidua funerea (Tarragon)

This species of combassou is the least known of the three. Inasmuch as a good part of its range lies in areas where there are numerous resident observers, I hope that additional observations will be made. The following data comprise what we know thus far.

DISTRIBUTION

The dusky combassou ranges from the eastern Cape Province, Natal, Transvaal, the extreme northern part of South-West Africa (near the Angola border), north to Mozambique, Nyasaland, the Rhodesias, Angola, to the Kasai, Manyema and Kivu Districts of the Belgian Congo, and to north-central Tanganyika. It has become differentiated into three slightly marked races whose ranges are:

Vidua funerea funera: Eastern Cape Province, Natal, southern Mozambique, Nyasaland, and the Rhodesias (northern limit not yet worked out). It has spread throughout a good part of eastern Cape Province in recent years. It was first recorded near East London in 1916, and by 1922 it had reached Somerset East (Anonymous, 1932, p. 96).

Vidua funerea nigerrima: Northern Mozambique, southern and eastern Belgian Congo (Katanga, Manyema, and Kivu Districts) east to Ukerewe Island, Lake Victoria, and west to Angola, south to extreme northern South-West Africa (Oshikanga), and north in eastern Africa to southern and central Tanganyika. The identification to this race of the Oshikanga record is a geographic guess, as no specimen from there has been examined.

Vidua funerea wilsoni: From the Turkwel River area, extreme northwestern Kenya Colony, west through the Sudan (Equatoria) to northeastern Belgian Congo (Dungu, upper Uelle District), Cameroons, Nigeria, Ghana, Portugese Guinea and to Senegal. Chapin (1954, p. 566) questioned the record from northeastern Belgian Congo as to subspecies.

The altitudinal range of the species appears to be up to 5,500 feet. It is essentially a lowland bird.

Breeding Season

The following data give us an outline, of the breeding time of the dusky combassou in the various parts of its range:

South-West Africa: Oshikanga (just south of the Angola border), May, egg attributed to this species (A. Roberts, 1939, pp. 115–117).

Natal: Richmond district, no data, egg (A. W. Vincent, 1949, p. 668).

Nyasaland: April, May, and July, males collected with enlarged gonads (Benson, 1941, pp. 45–46).

Mozambique: Sul do Save, mid-December, birds collected in breeding condition (Lamm, in litt). Movene, January 28, male collected with enlarged gonads (Lamm, in litt). Northern Mozambique, February, March, May, June, and July specimens collected in breeding condition (J. Vincent, 1936, pp. 112–113).

Tanganyika: Matengo Highlands, begins to breed in April (Meise, 1937, p. 155). Birds in breeding condition in January (Mackworth-Praed and Grant, 1955, pp. 1044–1045).

Belgian Congo: Southeastern Congo, males in breeding plumage from December to early June. Kasai, November 19 to May 7 at least. Uelle District, October and November (Chapin, 1954, pp. 564–566).

Songs and Calls

The few comments in the literature and the few others sent me by observers suggest that the vocalisms of the dusky combassou are similar to those of other combassous. J. Vincent (1936, pp. 112–113) stated that the "call or twitter" (probably the song) reminded him of that of a linnet both in duration and in tone. He observed that the song is usually given by birds from fairly prominent perches. In this respect, too, this species resembles its congeners.

According to Irwin (1952, p. 115) the song ceases before the postnuptial molt commences. In Mashonaland he noted that the males stop singing and begin to flock in the first half of April, even though they are still in full breeding plumage.

Courtship, Territorial Behavior, and Mating

The courtship display of the dusky combassou as described by Hamling (1953, p. 16) is essentially similar to that of the pin-tailed widow bird—the former "dancing in the air in front of the hen, although much less vigorously and for a much shorter period." The seeming discrepancy in "vigor" may, however, be due to the presence of long rectrices in the pintail, which create an accentuated impression of the jerky, bouncing movements of the bird. I saw both this species, *Vidua funerea*, and the glossy combassou, *V. amauropteryx*, displaying in Southern Rhodesia, and did not see any difference between them in this respect. In the Blythswood area, eastern Cape Province, Godfrey (1929, p. 118) saw a male *funerea* give a, "mid-air display suggestive of the aerial dance of the Pied Widow. Along with two females he was chattering fifteen minutes before sunset, on the pinnacle of a bare blue-gum; he rose in the air and fluttered thrice in succession over one of the females, then returned to his perch."

The only evidence for or against territoriality in the dusky combassou are the observations that the individual males spend hour after hour at the same singing post. Lamm (in. litt.) observed this behavior in Mozambique from mid-December to mid-April, and considered it a sign of territorial attachment. In Southern Rhodesia Irwin (in litt.) noted somewhat similar behavior by both this species and the glossy combassou, and concluded that the singing males in a given area appear to be aware of each other's territories and do not intrude. When he shot a singing male, however, he found that its place on the same singing tree was quickly taken by another individual. Hamling (1944, p. 42) noted, in the eastern Caprivi corner, that the male dusky combassou can be seen "perched on an exposed branch in the broiling heat, when nearly every other bird is safely hidden in the shade. He uses the same branch day after day, and spends many hours upon it."

Chapin (1954, p. 566), writing of the race *Vidua funerea purpurascens* (a synonym of *nigerrima*), stated that "either this or a closely related form in southwest Tanganyika Territory is reported to remain in flocks until early May, then each male selects a tree from the top of which he delivers his weak twittering or warbling song. To this tree he returns constantly during the next several weeks." He doubted, however, that true pairing takes place but gave no evidence, and indeed there appears to be no evidence available as to what conditions really prevail. I am not aware of what data are behind his words that "it seems all but proved that pairs are not formed." His belief may have stemmed from the fact that some males in breeding plumage and condition were found in loose, small flocks all through the breeding season, and others were found apparently largely restricted to their individual singing posts.

Eggs and Egg Laying

J. Vincent (1936, pp. 112–113) wrote that he collected the "pure white egg" of the dusky combassou from a waxbill's nest in Natal. He gave no measurements and no indication how the identification was made. Without such information we can look upon his statement as merely an assumption, even though a fairly probable one. Other eggs, also pure white, referred to the dusky combassou measure 14.9 by 12.3 mm. (A. W. Vincent, 1949, p. 668) and 15.2 by 12.3 mm. (A. Roberts, 1939, pp. 115–117). A completely authenticated egg of the dusky combassou is still needed, no matter how safe it may seem to predict that the egg will be pure white and of the dimensions given above. Bannerman (1953, p. 1499) cited J. Vincent's statement, but his account credited the egg to the West African race, *Vidua funerea wilsoni*, to which it does not belong.

One female, collected by J. Vincent, appeared to be getting ready to lay 6 eggs; at least it showed that many enlarged ova.

Hosts

Three species of weaver birds have been reported as hosts of the dusky combassou, but, while some of the instances are highly probable, not one can be considered as proved. I know of no completely authentic eggs or nestlings of this parasite having been collected. All that can be said in critical support of the individual cases is presented below in such detail as is available and as seems worthwhile. Obviously, here is another opportunity for naturalists resident within the range of the bird to make a definite contribution to our knowledge.

Red-bellied fire finch: *Estrilda senegala* (Linnaeus) [70]

At Oshikanga, South-West Africa, just south of the Angola border, in May 1937, A. Roberts (1939, pp. 115–117) found a nest of this fire finch (race *E. s. rendallii*[71]) with 3 eggs in it. One of the eggs was larger than the others, this egg measuring 15.2 by 12.3 mm., as compared with 14.5 by 11.9 mm. and 14 by 11 mm., the measurements of the other two. Roberts never saw the fire finches at the nest, which was apparently deserted, but on several occasions he saw a male dusky combassou near it. Inasmuch as no other combassous were seen in the area, he assumed that the larger egg was referrable to this species—hardly a safe identification even though it may be a correct one. Winterbottom (1951, p. 38) listed this fire finch as a victim of the dusky combassou without further data, undoubtedly on the basis of Roberts' record.

Gill (1945, p. 32), based on Roberts, listed *Lagonosticta rubricata* [72] as a host. He may have mistaken this species for *Estrilda senegala* as I know of no record of the dark fire finch in this capacity.

There is reason to ask whether all these statements actually refer to the dusky combassou, *Vidua funerea*. True, this is the name used by Roberts for the combassou seen at Oshikanga, but the bird may actually have been the glossy combassou, *V. amauropteryx*. This species is known to occur in South-West Africa, while *V. funerea* has not been recorded south of Angola in the western part of the continent.

---

[70] *Fringilla senegala* Linnaeus, Systema naturae, ed. 12, vol. 1, 1766, p. 320 (Senegal).

[71] *Lagonosticta senegala rendalli* Hartert, Nov. Zool., vol. 5, 1898, p. 72 (Upper Shire River).

[72] *Fringilla rubricata* Lichtenstein, Verzeichniss der Doubletten des zoologischen Museum . . ., 1823, p. 27 (Kaffirland).

Oshikanga is, however, close to the Angola border, and probably Roberts correctly identified the bird that he saw.

Common waxbill: *Estrilda astrild* (Linnaeus) [73]

The common waxbill is the bird most frequently mentioned as a host of the dusky combassou ever since J. Vincent (1936, p. 109) reported that in Mozambique the local race *E. a. cavendishi* [74] was parasitized by the dusky combassou and by the pin-tailed widow bird. He recorded a nest with two eggs of the common waxbill, three of the pintail, and one of the dusky combassou. In the same area and at the same time he found the dusky combassou to be in full breeding condition, but gave no further evidence supporting the identification of the egg referred to this species. He related (p. 113) that he had taken, some time previously, the egg of the dusky combassou in nests of the common waxbill in Natal. Some years later A. W. Vincent (1949, p. 668) recorded the same combination of parasites, the dusky combassou and the pintail, *Vidua macroura*, laying in the nests of the common waxbill in the Richmond District, Natal. Again, as far as supporting evidence goes, the identification of the dusky combassou eggs was an assumption based on the occurrence of that bird there, and cannot be looked upon as proved. A. Roberts (1939, pp. 115–117) apparently accepted J. Vincent's record and identification. On the basis of Roberts' record, Gill (1945, p. 32), treated the identification as an apparently accepted fact. Bannerman (1953, p. 1499) wrote of the West-African race *Vidua funerea wilsoni* that the "pure white eggs of this indigo bird have been taken in the nest of the common waxbill." This record is based on J. Vincent (1936), and refers to the nominate race of the dusky combassou in Natal.

Bishop bird: *Euplectes* sp.

In the egg catalogue of the Victoria Memorial Museum, in Salisbury, Southern Rhodesia, there is an entry for a set of three eggs of the dusky combassou and one of a "bishop bird" in the nest of the latter, collected at Gokwe, Southern Rhodesia, January 9, 1933, by "A. N. C.," who reported having seen a hen dusky combassou leaving the nest. I could not find the eggs, however, and so was not able to examine and measure them when I was in that museum in January 1951.

FOOD AND FEEDING HABITS

According to de Klerk (1942, p. 63), the food of the dusky combassou consists of grain, grass seeds, small flowers, and insects. Belcher

---

[73] *Loxia astrild* Linnaeus, Systema naturae, ed. 10, vol. 1, 1758, p. 173 (Canaries, America, Africa=Capetown).

[74] *Estrilda cavendishi* Sharpe, Ibis, ser. 7, vol. 6, 1900, p. 110 (Mapicuti, Cheringoma District, Mozambique).

(1930a, pp. 336–337) noted a flock that came every day to pick up machewere seeds in a fowl yard at Nyambadwe House in the Shire Highlands, Nyasaland.

I have seen these birds feeding on small seeds along paths in Southern Rhodesia, but as the birds were near habitations, I did not feel free to collect any.

Plumages and Molts

Vidua funerea funerea

Adult male in breeding plumage: Similar to the corresponding stage of *V. amauropteryx*, but black plumage with much darker, dull, velvet-like sheen, blackish Dusky Dull Violet-Blue. Bill white or pale pinkish white. Feet coral red, orange, and flesh pink or even whitish (according to various describers, but I cannot help but question the extremes in the above-mentioned series). Iris dark brown or blackish. Wings 65–71 mm.

Adult male in nonbreeding plumage: Similar to that of *V. amauropteryx*, but more distinctly streaked above, more like *V. chalybeata* in this regard, but somewhat warmer brown than the latter.

Female: Similar to that of *V. amauropteryx*, but averaging somewhat paler. Not distinguishable with certainty from nonbreeding males. Wings 62–66.5 mm.

Juvenal (sexes alike): Not distinguishable with certainty from same stage of *V. amauropteryx*.

Vidua funerea nigerrima

Adult male in breeding plumage: Similar to that of nominate race, but less glossy, and the gloss darker. Very dark violet wash over black feathers. Bill white or pinkish white. Feet white or very pale flesh color. Iris blackish brown. Wings 64–70 mm.

Adult male in nonbreeding plumage: Not distinguishable from the corresponding stage of nominate race.

Female: Similar to male in nonbreeding plumage and to female of nominate race. Wings 62–66 mm.

Juvenal (sexes alike): Not distinguishable from that of nominate race.

Vidua funerea wilsoni

Adult male in breeding plumage: Similar to that of nominate race, but slightly more glossy and smaller. Wings 63–67 mm.

Adult male in nonbreeding plumage: Similar to that of nominate race, but slightly paler in color, and smaller.

Female: Similar to that of nominate race, but slightly paler in general coloration, and smaller. Wings 60–61 mm.

JUVENAL: None seen, but said to be indistinguishable from that of nominate race.

NATIVE NAMES

The only native name that I have noted is "Insimbi," a Kikerewe tribal name on Ukerewe Island, Lake Victoria.

Black-Winged Combassou

Vidua chalybeata (Muller)

Plate 6

DISTRIBUTION

The black-winged combassou differs from the other species of combassous in the blackish (not brownish) remiges of the breeding plumage of the adult male. It ranges from Northern Rhodesia, Nyasaland, Tanganyika, Kenya, Uganda, and the Belgian Congo, north to Ethiopia, Sudan, and French West Africa, west to Nigeria, Gambia, and Senegal. It has become differentiated into five races with the following ranges:

Vidua chalybeata chalybeata: Savannas and bush country of Upper Guinea from the French Sudan, possibly the French Niger Territory, west to Sierra Leone, Gambia, and to Senegal (Dakar, Kirtaona, Dagama, Richard Toll).

Vidua chalybeata neumanni: Northern Cameroons (Mayo Sola, Rei Bouba), northern Nigeria (Zaria, Lokoja, Bauchi, Kano), and northern Ghana (Morago River), and the Lake Chad area south to Fort Lamy, and east to Darfur Province, Sudan.

Vidua chalybeata ultramarina: Southeastern Sudan (Lado, Mongalla, Bahr-el-Ghazal) to Ethiopia (Addis Ababa, Harar, Hawash area, Arussi-Gallaland), north to Bogosland, Tacazzi and to southwestern Eritrea (Archico on the coastal plain of Cunana; not recorded from Dancalia, but said to be fairly generally distributed otherwise in this former Italian colony, chiefly in the hot lowlands in the Acacia savannas), and to Somaliland (Abrona).

Vidua chalybeata orientalis: Northern half or so of Tanganyika (Pare Mountains, Moschi), Kenya (Taveta, Voi, Machakos, Fort Hall, Kisumu, and many other localities), and Uganda (Entebbe, Jinja, Mabira, Npumu, Buvuma, and Rusinga Islands in Lake Victoria), and the eastern Belgian Congo (Barata, Gabiro, Kisenyi, Rutshuru, Urundi, Usumbura, and Uvera).

Vidua chalybeata codringtoni: Northern Rhodesia (Molilo's, near Petaukve, and Lupande River, Loangwa Valley), Nyasaland, and Tanganyika (north to Iringa).

BREEDING SEASON

What little is known of the time of breeding of the black-winged combassou is based on the following evidence:

SENEGAL: Richard Toll (a town), October 27, eggs (G. Morel and M. Y. Morel, 1955, pp. 281–282); February 22, egg (G. Morel, 1959, pp. 158–159).

GAMBIA: No date, nestling, Hopkinson (cited by Chapin, 1954, p. 569).

French Sudan: Ké Masina, January 30, hen with oviduct egg (Bates, 1914, p. 710).

Nigeria: Lukoja, June 19, egg (Jourdain and Shuel, 1935, p. 662). Kano, August 9, hen with developed ova (Bannerman, 1949, pp. 373–375). Nasarawa, August 12, male with greatly enlarged gonads (Serle, 1940, p. 45).

Sudan: Darfur, October and January, "probably breeding" (Mackworth-Praed and Grant, 1955, p. 1042).

Belgian Congo: Kasenyi, August and September, males with enlarged gonads (Chapin, 1954, p. 568).

Uganda: Entebbe, April and May, eggs (identification only probable, Pitman, in litt.). Pairing in January V. G. L. van Someren, 1916, p. 426).

Kenya: Kisumu, May and June, "breeding" (V. G. L. van Someren, 1916, p. 624) near Fort Hall, late March and early April. Birds with enlarged gonads collected (Lönnberg, 1911, p. 107).

Ethiopia: Dangila, September 19, female, supposedly nest building, (Cheesman and Sclater, 1936, p. 194).

Tanganyika: Iringa, March, breeding female collected "about to lay her last egg" (Lynes, 1934, pp. 128–129). No locality, January, breeding condition (Mackworth-Praed and Grant, 1955, p. 1042).

Songs and Calls

The vocal utterances of the black-winged combassou are similar to those of the other combassous. In the country around Taveta, Kenya Colony, I noted the call note of the eastern race, *Vidua chalybeata orientalis*, as an emphatic, slightly harsh *dzip* and concluded that it is not given as often or as repetitively as it is by some widow birds. The song is a rapid but rather formless series of notes, quite similar to that of the pintail, *Vidua macroura*, but slightly huskier and buzzier. In western Africa Bates (1930, p. 515) noted the nominate subspecies singing "a few scattering notes."

Courtship and Mating

At Taveta, Kenya Colony, in late March and the first 3 weeks of April, I often watched male black-winged combassous go through their display. It is a bouncing, aerial dance, the airborne segments of it being a quivering affair somewhat similar to the hovering display of the pin-tailed widow bird but of shorter duration. Between each of the bounces, the cock returns to the ground and then immediately leaps up again. He repeats 3 to 10 times. The whole display may last as long as 3 seconds, and is accompanied by a rasping, beady "song," the notes unmodulated and jerky as though the rhythmic bounces of the bird interfered with its delivery. The bird rises only a foot or two above the hen (or hen-plumaged bird), which is usually on the ground.

Mackworth-Praed and Grant (1955, p. 1041) wrote that the northeastern subspecies *ultramarina* often breeds in immature plumage. This statement implies that courtship also precedes the development of nuptial feathering, but I have seen no evidence to support this statement unless it is Chapin's (1917, p. 257) comment to the effect that he had observed "the black males of *Hypochera*, or even brown immature individuals hovering in the air beside their mates in the same way as cocks of *Vidua serena* [= *macroura*]." As far as is known, however, no viduine species begin to breed before their second year.

Eggs and Egg Laying

Olsen (1958) bred the black-winged combassou in captivity with *Estrilda senegala* as the host. He noted that the eggs of the parasite were pure white, slightly larger and more rounded than those of the host. He failed to measure the eggs as he did not want to disturb the birds. Aside from this record, no completely authenticated egg of this species of combassou has been described. Shuel (*in* Jourdain and Shuel, 1935, p. 662) found a dead black-winged combassou with an egg ready to be laid just outside the nest of an apparent intended host. While Shuel failed to describe the egg, he assumed that the nest belonged to this combassou. Because the nest contained four pure white eggs 13.4–13.7 by 10.7–10.9 mm., it seems likely that if the egg still in the body of the bird had been very different he would have been less prone to think the nest belonged to the same species. There is no reason to think that the egg of this combassou is ever anything but unmarked white, as are the known eggs of all the viduine weavers. Eggs, assumed by the collectors to be of the black combassou (but which may have been of the pin-tailed widow bird) from Entebbe, Uganda, are indistinguishable from those of the latter, these eggs being pure white and measuring 14.4–14.7 by 10.9–12.0 mm.

In the Gambia, many years ago, Hopkinson (1909, p. 7) described the eggs of the black-winged combassou as white, but I am not sure what eggs he was describing, as he assumed that this bird made its own nest and cared for its eggs and young in normal fashion.

Another similarly uncertain case was reported from Denton Bridge, Gambia, by Ross A. Walton. On October 20, 1943, he collected an old nest of an unidentified species of weaver that contained five fresh, pure-white eggs measuring 13.85–14.2 by 10.3–11.1 mm. A hen black-winged combassou was seen leaving the nest after the first egg was laid. The eggs are now in the collection of R. Kreuger, of Helsingfors, to whom I am indebted for this information. While this record cannot be considered as acceptable, I list it here in the hope that additional knowledge in the future may help to elucidate it.

Three other authors failed to place on record any corroborating details, so their statements are less useful than they would otherwise have been. Russ (1880, p. 681) stated that he bred the black-winged combassou in his aviary, but gave no further information, and thus left no record of what the eggs were like, their number, and their incubation period. Steinmetz (1937, pp. 352–354) wrote that a combassou probably of this species laid four eggs in the Berlin Zoo. Olsen (1958) recorded the incubation period (in captivity with *Estrilda senegala* as the incubating host) as 11 days.

HOSTS

Only two species of small waxbills have been recorded as parasitized by the black-winged combassou, the bronze mannikin and the red-bellied fire finch.

Bronze mannikin: *Spermestes cucullatus* Swainson [75]

V. G. L. Van Someren (in litt.) informed me that he had definite records of the black-winged combassou using nests of the bronze mannikin as receptacles for its eggs in the vicinity of Kisumu, Kenya, in July 1912 and 1913. How many such instances came under his observation is not known, and unfortunately no details are now available.

Red-bellied fire finch: *Estrilda senegala* (Linnaeus)[76]

At Burrem, French Sudan, in October, Bates (1934, pp. 709–710), saw "some little sparrowy [female?] Indigo-Finches entering with Fire-Finches through the holes in the nest ceiling of a house . . . and . . . saw something similar at Timbuktu. . . . The two species may always breed together—unless, indeed, the Indigo-Finch is parasitic on the Fire-Finch."

At Lokoja, Nigeria, June 19, Shuel (*in* Jourdain and Shuel, 1935, p. 662) found nests of the red-bellied fire finch with eggs measuring 13–13.5 by 10.4 mm. But in one nest, one egg measured 14.7 by 11.5 mm., and was, in all probability, a black-winged combassou's egg. Shuel found a similar nest with a four pure white eggs measuring 13.4–13.7 by 10.7–10.9 mm. He thought that this nest belonged to the black-winged combassou because a dead and partly decomposed female of this species lay just outside the nest and had an egg in its oviduct. Chapin (1954, p. 569) interpreted the incident to mean that the hen black-winged combassou probably got her foot entangled as she came to the nest to lay in it, "and her struggles and death caused the fire finches to abandon their home."

As further noted by Chapin, in Gambia Hopkinson found a nest of this fire finch out of which flew two young fire finches and one young black-winged combassou. Even after he captured the young combassou, the adult fire finches continued to bring food to it.

---

[75] *Spermestes cucullatus* Swainson, Birds of western Africa, vol. 1, 1837, p. 201 (Senegal).

[76] *Fringilla senegala* Linnaeus, Systema naturae, ed. 12, vol. 1, 1766, p. 320 (Senecal).

G. Morel and M. Y. Morel (1955) found a nest of this fire finch at Richard Toll, Senegal, October 27. It contained three young of the host and one of the black-winged combassou. The mouth markings of the two species were noted as being very similar. I am indebted to the observers for the photograph of the two kinds of nestlings (plate 6).

In the Ngong area, Kenya, V. G. L. van Someren (in litt.) saw a young black-winged combassou in a little flock of red-bellied fire finches feeding in a chicken run. The fledgling combassou was quivering its wings and begging for food. "They were disturbed before I could actually note a female *Lagonosticta* feeding it, but I have no doubt that it was fostered by a *Lagonosticta* (fire finch) who had her own youngsters with her." Van Someren's record refers to the East African race of the host *Estrilda senegala kikuyuensis*,[77] whereas the Senegal and Gambia records have to do with the nominate race of the host.

Because this fire finch is known to be victimized by the black-winged combassou, it should be noted that in the French Sudan, Guichard (1950, pp. 194–195) found that the two species seemed to share a tendency to live close to villages and to be scarce away from human habitations—in other words, to have the same ecological preference. Furthermore, G. Morel and M. Y. Morel (1955) wrote that in Senegal the black-winged combassous come into breeding plumage at precisely the same time that the fire finches come into breeding condition.

Recently, G. Morel (1959, pp. 158–159) made the most important discoveries thus far about the black-winged combassou and this fire finch. At Richard Toll, he found 33 nests at least 13 of which were parasitized by the blackwing. He noted that the female parasite first showed interest in the nests while they were being built. The hens frequently visited them as if checking on their progress. When the fire finches commenced laying, the nesting area was literally assailed by the female blackwings, which came and looked into the nest entrances, and as many as 5 of which disputed advent to a nest at certain times. Most of the nest visiting took place between noon and 3 p.m., the hottest hours of the day.

On February 22, 1957, from noon onward, a female black-winged combassou was noted busily coming and going close to a nest. At 12:53 p.m., it came to the nest, entered it, but left in about half a minute. Morel examined the nest immediately and found that the female fire finch was in it but that the blackwing had not laid during its brief visit. The fire finch continued to sit on the eggs in spite of the examination. At 1:25 p.m., a female blackwing (supposedly the same as before) resumed its fluttering flight close to the nest. Its actions

---

[77] *Lagonosticta senegalla kikuyuensis* van Someren, Bull. British Ornith. Club, vol. 40, 1919, p. 55 (Nairobi)

followed a pattern: It lighted on a perch over and in front of the nest, then rose to the full height of its legs without leaving the perch, and then dropped down to the entrance and looked in. Occasionally, the female fire finch appeared to repel the intruder, but not regularly or violently. At 1:35 p.m., the blackwing came to the nest, slowly entered it, remained inside a few minutes, and then left. Examination of the nest just after this visit revealed one egg of the parasite together with those of the host. The egg was laid in the presence of the incubating host. While the domed character of the nest prevented Morel from observing the act of ovulation or of any interaction between the birds, the end result indicated a complete tolerance of the intruder by the fire finch.

Nestling Stage

As in the other parasitic weavers, the black-winged combassou nestling grows up together with its nest mates and not at their expense. The case already cited and the illustration (plate 6) supplied by G. Morel support this inference. In captivity with the red-bellied fire finch as the host, according to Olsen (1958), the nestling stage lasted 18 days.

Young Out of the Nest

As was mentioned in our discussion of the red-bellied fire finch as a host of the black-winged combassou, V. G. L. van Someren saw a fledgling of the latter begging for food in a small flock of the former species. Hopkinson's Gambia record also showed that the fosterers continued to feed their parasitic fledgling after it had left the nest. G. Morel and M. Y. Morel (1955) recorded young black-winged combassous with groups of equally young fire finches, which continued to be fed by the male red-bellied fire finch after they had left the nest. It is not known, however, how long after quitting the nest the young parasite is attended and cared for by its foster parents.

Food and Feeding Habits

I watched black-wing combassous feeding on the ground by picking up what seemed to be small seeds from the grasses and other low vegetation. All of the birds collected had only small seeds in their gizzards. One individual had at least a hundred such seeds. In the French Sudan, Bates (1934, pp. 709–710) found this combassou feeding on the seeds of a particular plant, *Eleusina coracana*, but I did not note a preferred food source in my field notes. These combassous drink water regularly. A. L. Butler (1905, p. 316) saw them at Khartoum occasionally entering house verandahs to drink from the large earthenware filters.

PLUMAGES

Vidua chalybeata chalybeata

ADULT MALE IN BREEDING PLUMAGE: Like that of *V. amauropteryx*, but primaries and rectrices darker, Fuscous to Fuscous-Black with no paler external margins. Plumage of head, body, and upper wing-coverts black with moderately pronounced Dusky Greenish Blue gloss. Bill white or pinkish white. Feet Apricot Orange to Cinnamon-Rufous. Iris brown. Size slightly smaller, with wings 59–65 mm., tail 36–40 mm., culmen from base 9.4–10.8 mm., and tarsus 12.5–13.5 mm.

ADULT MALE IN NONBREEDING PLUMAGE: Like that of *V. amauropteryx*, but less uniform in appearance above. Edges of the feathers paler, between Pinkish Cinnamon and Pinkish Buff, making the dark centers stand out more in contrast. Center of crown Cinnamon-Buff. Sides of head, chin, throat, breast, sides, and flanks more tawny, light Cinnamon-Buff.

FEMALE: Like female of *V. amauropteryx*, but generally slightly paler above and below. Throat and breast averaging less brownish, more grayish. Not certainly distinguishable from nonbreeding adult male of its own species. Slightly smaller in size, with wings 58–62 mm., tail 34–37.5 mm., culmen from base 9–10.3 mm., and tarsus 12–13 mm.

JUVENAL (SEXES ALIKE): Like juvenal of *V. amauropteryx*, but very slightly more rufescent above. Edges of feathers of back, upper wing-coverts, and remiges slightly paler, dusty Tawny-Olive. Cheeks, chin, throat, and breast also more tawny, Cinnamon-Buff.

Vidua chalybeata codringtoni

ADULT MALE IN BREEDING PLUMAGE: Like that of nominate race, but larger, with wings 66–70 mm. Gloss of plumage more greenish. General color dull bluish black with a dark Bottle Green wash. Feet apparently averaging paler, salmon pink (but very few specimens were examined.)

ADULT MALE IN NONBREEDING PLUMAGE: Like that of nominate race, but larger. Said to have top of head blackish with broad central buff stripe. Sides of head and supraorbital stripe buff. Broad blackish patch behind the eye (suggesting onset of prenuptial molt). Upper back streaked blackish and buff. Rump plain earth brown indistinctly mottled with dusky. Remiges and rectrices blackish with buffy edges. Chin buff. Center of abdomen and under tail-coverts white. Under wing-coverts mottled brown and white. This description, taken largely from Mackworth-Praed and Grant, differs from that of the nominate race more than I would expect of actual specimens. I have not seen any actual specimens.

FEMALE: Like nonbreeding male, but somewhat smaller, with wing 64 mm.

JUVENAL: Apparently unrecorded.

Vidau chatybeata neumanni

ADULT MALE IN BREEDING PLUMAGE: Like that of nominate race but with more bluish sheen, between Dusky Blue and Indulin Blue. Wings 61–64 mm.

ADULT MALE IN NONBREEDING PLUMAGE: Not distinguishable with certainty from the corresponding stage of nominate race.

FEMALE: As in nominate race. Wings 60–66 mm.

JUVENAL (sexes alike): Similar to adult female, but slightly paler above and below. Throat and breast averaging less brownish, more grayish.

Vidau chalybeata orientalis

ADULT MALE IN BREEDING PLUMAGE: Like that of nominate race but slightly less glossy and sheen less greenish, more bluish, dark Dusky Blue. Iris blackish brown. Bill white. Feet pale brown. Wings 62–72 mm.

ADULT MALE IN NONBREEDING PLUMAGE: Not distinguishable with certainty from that of nominate race.

FEMALE: As in nominate race. Wings 62–65 mm. From his extensive East African material, V. G. L. van Someren (1922, p. 158) found that as the females begin to come into breeding condition they tend to become noticeably duskier on the crown, upper back, and breast than they do in the nonbreeding season. He noted that occasionally the breast becomes deep ashy brown, a condition that I noticed very markedly in three hens collected by Grauer in the Kageru-Kivu region (specimens now in American Museum of Natural History). Van Someren also stated that the female plumage—

> is very like that of the nonbreeding male, but even darker. The character of white under-tail coverts mentioned (in literature) in connection with these birds is not reliable, and simply indicates remains of the off season dress, these feathers being almost the last to be moulted. With regard to the brownish wings in certain birds of this group, it is quite noticeable that males which have gone through the nesting season, although showing very little abrasion of the tips of the primaries and secondaries, yet have these feathers much browner than in the freshly moulted, adult breeding bird. The first young plumage is like that of the females in off plumage, but altogether duller and paler on the breast.

JUVENAL (SEXES ALIKE): Like that of the nominate race.

Vidua chalybeata ultramarina

ADULT MALE IN BREEDING PLUMAGE: Like that of nominate race, but with gloss on black plumage more pronounced and darker and somewhat more violaceous, less greenish blue, very dark Dusky

Slate-Blue. Bill white. Feet coral or orange-red. Iris brown. Wings 57–70 mm.

ADULT MALE IN NONBREEDING PLUMAGE: Like that of nominate race.

FEMALE: Like that of nominate race. Wings 59–65 mm.

JUVENAL (SEXES ALIKE): Like that of the nominate race.

NATIVE NAMES

Very few native names for the black-winged combassou have been reported in the literature. I note that the Joloff name "kumbassooban" may have been the origin of the term combassou, which was first applied to these birds by the aviculturists and since then adopted more widely by ornithologists.

Native Name	*Tribe*	*Locality*
Kumbassooban	Joloff	Gambia
Nyanna-Fintong	Mandigo	Gambia
Sannafintong	Mandigo	Gambia
Tioukhoum	Arabicized	French West Africa
Tchorelli	Ukamba	Kenya Colony

Long-Tailed Widow Birds: Subgenus *Vidua*

The four species of long-tailed widow birds, so called because the breeding adult males have the two median pairs of rectrices greatly elongated, constitute the typical section or subgenus of the genus *Vidua*. They are remarkably dissimilar in the male nuptial dress, so dissimilar that at one time they were placed in three genera, but the differences are not of more than specific value. In their other plumages and in their general life histories, the species are very similar. For the benefit of field students and of museum workers, it is useful to have the differences between the females and the nonbreeding males of the included species outlined here. For further details, reference should be made to the plumage descriptions given near the end of the account of each species. In general, it is not readily possible to distinguish between males in nonbreeding dress and adult females of the same species.

The top of the head is buffy white with a blackish-brown stripe on either side in all but the straw-tailed widow bird, *Vidua fischeri*, whose crown is brown with dusky marks. Concerning the other three, the superciliary streak is white in the shaft-tailed widow bird, *V. regia*, and buffy varying from rufous buff to pale buff in the other two. The latter two may be told apart by the inner margins of the inner webs of the primaries, which are very narrowly edged with white in the pin-tailed widow bird, *V. macroura*, and more broadly edged with white in the blue widow bird, *V. hypocherina*. The latter also has a dusky mark in the loreal area, which is not present in the pintail.

Blue Widow Bird

Vidua hypocherina J. and E. Verreau[78]

PLATE 7

DISTRIBUTION

The blue widow bird is widely distributed but rather local in the drier bushveld country of eastern Africa from Ethiopia (from Shoa-Hawash, Addis Ababa, Ourso, east to Harar, and south through the Arussi-Gallaland and Boran areas),[79] British Somaliland (Hargeisa, Arabsiyo, Daboloc), Italian Somaliland (Wante and El Uak in Jubaland), Kenya (chiefly in the northern and eastern parts of the country, not in the highlands; Doinyo Narok, Tsavo, Voi, Bura, Mwatate, Lake Jipe, Marsabit, Turkwell River, Tana River, Isciolo, Serenli, Odda, Mackinnon Road, Nguruman, Kisumu), Uganda (Karamoja in the northeast and Buddu on the west shore of Lake Victoria) south to central Tanganyika (slopes of Kilimanjaro, Moschi, Makamija in Usambara, Kipera, Kilosa, Dodoma, Morogoro, Dar-es-Salaam, Ngumumova, Kiparaja, Useguha, and Ugogo).

The altitudinal range of this bird is from sea level (Dar-es-Salaam) to about 4,500 feet. It is not generally recorded above 4,500 feet in Kenya and Tanganyika. Its ecological and geographical distribution from Ethiopia to central Tanganyika corresponds fairly close to that of the straw-tailed widow bird (*Vidua fischeri*), but the latter has been also reported (but not collected) a little farther west, in the southeastern part of the Sudan, not far from the Uganda border. Because of its discontinuous, spotty distribution, the blue widow bird is often missed by naturalists. When I was in Kenya, I made many special searches for it but found it in only a few places—in the low hills between Bura and Mwatate, at Voi and at Tsavo—always in thorny *Acacia* tangles.

When first described, this species was thought to occur in Upper Guinea (Casamanse and Gambia), but this belief has long since been proved to be false.

BREEDING SEASON

There is no reason to assume that the blue widow bird is migratory even on a small scale. Its breeding range should therefore coincide

---

[78] *Vidua hypocherina* J. and E. Verreau, Rev. Mag. Zool., 1856, p. 260, pl. 165 (West Africa, probably East Africa).

[79] The record from Dangila, in northwestern Ethiopia, of Cheesman and Sclater (1936, p. 194) is in error; the specimen is actually *Vidua chalybeata ultramarina*. For checking this specimen and correcting the identification, I am obligated to J. D. Macdonald.

with its total distribution. The following are the only definite data known to me of breeding dates and localities:

ETHIOPIA: Yavello, June 29, male with enlarged gonads collected.
BRITISH SOMALILAND: Baboloc, September 12, fully fledged young.
KENYA: Kisumu, July, breeding records. North Kavirondo, June, "breeding."
TANGANYIKA: Ngumumvu, February 8, male with enlarged gonads collected. Morogoro, June 19, fully fledged young.
UGANDA: Latome, Karamojo, September 17, "breeding."

SONGS AND CALLS

The only notes that I ever heard from the blue widow bird were monosyllabic, rather weak but high chipping notes not distinguishable to my ear from the ordinary call notes of the pintail, *Vidua macroura*. I never heard what may be the true courtship song, and no one else has recorded anything about it.

COURTSHIP

At Tsavo, Kenya, May 6, 1925, I saw a male blue widow bird in full nuptial plumage together with two birds in the "sparrowy" plumage—either females or immature males flitting about in a dense thorny tangle on the river's edge. The birds then settled on the ground, and the male flew up and hovered over one of the brownish birds, just as the pin-tailed widow bird does in its courtship. The wings beat rapidly, the long tail feathers jerked with the wing beats so that they seemed to cascade over the "female," and white patches on either side of the rump showed as the bird moved. The male remained in one spot for approximately half a minute in this hovering performance. I could not hear if it made any vocal sound, as I was watching from some distance through field glasses. The action was slightly less vigorous than it is in the pintail, but I cannot say if the lone instance observed is entirely typical in this respect.

Recently V. G. L. van Someren (1956, p. 505) watched a male display "before the hens in much the same way as the pied whydah [pin-tailed widow bird] though not so elaborately."

HOSTS

R. Neunzig (1929b, pp. 9–11) assumed that an egg or a nestling recorded by V. G. L. van Someren (1918, p. 282) as the pintail in a nest of *Estrilda erythronotos delamerei*,[80] really ought to be considered as the blue widow bird, but for this reidentification he presented no valid basis. The only arguments that he cited are the general similarity of the juvenal plumages of the *Estrilda* and of the blue widow

---

[80] *Estrilda delamerei* Sharpe, Bull. British Ornith. Club, vol. 10, 1900, p. 102 (Athi River, Kenya).

bird and the extensive coincidence of their geographic ranges. He dismissed the fact that the juvenal plumage of the pintail (van Someren's original identification) is equally like that of the host species, and its geographic range is even more completely coincidental with that of the *Estrilda*. I include this host record in the account of the pintail especially since there are other instances of this species parasitizing this waxbill. Boetticher (1952, p. 51) appeared to accept Neunzig's reidentification of the parasite, but gave no further information.

The only bird said to be victimized by the blue widow bird is the bronze mannikin, *Spermestes cucullatus*, which V. G. L. van Someren (in. litt. November 23, 1950) found to be so affected near Kisumu, Kenya, in July 1912 and 1913. More recently, however, he (1956, p. 503) qualified this statement by writing that he saw the hen blue widow bird at the nest of the bronze mannikin, which "suggests that the species is parasitic . . . but proof positive is lacking."

FOOD AND FEEDING HABITS

Hawker (1899, p. 60), in British Somaliland, noted blue widow birds mixing with flocks of other small finches feeding on the "jowari stubbles." I have not been able to identify "jowari" but assume that it is a local grass or grasslike plant. Jackson (1938, pp. 1528–1529) saw the blue widow bird come to a rock pool to drink at various times between noon and 5 p.m. Fischer (in Reichenow, 1904, p. 217) saw it in loose flocks of from 10 to 30 individuals together with firefinches, in abandoned fields.

The gizzard of a specimen collected at Isciolo, Kenya, contained many small grass (?) seeds.

PLUMAGES

ADULT MALE IN BREEDING PLUMAGE: Entire head, back, rump, upper wing-coverts, upper tail-coverts, breast, and abdomen glossy Dusky Violet-Blue. Small, often concealed, whitish patch on either side of the rump. Remiges Fuscous, narrowly edged externally with whitish and basally broadly so internally. Under wing-coverts and axillars white. Four median rectrices very elongated, dull Black with faint bluish gloss laterally. Other rectrices Fuscous-Black to Black, narrowly tipped with white. Iris brown. Bill fleshy brown at base, dusky brown terminally. Tarsi and toes pale grayish brown. Wings 59–67.5 (64) mm. Tail 40–47 (44) mm. Median rectrices up to 205 mm. Culmen 9–10 mm. Tarsus 13.5–16 (15) mm.

ADULT MALE IN NONBREEDING PLUMAGE: Very similar to the corresponding plumage of *V. macroura*, from which it differs in having the remiges broadly edged with white on their inner webs, and in having the under wing-coverts and axillars white. Paler portions of upper parts more whitish, less tawny ochraceous than in *V. macroura*, and darker centers of feathers paler, dark olive brown, as compared with Black in *V. macroura*. Under parts of body more whitish, less tawny than in *V. macroura*. Also slightly smaller (wing length 63 to 67 mm., as compared with 66 to 78 mm. in *V. macroura*). Cannot be distinguished from the adult female *V. hypocherina* with certainty.

ADULT FEMALE: Similar to male in nonbreeding plumage, averaging slightly smaller, but not to such an extent that size may be used to distinguish one from the other. Specimen material examined for plumage characters does not permit me to discriminate between breeding and nonbreeding females, or between fully adult birds and younger postjuvenal ones.

JUVENAL (sexes alike): Differs from corresponding stage of *Vidua macroura* in having lores blackish, under wing-coverts and axillars white, and under tail-coverts grayish tawny. General tone of entire upper parts of head and body is slightly grayer, Buffy Brown (Olive Brown in *V. macroura*), but this color difference is slight and may even disappear in longer series.

Pin-Tailed Widow Bird

Vidua macroura **(Pallas)**[81]

Plates 8, 9, 13–15

DISTRIBUTION

The pintail is the best known, the commonest, and the most widely distributed of all the parasitic weaver birds. It occurs on nearly all types of land, except dense forest lands and true deserts, from the grasslands south of the Sahara, from Senegal east to the middle and lower part of Ethiopia, to Eritrea, south to Cape Province, on the islands of Fernando Po and São Thomé in the Gulf of Guinea, on Zanzibar and Mafia Islands, and on Mayotte Island in the Comoro group in the Indian Ocean. Its altitudinal range is from the seacoast to as high as 7,500 feet.

The pintail is found in open, tree-dotted, or bushy areas. It avoids semiarid places, and sometimes is commonest in or close to semimarshy spots. I have not, however, found it in true marshes.

The recorded localities for the pintail are so numerous that there is little point in attempting to list them all. Furthermore, this species has no recognizable (or described) geographic races. It has been recorded from every country or political area in its entire range, except

---

[81] *Fringilla macroura* Pallas, Adumbrat, *in* Vroeg, Catalogue . . . de quadrupedes et d'insectes . . . , 1764, p. 3, No. 144 (East Indies-Angola, ex Edwards and Brisson).

British and French Somaliland, where it probably will be found to occur as well. Wherever it is found, it seems to be fairly common.

There is little evidence that the pintail is even locally migratory, although some writers have made this suggestion. The probable reason for such statements is that the observers did not recognize the species in its nonbreeding plumage, when it is admittedly not too easily distinguished in the field from other nonbreeding weavers. However, Hopkinson (*in* Bannerman, 1949, p. 382) wrote that in Gambia the numbers of pintails increase greatly in June when the males assume their distinctive feathering, "a real immigration for breeding here during the rains, not a merely apparent increase because the cock then becomes more noticeable."

My own field work in southern and eastern Africa permitted me to see the pintail on countless occasions, and I had the opportunity to take many notes on its habits. These notes are incorporated with the other data in the following account.

Breeding Season

A résumé follows of the evidence indicating the breeding season of the pintail in various parts of its enormous range. These data are taken from published observations, from labels on museum specimens, and from unpublished observations of a number of contributors.

GAMBIA: Breeds during the rains (probably in August).

SIERRA LEONE: Gandorhun, August 1, males seen displaying.

LIBERIA: June, "establishing territories" (H. A. Beatty). Lenga Town, August 21, female with well-developed ova collected.

IVORY COAST: Béoumi, 200 miles north of Grand Bassam, November 28, female collected with egg in the oviduct.

NIGERIA: Courtship display and copulation recorded in June and July. Southern part of the country, males in nuptial plumage, March to November. Enugu, females with ovarian eggs well developed, September 9 to October 20.

BELGIAN CONGO: Uelle and northern Ituri, males assume breeding dress in May, but breeding delayed until August to October. Kasenyi, September 8, egg. Lake Albert, prenuptial molt in May, but at Lake Edward in December. Luluabourg, Kasai, January 23, newly fledged young. South of the forest in the Kasai, males in breeding plumage from October to January.

SUDAN: Kagelu, Equatoria, November, eggs. Darfur, copulation observed September 20. Said to breed April to July, and September to November.

UGANDA: Entebbe, eggs, October 4, November 11. Said to breed March to November.

ETHIOPIA: Alghe, November 4, male with swollen gonads collected. Said to breed August to November.

KENYA: Said to breed throughout the year. Actual records from November to January and April to July.

TANGANYIKA: Iringa, January and March, specimens in breeding condition collected. Said to breed irregularly throughout the year.

ZANZIBAR: April 18, female collected with well-developed ova. Said to breed December to May.

MOZAMBIQUE: Zimbiti, October 24, egg. Said to breed March to June.

SOUTHERN RHODESIA: Marandellas, March 24, April 2, eggs. Said to breed February to May.

NYASALAND: Said to breed December to April.

TRANSVAAL: November 27 to February 26, eggs.

NATAL AND ZULULAND: November 26 to April 4, eggs.

CAPE PROVINCE: April 15, female with egg ready to be laid. April 18, eggs.

SONGS AND CALLS

The vocalisms of the pintail are not remarkable. The usual call notes are weak, high, but sharp *tsips*. When a band of birds call simultaneously and rapidly, they produce a light twittering chorus. The song proper is a rapid but slightly modulated repetition of the call note, and usually consists of from 5 to 10 syllables, occasionally up to 15 or even more. The song is given in flight as well as at rest. Bates (1909, pp. 53–54) referred to a vigorous twittering given during courtship flight. Skead (in litt.) wrote that the call of the male is a quiet, rather wispy *peetzy, weetzy*, and also a single *thwee* whistled note. He also wrote that the female gives a plaintive *peet-peet* note. In the eastern Belgian Congo, Collias (in litt.) observed that the hen often gives a low-pitched, harsh "threat" note when approached by the cock. Usually, I found that the notes in the two sexes sounded alike.

COURTSHIP

Courtship is commonly indulged in by the pintail. In this respect, it and the other parasitic viduines are more like the cowbirds than the cuckoos and, especially, the honey-guides.

The courtship display of the male pintail has been seen and described by many authors. I also have observed it many times in many places. The first time that I witnessed it was on December 1 at Woodbush, in the northern Transvaal. The male flew up from the ground where it had been feeding with a female (a bird in the "sparrowy" plumage), and hovered about 2 feet in the air directly over her, with his body feathers slightly ruffled and his wings beating rapidly. With each wing beat the four long rectrices were jerked violently and were caused to stream boisterously over the hen, much like the cascade type of tail display of the red-throated whydah, *Coliuspasser ardens*,[82] and the long-tailed widow bird *Diatropura progne*.[83]

On another occasion, in Kenya, I saw a male display to a female perched in a thorn tree. The display was similar to the one described above. The male hovered about the same distance above the hen.

---

[82] *Fringilla ardens* Boddaert, Table des planches enluminéez d'histoire naturelle, 1783, p. 39 (Cape of Good Hope).

[83] *Emberiza progne* Boddaert, Table des planches enluminées d'histoire naturelle, 1783, p. 39 (Cape of Good Hope).

The distance of the hen from the ground appeared to be less important than the distance of the male above her. On several other occasions I watched males courting where there were several brownish hen-feathered birds present. I noticed frequently that the male (only one in each group) tended to confine his attentions to one particular bird. Apparently there was only one adult female, and the other hen-feathered birds were year old individuals of either sex. Once I shot the whole band (five brownish birds) and found that one was a female with an enlarged ovary, and that the rest were in nonbreeding condition. Three of them were males, and the other was too badly damaged for its sex to be determined with certainty.

Several variations of the courtship flight were reported. Granvik (1923, pp. 183–184) wrote: "When the male saw that he was observed he would fly a little distance off and drop to the ground, where he executed and continued the dance in about the same manner as *Drepanoplectes jacksoni*, that is to say, he would rise about a meter into the air, then fall to the ground. Without stopping he kept up in this way for a long while." Hamling (1944, p. 42) recorded another variation in Southern Rhodesia. A male bird "was perched on a leafless branch, when a hen flew up and joined him; the cock promptly flew off and gave the ordinary dancing performance. Then bobbing back he made as if to alight on the branch again, but instead of doing so he held himself suspended in the air a few inches from the hen, moving neither up nor down, and maintained this position for some moments; in fact by rapid wing beats he held himself almost upright and completely stationary in the air."

Collias (in litt.) noted a very similar performance near Tshibati in eastern Belgian Congo. The male hovered a few inches over the female and held his body almost vertically while jerking his long rectrices up and down in a vertical arc of 30 to 40 degrees and waving them slightly laterally. The hen responded by crouching forward with raised shoulders and tail and quivering wings. This was apparently the position of invitation, but the male continued displaying and made no attempt at coition.

The display dance flight is obviously correlated with the long central rectrices of the nuptial plumage, but the birds do not always wait until the prenuptial molt is complete. Thus, Moreau (*in* Sclater and Moreau, 1933, p. 417) noted birds in winter plumage on July 31 in Tanganyiki fluttering over each other in the same way that the long-tailed males do. One of them was collected and proved to be a male with well developed testes.

Other writers have also made similar observations. In Mozambique, J. Vincent (1936, pp. 113–114) noted a male still in immature or nonbreeding plumage courting and giving the full song of the species. Skead (in litt.) once saw a male going through a display dance with his nuptial tail plumes still short but started in their growth. A case of fully consummated display was observed in Ghana by Donald W. Lamm, who sent me the following notes: "At the end of August, males were displaying regularly to females, dancing up and down in front of them. One female was on a telegraph wire with a male bouncing directly over her. The up and down movement of the tail is obviously an important element in display, and the males seem to be in an absolute frenzy of emotion. Finally he dropped on her back and copulated. She then flew off and he flew down to the ground. In each case of full display there were only the two birds (one male, one female) present."

An extreme development of the usual courtship of the pintail was described by Boosey (1956, p. 79), who liberated a number of them from his aviary in England. They stayed in the immediate vicinity and returned regularly to feed in the cages left open for this purpose. Boosey wrote that "tirelessly the male Whydahs would fly higher and higher into the sky. Then suddenly they would turn and do their 'bolt from the blue' act, descending rapidly in a steep spiral with their long supple black tail feathers streaming out behind them." As far as I know, this "bolt from the blue" is a variation from the courtship dance that has not been reported for this species in a completely wild state. The variation also suggests a possible root for the development of the aerial diving performance of the paradise widow bird (see pp. 144–145).

Recently V. G. L. van Someren (1956, pp. 501–503) described quite vividly the onset of courtship and the breaking up of the "winter" flocks near Ngong, Kenya Colony.

> Probably long before the flock has split up there will have been some evidence of approaching sexual activity; males will have displayed, jumping up and with rapid wing beats hovering for a few moments, then dropping among the feeding flock again. This display will be maintained, developed and exaggerated by the remaining cocks. While the few hens are quietly feeding on the ground a male jumps up and hovers in front of a hen, his tail "plumes" waving and bending as he rises and falls. The hen makes off and flies to a bush . . . [and] the male pursues her. He starts hovering again, and as he moves from side to side in the air the hen crouches and watches him with moving head and clicking bill. This is a preliminary to a further split in the small flock; if two males have remained, one will go off with two or three hens to some other area. The remaining cock increases the frequency of his display and then one may see the mating taking place. But the hen does not accept the male readily, and he redoubles his antics. As he hovers the bird is held upright, the head just a little forward and the tail well down, so that with each jerky movement the long tail feathers move in a series of waves and curves."

Van Someren also wrote that the males at times may be polygamous. He had a male and three females under close observation in his sanctuary. "The male has displayed before all three hens, and I have seen him mating with all of them. Moreover, when I have known that a female has gone to the nest of an *Estrilda* to lay, the male has mated with one of the remaining hens." This case will be discussed more fully in the following section on territorial and mating behavior.

When going through the dancing flight, the male bird makes a twittering *tseet* noise that seems quite forceful and vigorous close up but does not carry very far. This note seems to be synchronized to the beat of the wings.

Territorial Behavior and Mating

In the discussion of courtship behavior, I quoted V. G. L. van Someren's discussion of the onset of the reproductive cycle and the break-up of winter flocks. This onset is, of course, intimately related to the expression of territoriality in the pintail. No one has yet made a real study of the territorial behavior of the pintail, but the following data give us something to go by for the present.

On November 24, at Woodbush, Transvaal, I saw an adult male in full breeding plumage. He was perched on a bush in an open grassy field, and as I approached, he flew off to a nearby bush and then to another not far off as I came close again. He made a small circling flight and came back to the original bush. On and off during the rest of the day, each time that I visited the spot I found by repeated trials that he could not be induced to leave. He had apparently established his territory there. Apparently the bush in which he was first found was his singing perch. The next day I spent a couple hours watching and tried to make him fly off, but he would not go more than about 100 feet and would then circle back gradually. There was only one henlike bird in the immediate vicinity. I shot the male and found the testes were much enlarged. The plumage was still very fresh. In fact the long central retrices still retained a little of the sheaths basally, and one of them was so loose that it came out when I skinned the bird.

In the same region I watched two other males that also seemed to have established their individual territories. I watched one of them for three successive days, and he was apparently without a mate as yet. He had a territory about 400 yards in diameter, considerably larger than that of the first male, but more open, less bushy, and probably contained possibilities of no greater number of nests to parasitize than the other. The other male had a smaller breeding area and was usually accompanied by three or four brownish henlike birds. I shot one of these birds and found it to be a male—a year-old bird in first nuptial plumage.

Several observers have reported territorial fighting between males. At Tshibati, Belgian Congo, on December 9, 1956, Collias (in litt.)

noted that a male in full plumage was in daily "ownership" of a section of a field, about 35 by 100 feet in extent, and had been so for some weeks. Another cock bird, banded with pink bands on both legs on December 6, invaded his territory, and both began to fight viciously on the ground and in the grass. They gripped claws and pecked at each others' heads. The fight continued for three minutes, when one of the birds flew off and left the other temporarily exhausted on his back in the grass. He soon recovered and pursued the other and renewed the battle, this time for two minutes. Another such territorial fight between the two was noted again on December 14. During the next two months the individual marked with pink bands was rarely met with, but on May 5 this bird was found back at his old stand, apparently with no rival in sight. He was courting females all around the area. In other words, this male, color banded early in December, was courting hens nearly 5 months later in the same territory, but in the interval he was known to have been evicted from it at least once by another male, who was apparently a previous occupant. V. D. van Someren (1958, p. 165) reported the male pintail as "pugnaciously territorial and allows no other cock near at any time in the area he has selected."

Recently Beatty (*in* Rand, 1951, p. 646) noted that in Liberia at about "April the males commenced to select females and by June little groups consisting of one or two males and perhaps a dozen females establish territories. These territories were vigorously defended against intruding males." While I consider that this writing is rather loose, without detailed critical evidence behind it, it reflects the general picture of territorial behavior.

Serle (1957, p. 682) gave a somewhat similar account in eastern Nigeria. He noted that after they acquired breeding plumage, the males left the flocks and established territories, each of which was shared with three or four birds in the "sparrowy" plumage. No attempt was made to determine whether they were females, nonbreeding males, or immature birds. Unlike Beatty, Serle found only one adult male in each such territory. V. G. L. van Someren (1956, pp. 501–503), in Kenya, knew of a male and two females that frequented a strip of grassland near the forest at Ngong. He noted that they "ranged over about two acres in one direction and an acre to the south around the corner of the forest."

Various authors have commented to the effect that this bird is promiscuous, polygamous, and monogamous in its breeding. In fact, the observational data vary so much that at times even the same observer has been led to opposite conclusions. Thus V. G. L. van Someren (1956, pp. 501–503) gave evidence of polygamous behavior in a male pintail, but in an earlier paper (1922, p. 153) based on much experience, decided that it is not polygamous. "Although parasitic on other Finches, especially *Estrilda*, I have never seen more than one female with a male, when the former are laying. I have seen the female accompanied by the male enter the nest of an *Estrilda*, deposit its egg, and then fly off with the male. Most of the so-called females accompanying the males when these birds 'flock' are young males and a few young females." J. Vincent (1936, pp. 113–114) was unable to decide whether the species is polygamous or not "for of the three or four drab looking companions to a male in breeding season . . . thought to be females were often immature males which, although apparently a year or more in age, have not yet developed breeding dress." Lynes (1924, p. 678) suspected that the males do not acquire breeding plumage in their first year "and that the harems or polygamous habit commonly attributed to these birds will prove to be merely the same hanging-on of first year, *i.e.*, immature birds of both sexes, but it will require proof."

My own experience, based on study of a large number of these small "flocks" during the breeding season, leads me to conclude that the pintail is usually monogamous. I have never seen two courting full plumaged males in any one of the breeding season flocks. Chapin (1954, pp. 573–577) believed that the males are promiscuous rather than polygamous.

Jackson (1938, pp. 1525–1528) gave a valuable summary of his long experience with the pintail in Kenya and Uganda as follows:

> There is, or was, a very widespread conviction that this bird and the majority of, if not all, the long-tailed *Viduinae* are polygamous. . . . personal observations extending over a period of thirty-two years have led me to the firm belief that not one of those found within Kenya Colony and Uganda is polygamous. . . . Between the breeding seasons, and even during them, flocks of half a dozen up to sixty or more may be met with. The great majority are either females or young male birds, in the striped plumage, and it is extremely difficult, even with binoculars, to tell one from the other.
>
> In such flocks there are generally one or more adult male birds in worn full plumage, some with or without the long black tail, while others have a black tail, but otherwise still in the striped dress of the female. At such times these adult males may be seen dancing and pirouetting in the air above the birds feeding on the ground, in the same manner as courting but with less persistence.
>
> Occasionally a bird in striped dress and with no sign of the black tail will follow suit, and it has often occurred to me that it is not improbable that the older birds are showing the younger ones how it is done. Anyhow it is obvious that they are not courting, and yet it is quite conceivable that their dancing amidst a large flock has added weight to the assumption that the bird is polygamous.
>
> During the breeding seasons, between April and June and in November and December, if a cock-bird in full dress is seen by himself within a limited area of a few acres in extent, it may safely be assumed that it is a breeding bird, although there is no sign of its mate. He will fleck and fossick about from bush to bush or other coign of vantage, and will attack furiously any other bird of more than double its size and weight that may venture to show itself within its domain.

Lynes (1924, p. 678) concluded, from his Darfur specimens and notes, that the pintail, like the paradise widow bird and some of the bishop birds, does not assume adult plumage or begin to breed until the second year. His conclusion also accounts for the difference between the apparent and the true picture of the constituents of the small flocks found in the breeding season. Chapin and V. G. L. van Someren are also of the same opinion.

There may be more pintail males than females, a situation common in parasitic birds such as cowbirds and other widow birds. V. G. L. van Someren (1919, p. 414) once collected 30 live birds in off-season plumage for his aviaries in January, and found that only 7 turned out to be females. The birds were alike until April, when the males assumed their nuptial feathering. In the small breeding season flocks that I studied, random collecting revealed more immature or nonbreeding males than females.

EGGS AND EGG LAYING

The eggs of the pintail are pure white, and vary from 14.5 to 16.6 by 11.0 to 12.2 mm. They are definitely known from eggs laid by captive birds (Bolus, 1909, p. 113, and Feo, 1910, pp. 145–146) and from fully shelled oviduct eggs taken from wild killed pintails (Bannerman, 1923, p. 682; Godfrey, 1929, pp. 117–118). There are other eggs whose identity seems in no doubt and that may also be taken as authentically known reference specimens, such as several sets from the Karkloof District of central Natal where the pintail is the only species of *Vidua* present.

In the majority of cases only a single egg is laid in any one nest, but I have data on numerous nests with two, three, and four eggs of the parasite. There are no data whether these multiple eggs are the product of one or of several hens. No one has witnessed the bird actually laying its egg, although several observers have noted hens entering nests of waxbills. Therefore, we do not know positively whether the laying hen destroys or removes an egg of the host before laying its own, although there are pronouncements on this matter in the literature. Thus, A. Roberts (1939, pp. 106–107; 1940, p. 361) stated that an egg of the host is "destroyed to make room for each of those of this parasite, and thereafter the young grow with the others in amity." Neuby-Varty (in litt.) wrote me that the pintail may remove some eggs because he has never found parasitized nests of the common waxbill with as many eggs as in unmolested nests. Chapin (1954, pp. 573–577) noted that the "laying widow bird has been accused of destroying one of the legitimate eggs." On the other hand V. G. L. van Someren (1956, pp. 501–503) stated: "One, two, or rarely three eggs may be laid in the foster parent's nest. It depends on the number of nests available, and I doubt if each whydah lays more than four or five eggs. No attempt is made to destroy the eggs of the foster bird, nor does the nestling *Vidua* eject any of the rightful chicks." In an earlier paper van Someren (1922, p. 153) wrote that he had "seen the female accompained by the male enter the nest of an *Estrilda*, deposit its egg, and then fly off with the male." In his 1956 account, he stated that he saw "the male accompanying the hen to two known *Estrilda* nests. Quite often, in the vlei land, I have seen a male fly from a bush and drop to a certain patch of grass, then leave (from there) with a hen. That patch has held an *Estrilda* nest. I have located waxbills' nests by watching the movements of the hen and cock pintail." It would seem that if the female often removed one of the eggs before depositing its own, van Someren would have seen some sign of it.

Delacour and Edmund-Blanc (1934, p. 85) wrote that the hen pintail accompained by the cock enters the nest of the host and lays its egg. There is no indication that these authors had any original observations on this point, and their statement is probably based on V. G. L. van Someren's published notes. Probably the male pintail does not actually enter the nest together with its ovulating mate. In the northern Transvaal near Potgieters Rust, I saw a male in full breeding plumage near a waxbill's nest (about 2 feet from it, in the same bush) from which a female pintail flew as I approached, and was joined in flight by the male. The nest proved to be empty.

Mörs (1925, p. 168) watched a hen pintail go into a nest of a common waxbill from which it did not emerge until about half an hour later. The time elapsed is much more than would be required merely for egg-laying, but no indications were given about what the bird was doing. On examination the nest was found to contain five eggs of the waxbill and two of the pintail.

Nothing is known of the number of eggs laid by one hen in a season. I have never found more than four discharged follicles in the ovary of any bird, but there is no evidence whether the bird may lay the equivalent of more than one clutch a season with a sufficient interval between clutches to allow the follicles time to disintegrate. Similarly we do not know whether one female lays all its eggs in nests of a single species of victim, but since the great majority of known instances of its parasitism involve a group of closely related waxbills and fire-finches, this question of definite host specificity may be less important here than in other brood parasites, such as cuckoos and cowbirds.

Years ago A. Roberts (1912, pp. 45–46) wrote that the hen pintail may first deposit her egg on the ground and then carry it to the nest of some other bird; however, he based this erroneous guess on the fact that a captive bird in an aviary laid its egg on the bare ground (Bolus, 1909, p. 113). V. G. L. van Someren's observations (quoted above) are evidence to the contrary. Roberts was probably influenced by the then current ideas about the egg laying of the European cuckoo.

Recently Mackworth-Praed and Grant (1955, pp. 1046–1047) noted that the hen pintail may at times lay the first egg in the nest. Although no basis for this statement was given, it is apparently taken from J. Vincent (1936, p. 114), who wrote that the common waxbill does not appear to resent the intrusion of the parasite "as in some instances it has been almost certain that the whydah was the first to lay." Unfortunately, the details that seemed to make this "almost certain" were not recorded.

A few observations have also been made about the incubation period. Skead (1957) found a nest of the common waxbill containing seven eggs of the owner and one of the pintail, on November 30. On December 10 the pintail and four of the waxbills hatched. The last of the waxbill's eggs hatched on December 13. From November 30 to December 10 is 11 days, so that the incubation period of the pintail must have been something over that. In his acount of this waxbill, V. G. L. van Someren (1956, p. 493) wrote that its incubation "lasts about eleven days."

Another estimate of the incubation period, based on a breeding instance in the aviary of H. David and kindly sent me by G. A. Radtke, is somewhat longer. The egg was found freshly laid in a deserted nest of a pair of zebra finches (*Taeneopygia castanotis*), and was then placed under a brooding bengalese finch (*Lonchura striata*), whose own eggs proved to be infertile. The egg hatched "within a fortnight or so," but no accurate time record was kept.

The question of mimetic similarity between the eggs of the pintail and those of its hosts seems to have been avoided because most of the victims (the various species of waxbills) lay unmarked white eggs much like those of the pintail; however, the pintail is not completely restricted to victims with similar egg types. The tawny-flanked longtail lays eggs varying from bluish green to salmon pink and pale brown pencilled or blotched with purplish gray or brown. The spot-backed weaver lays brown-spotted blue, green, or whitish eggs. The red-collared whydah's eggs are bluish green, tinged with pale lavender gray, and speckled with brown. The streaky seed eater lays bluish or whitish eggs with fine brownish scrawls on them.

Old accounts in the literature describing the nests and eggs of the pintail (von Heuglin, Stark, Alexander, Teschemaker, 1910b, and others) are erroneous and should be disregarded. A most confusing statement was made years ago by Knauer (1889, p. 396), who wrote that in the Vienna Zoo the pintails diligently built nest after nest, and that out of over 100 individuals only 2 died in the period of a year. It is probable that he was referring to weaverbirds in general, and not specifically to the pintail.

HOSTS

The known hosts of the pintail are all species of weavers with the exception of two warblers and two finches—a fairly limited range of related type birds. With the exception of the finch, all these birds have domed nests with openings on the side. There are enough data on the pintail, and on the commoner warblers, flycatchers, thrushes, and bulbuls to enable us to say that this limited choice of hosts is real and not merely due to insufficient observations. The birds parasitized are generally small species, most of them being about the same body size as the parasite or even smaller, and in most cases the eggs of the host are somewhat smaller than those of the parasite. Over 77 records for all hosts refer to 18 species, or 26 forms including races, and do not include 3 other species that cannot be considered definitely established as victims. Of the 18 species, 11 are waxbills, fire finches, or mannikins; 1 is a long-tailed whydah; 2 are larger weavers; 2 are true finches; and 2 are grass warblers. The identifications of the parasitic eggs are by no means always as definite as I would wish. They are individually appraised as far as the available evidence permits. Of the 77 records, all but a few relate to waxbills; in fact 41 are for one species, the common and widely distributed *Estrilda astrild* (and races).

Considering the very great geographic range of the pintail, the recorded list of victims of its parasitism amounts merely to the beginning of a definitive list of hosts. There are some species not on the list whose absence is surprising, because they would seem to be as suitable as some that do appear in the subjoined list and whose nests have been examined in sufficient numbers to make it apparent that they are not victimized (at least not to any extent). The cordon bleu, *Estrilda angolensis*, is such a species. In fact, Plowes (1947, p. 153) examined many nests of this bird at Ladysmith, Natal, where the pintail is common, and was led to conclude that the pintail does not make use of the nests of the cordon bleu. On the other hand, the waxbills, fire finches, and their close relatives (the most "likely" victims) all lay small pure white eggs similar to those of the pintail, and it is quite possible that the eggs of the latter may have been overlooked.

That more than half the cases of parasitism of the pintail have to do with the common waxbill supports R. Neunzig's contention (1929b, pp. 3–6) that it is the usual, "normal" host. There is ample evidence, however, that it is by no means the only one, as may be seen from the following annotated list of recorded victims. The close similarity in the pattern and color of the palate markings and the gape wattles of the *Estrilda* and its parasite are not due to any evolutionary mimetic process, but reflect the close phylogenetic relationship between them

Tawny-flanked longtail: *Prinia subflava* (Gmelin) [84]

One record refers to a nest containing three eggs of this warbler (race *P. s. affinis*) and one of the parasite, found in tall weeds among. some rocks in one of his tobacco fields on his farm near Marandellas, Southern Rhodesia, by B. M. Neuby-Varty, to whom I am indebted for this information. He collected the eggs on February 15, 1957, but had found the nest with all the eggs already present a week earlier. He had left them to hatch and took them only after it had become obvious that the nest had been deserted.

This record, the only one for a longtail as a host of the pintail, recalls the similarly unique one for the shaft-tailed widow bird in the Transvaal.

The tawny-flanked longtail is one of the few birds used by both parasitic widow birds and cuckoos (*Chrysococcyx caprius* [85] and *Chrysococcyx klaas* [86]), but, except for the present record, it has not been reported as a victim of, and is probably infrequently parasitized by, the pintail.

Tawny-capped grass warbler: *Cisticola fulvicapilla* (Vieillot) [87]

One record refers to the race *C. f. ruficapilla.* Neuby-Varty (in litt.) found a nest of this grass warbler on his farm "Torre" near Marandellas, Southern Rhodesia, on March 5, 1951. The nest contained three small white eggs but none of the grass warbler. Measuring 16 by 12, 16.25 by 12, and 16 by 12.25 mm., these eggs must have been laid by the pintail, the only parasitic widow bird occurring there. The parasite could have removed the eggs of the host as it laid its own in the nest.

This record is of an unusual host and suggests that occasionally two parasitic weavers, the pintail and the cuckoo finch overlap in their choice of victims.

Spot-backed weaver: *Ploceus cucullatus nigriceps* (Layard) [88]

In southern Tanganyika, Grote (1925, pp. 34–35) hired native boys to bring him young weaverbirds out of arboreal nests. Among a

---

[84] *Motacilla subflava* Gmelin, Caroli a Linné . . . systema naturae, ed. 13, vol. 1, 1789, p. 982 (ad fluvium *Senegal*).

[85] *Cuculus caprius* Boddaert, Table des planches eliminéez d'historie naturelle, 1783, p. 40, No. 657 (Cape of Good Hope).

[86] *Cuculus klaas* Stephens, *in* Shaw, General zoology . . ., vol. 9, 1815, p. 128 (Platte River, ex Levaillant).

[87] *Sylvia fulvicapilla* Vieillot, Nouveau dictionnaire d'histoire naturelle, vol. 11, 1817, p. 217 (Camdeboo, ex Levaillant).

[88] *Hyphantornis nigriceps* Layard, Birds of South Africa, ed. 1, 1867, p. 180 (Kuruman).

number of young spot-backed weavers brought was a nestling pintail. Grote concluded that the parasite lays its eggs in nests of this weaver occasionally. It appeared more likely that this chick was raised in such a nest than that his native assistants had gotten it elsewhere and had mixed it up with the *Ploceus* nestlings brought to him at the same time. The possibility of confusion, however, makes this unique record uncertain.

Red-collared whydah: *Coliuspasser ardens* (Boddaert) [89]

A nest containing a single egg of the owner and one of the parasite was found at Kilgobbin, Natal, on March 19. The eggs are now in the collections of the Transvaal Museum (A. Roberts, 1939, pp. 106–107). This record refers to the nominate race of the host.

Magpie mannikin: *Lonchura fringilloides* (Lafresnaye) [90]

A nest was found containing five eggs of the host and one of the parasite, at Zimbiti, near Beira, Mozambique, October 24. The eggs are now in the Transvaal Museum (A. Roberts, 1939, pp. 106–107).

Bronze mannikin: *Spermestes cucullatus* Swainson [91]

The eastern race *S. c. scutatus*[92] has been recorded occasionally as the host of the pintail. Jackson (1938, pp. 1525–1528) wrote that he and his assistant Baraka found several parasitized nests of this mannikin in Kenya. H. W. Bell-Marley collected a set of five eggs of this mannikin and one of the pintail at St. Lucia Lake, Zululand, April 4, 1929. This set is now in the U.S. National Museum. At Verulam, Natal, November 26, a nest containing four eggs of the builder and one of the parasite was collected for the Transvaal Museum (A. Roberts, 1939, pp. 106–107). V. G. L. van Someren (1956, pp. 501–503) reported that in Kenya he once found two eggs of the pintail in a nest of this mannikin. In northwestern Ethiopia, Cheesman (*in* Cheesman and Sclater, 1936, p. 194) saw a female pintail going into a nest of this mannikin, but did not have the chance to examine the nest itself. Winterbottom (1951, p. 37) listed this mannikin as an occasional host of the pintail.

Cape fire finch: *Estrilda rubricata* (Lichtenstein) [93]

Haagner and Ivy (1907a, p. 81) reported a nest of this finch with eight eggs, some of which were larger than the others, and which

---

[89] *Fringilla ardens* Boddaert, Table des planches enluminéez d'histoire naturelle, 1783, p. 39 (Cape of Good Hope).

[90] *Ploceus fringilloides* Lafresnaye, Mag. Zool., 1835, pl. 48 (India = Liberia).

[91] *Spermestes cucullatus* Swainson, Birds of western Africa, vol. 1, 1837, p. 201 (Senegal).

[92] *Spermestes scutatus* Heuglin, Journ. Ornith, vol. 11, 1863, p. 18 (Dembea, Abyssinia).

[93] *Fringilla rubricata* Lichtenstein, Verzeichniss der Doubletten des zoologischen Museums . . ., 1823, p. 27 (Kaffirland).

they considered as probably those of a parasite. Considering that this record was made when A. Roberts first demonstrated that the pintail is a brood parasite, the caution of the above authors is understandable. Probably their record refers to the pintail.

Black-bellied fire finch: *Estrilda rara* (Antinori) [94]

Myers reported (*in* Bannerman, 1949, p. 386) finding a nest of this finch near Kagelu, Equatoria Province, Sudan, in November. It contained three well incubated eggs of the host and two fresh ones, "which may belong to *Vidua macroura* which is very common here." While not improbable, this record must be looked upon as uncertain.

Red-bellied fire finch: *Estrilda senegala* (Linnaeus) [95]

At least three races of this finch have been recorded as victims of the pintail: *E. s. rendalli*, *kikuyuensis*, and *ruberrima*.[96] The data are as follows: In Kenya and Uganda, Jackson (1938, pp. 1525–1528) wrote that he and his native assistant, Baraka, found eggs attributed to the pintail in nests of the races *kikuyuensis* and *ruberrima*. V. G. L. van Someren (1956, pp. 501–503) wrote that he once found a pintail's egg in a nest of this finch (race *kikuyuensis*), but gave no details. In an earlier paper (1918, pp. 281–282), writing of the parasitic breeding of the pintail, he listed "*Lagonosticta ruberrima*" (=*E. senegala ruberrima*) with the comment that "more often one egg or young to each nest, but occasionally 2 are found." This statement indicates that he must have seen a considerable number of instances in his field experience. Unfortunately, the data were not presented more fully. The records for the southern race, *rendalli*, are: A parasitized nest found in Nyasaland by Paget-Wilkes (1924, p. 23, published erroneously as the race *brunneiceps*,[97] which is now known to inhabit Eritrea and Ethiopia, east to Darfur), and a set of four eggs of this finch and one of the pintail, collected at Ndumu, Zululand, March 21, and now in the collections of the Transvaal Museum (A. Roberts, 1939, pp. 106–107). Winterbottom (1951, p. 38) listed this finch as a common victim of the pintail in southern Africa.

In all the above instances, the identification of the parasitic eggs as pintail eggs is merely probable. In no case were the eggs allowed to hatch, and in none of these cases did the observer state that other species of *Vidua* or of *Hypochera* were definitely absent from the immediate or adjacent area. In his discussion of this finch in the Belgian Congo, Chapin (1954, p. 530) wrote that it "is believed to

---

[94] *Habropyga rara* Antinori, Catalogo . . Uccelli . . ., 1864, p. 72 (between White Nile and Ghazal River).

[95] *Fringilla senegala* Linnaeus, Systema naturae, ed. 12, vol. 1, 1766, p. 320 (Senegal).

[96] *Lagonosticta brunneiceps ruberrima* Reichenow, Ornith. Monatsb., vol. 11, 1903, p. 24 (Victoria Nyanza).

[97] *Lagonosticta brunneiceps* Sharpe, Catalogue of the birds in the British Museum, vol. 13, 1890 p. 277 (Maragaz, Eritrea).

be the most frequent fosterer of *Hypochera*, so when any discrepancy of size is noticed among the eggs it will be wise to allow them to hatch and to study the nestlings closely."

Yellow-bellied waxbill: *Estrilda melanotis* (Temminck)[98]

Two races of this waxbill have been found parasitized—the nominate race in South Africa (two records), and race *E. m. kilimensis*[99] in Kenya (one record). In the collections of the Transvaal Museum is a set of four eggs of this waxbill with one of the pintail, taken at Karkloof, Natal, December 20 (A. Roberts, 1939, pp. 106–107). Pope-Ellis (1951, p. 126) reported seeing two fledgling pintails attended and fed by one of these waxbills near Mont-aux-Sources, in the Drakensberg Mountains, in Natal. The lone Kenya record is of a nest with an egg of the parasite, reported without further data by V. G. L. van Someren (1956, pp. 501–503).

Common waxbill: *Estrilda astrild* (Linnaeus)[1]

The common waxbill has been more frequently reported and is undoubtedly more frequently parasitized by the pintail. No less than six of the geographic races of this waxbill have been so recorded among 44 actual instances on which data are available. In addition to these cases, there are numerous statements in the literature by various observers that indicate a much larger number of other, individually unrecorded instances. The races definitely known to be parasitized are: *E. a. astrild, cavendishi,*[2] *minor,*[3] *massaica,*[4] *nyanzae,*[5] and *occidentalis.*[6] Other races will undoubtedly be found to be imposed upon as well.

The number of cases is sufficient to enable us to summarize the situation rather than to merely list them. In 32 out of the 44 cases, only a single egg of the parasite was found in one nest, with from 2 to 7 eggs of the host. In six instances there were two eggs of the pintail with from one to five eggs of this waxbill. In two nests there were three eggs of the pintail with two and six eggs, respectively, of the host. In each of three nests, one reported by A. Roberts (1939, pp. 106–107), and two collected at Karkloof, Natal, by R. E. Symons (these two sets are now in the Museum of Comparative Zoology), there were five eggs of the pintail. In the case reported by

---

[98] *Fringilla melanotis* Temminck, Nouveau recueil de planches coloriees d'oiseaux, livr. 37, vol. 3, 1823, pl. 221, fig.1 (Pays des Cafres, i.e., eastern Cape Province).

[99] *Coccopygia kilimensis* Sharpe, Catalogue of the birds in the British Museum, vol. 13, 1890, p. 307 (Kilimanjaro).

[1] *Loxia astrild* Linnaeus, Systema naturae, ed. 10, vol. 1, 1758, p. 173 (Canaries, America, Africa=Capetown).

[2] *Estrilda cavendishi* Sharpe, Ibis, ser. 7, vol. 6, p. 110 (Mapicuti, Cheringoma District Mozambique).

[3] *Habropyga minor* Cabanis, Journ. Ornith., vol. 26, 1878, p. 229 (Voi River, Kenya).

[4] *Estrilda astrild massaica* Neumann, Journ. Ornith., vol. 55, 1907, p. 596 (Njoro, Kenya).

[5] *Estrilda astrild nyanzae* Neumann, Journ. Ornith., vol. 55, 1907, p. 596 (Bukoba, Lake Victoria).

[6] *Estrilda occidentalis* Jardine and Fraser, *in* Jardine, Contributions to ornithology, 1851, p. 156 (Fernando Po).

Roberts there were no eggs of the host; all of this waxbill's eggs were replaced by the parasitic ones while the nest was under observation. Unfortunately, Roberts failed to record his observations of this unusual case history, other than to state that the nest was deserted eventually. This was at Kilgobbin, Natal, early in February. The two Karkloof sets, taken in January and February, each had two waxbill eggs as well as the five parasitic ones.

On April 3, near Taveta, Kenya, I found a nest of this waxbill containing four eggs of the owner and one of the pintail. The next day the nest was empty and deserted, probably because of some predator. Another nest, found a week later, with four eggs of the waxbill and one of the parasite, also came to grief within the next few days.

In Nyasaland Belcher (1930a, p. 333) found eggs of the pintail in about 40 percent of all the nests of the waxbill (race *cavendishi*) seen. In the Marandellas area, Southern Rhodesia, Neuby-Varty (in litt.) found eggs of the parasite only in nests of this waxbill. While these findings do not imply that no other birds were parasitized, they do suggest something of the relative frequency that the common waxbill is used as the host. That it is the commonest victim in Zululand as is indicated by an old Zulu saying that a young pintail is reared out of every nest of the waxbill (A. Roberts, 1907, pp. 9–11).

In the Transvaal Mörs (1925, p. 168) found that most nests examined of this waxbill contained eggs of the pintail, and concluded that an unparasitized nest was a relative rarity. For further details involving instances of this host species, reference may be made to the account of the development of the nestling pintail (pp. 113–116).

Although this waxbill is very frequently victimized by the pintail, no one seems to have found mixed flocks of adults of the two species even in areas where both species are numerous. Skead (in litt.) informed me that he saw a juvenal pintail with a flock of about 40 adult waxbills feeding on the ground. Numbers of observers have seen mixed groups of young birds of the two species, but once they pass the postjuvenal molt, they seem to part company.

It may be mentioned that this waxbill makes a nest with a secondary chamber above, in which the cock bird is said to sleep, and which is almost never used for eggs. There are no records of a pintail ever making the mistake of laying an egg in this false nest cavity; she seems to know the real nest from this roosting cavity.

Grey waxbill: *Estrilda troglodytes* (Lichtenstein) [7]

I note one very uncertain record. Chapin (1954, pp. 557–558) gave the measurements of a set of six eggs of the gray waxbill as vary-

---

[7] *Fringilla troglodytes* Lichtenstein, Verzeichniss der Doubletten des zoologischen Museums . . ., 1823, p. 26 (Senegambia).

ing from 11.5 to 15.5 by 9.5 to 11.25 mm. Bannerman (1953, vol. 2, p. 1482) also gave these measurements, and noted that this variation is considerable for so small an egg. Possibly the larger eggs are those of the pintail. The set of eggs was found by Shuel in Northern Nigeria.

Crimson-rumped waxbill: *Estrilda rhodopyga* Sundevall[8]

V. G. L. van Someren (1918, pp. 281–282) stated that this species is one of two (the other being *Estrilda astrild*) from whose nests he most frequently collected eggs or young of the pintail. Chapin (1954, p. 557) described a nest found at Kasenyi in the eastern Belgian Congo, September 8, containing six eggs, two of which were notably larger than the others, and which "no doubt had been laid by *Vidua macroura*, numerous and active in the vicinity."

Both van Someren's and Chapin's observations have to do with the Uganda race of the host, *E. r. centralis*.[9]

Zebra waxbill: *Estrilda subflava* (Vieillot)[10]

As far as I know, only the southern race *E. s. clarkei*[11] has been recorded as a victim of the pintail. Feo (1910, p. 146) was the first to record the zebra waxbill as its host. A. Roberts (1939, pp. 106–109) noted a set of three eggs of the waxbill and one of the parasite taken at Rayton, near Pretoria, Transvaal, on February 26 The eggs are now in the collection of the Transvaal Museum. D. C. H. Plowes (in litt.) collected a set containing four eggs of the host and one of the pintail, at Estcourt, Natal, on March 20. Symons (1919, p. 233) wrote that in the Giants Castle Game Reserve, Natal, the pintail, which is common there, generally lays its eggs in nests of the zebra waxbill and the common waxbill. In the R. Kreuger collection at Helsingfors is a parasitized set of *clarkei* eggs containing one egg of the pintail and one of the host, collected on March 10, 1947, near Bushmans River, Estcourt, Natal, by C. H. Jerome. Chapin (1954, p. 577) listed the zebra waxbill among the hosts to be expected in the Belgian Congo.

Inasmuch as this host uses a variety of old nests of other weavers, it would be of interest to know if it was more immune from the attentions of the pintail in some types of nests than in others. In other words, is the pintail attracted by the host or by the nest?

---

[8] *Estrilda rhodopyga* Sundevall, Oefvers. Kongl. Vetensk. Akad. Forhandlingar, vol. 7, 1850, p. 126 (northeast Africa, Sennar).

[9] *Estrilda rhodopyga centralis* Kothe, Ornith. Monatsb., vol. 19, 1911, p. 70 (Kisenyi, Lake Kivu).

[10] *Fringilla subflava* Vieillot, Nouveau dictionnaire d'histoire naturelle, vol. 30, 1819, p. 575 (Senegal).

[11] *Coccopygia clarkei* Shelley, Bull. British Ornith. Club, vol. 13, 1903, p. 75 (Richmond Road, Natal).

Fawn-breasted waxbill: *Estrilda paludicola* Heuglin [12]

At Entebbe, Uganda, on November 11, 1917, Belcher found a nest of this waxbill (nominate race) containing four eggs of the waxbill and one of the pintail. This record has appeared at least three times in the literature (Jackson, 1938, p. 1515; Bannerman, 1953, p. 1485; and Chapin, 1954, p. 539).

Black-cheeked waxbill: *Estrilda erythronotos* (Vieillot) [13]

A single record, unfortunately without further detail, seems to be all that is available on this waxbill as a host of the pintail. V. G. L. van Someren (1918, pp. 281–282) once found an egg of the pintail in a nest of the Kenya race of this waxbill (*E. e. delamerei*).

Streaky seedeater: *Poliospiza striolata* (Ruppell) [14]

V. G. L. van Someren (1956, pp. 501–503) listed this seedeater as a victim of the pintail "to my certain knowledge," but gave no further details. Van Someren's notes refer to the Kenya race *P. s. affinis*.[15] In a subsequent letter, he wrote that he knew of a nest of this seedeater in a certain thick bush and saw a female pintail fly out of the bush. Thereupon he looked in the nest and found that it contained three eggs of the builder and one of the pintail. This record is the only one known to me.

Golden-breasted bunting: *Emberiza flaviventris* Stephens [16]

V. G. L. van Someren found a parasitized nest on his grounds at Ngong, Kenya, near the similarly victimized nest of the streaky seedeater described above. These two records are the only ones known where the pintail laid in open, cup-shaped nests. Van Someren wrote me that there was no doubt about the pintail eggs in either and that he was amazed at the time.

UNVERIFIED HOST RECORDS: The following birds have appeared in the literature as hosts of the pintail, but the evidence is not sufficient to establish them even as "probable." There is no inherent reason why these species could not be parasitized, but so far there are no valid data available.

Cheesman and Sclater (1935, pp. 615–619; 1930, p. 194) recorded three species of grass warblers of the genus *Cisticola* (*brunnescens*, *cantans*, and *galactotes*) as hosts of the pintail in northwestern Ethiopia. However, all of these records pertain to the cuckoo finch

---

[12] *Estrilda paludicola* Heuglin, Journ. Ornith., vol., 1863, p. 166 (middle course of Bahr el Ghazal).

[13] *Fringilla erythronotos* Vieillot, Nouveau dictionnaire d'histoire naturelle, vol. 12, 1817, p. 182 (India=Kurrichane, western Transvaal).

[14] *Pyrrhula striolata* Ruppell, Neue Wirbelthiere zu der Fauna von Abyssinien gehorig, entdeckt und beschrieben. Vogel, 1840, p. 99, pl. 37, fig. 1 (Halai and Simen, Abyssinia).

[15] *Crithagra striolata affinis* Richmond, Auk, vol. 14, 1897, p. 156 (Kilimanjaro).

[16] *Emberiza flaviventris* Stephens, in Shaw, General zoology, vol. 9, 1815, p. 374.

and are discussed fully in my account of that species. As is often the case with errors, these records were cited in a few places in the literature before the error was detected, but these references may be disregarded.

Scaly weaver: *Sporopipes squamifrons* (Smith) [17]

One record of an egg attributed to the pintail refers to a nest of a scaly weaver by C. H. Jerome, and the tentative identification was confirmed by A. Roberts (1943, pp. 100, 102). This record is discussed in my account of the scaly weaver as a host of the shafttail, *Vidua regia*, where I believe it belongs.

Grosbeak weaver: *Amblyospiza albifrons* (Vigors) [18]

Calder (1944, p. 77) found a nest at Hillcrest, Natal, in the tall reeds of a reed bed, on December 14. It contained one fresh egg of the grosbeak weaver, the broken shell of another similar one, and also one small white egg (14.5 by 12 mm. as compared with 23.5 by 16.5 mm. for the host's egg). Nine days later he found another nest of this species with one small egg and none of the host's. He suggested that the small eggs were those of the pintail, which is not uncommon in the district, but rightly wondered why should it choose so large a host when waxbills are common there.

These two instances are at best uncertain. There are many small weavers that use nests of other species and then take care of their eggs in these adopted nests, and therefore cannot be ruled out as possible alternate identifications. Furthermore, Calder himself informed me that the dusky combassou occurs in the area, and might have been responsible for the parasitic eggs.

Long-tailed whydah: *Diatropura progne* (Boddaert) [19]

Masterson (1916, pp. 138–139) found a nest of Humansdorp, Cape Province, with five eggs of the builder and four assumed to be of the pintail. This record is poorly written, and is at best very doubtful. The data are given under *Vidua principalis* (= *V. macroura*) as follows: "Very common. I found a nest of the latter with nine eggs, five of the usual size and four slightly larger and rounder; the four I took to belong to the Whydah." The word "latter" appears to refer to the preceding species in his list, which is *Diatropura progne;* however, the eggs of the pintail are known to be much smaller, not larger and rounder, than those of the *Diatropura.*

---

[17] *Estrelda squamifrons* A. Smith, Report of the expedition for exploring central Africa . . ., 1836, p. 49 (South Africa).

[18] *Pyrrhula albifrons* Vigors, Proc. Zool. Soc. London, 1831, p. 92 (Algoa Bay).

[19] *Emberiza progne* Boddaert, Table des planches enluminéez d'histoire naturelle, 1783, p. 39 (Cape of Good Hope).

Orange-cheeked waxbill: *Estrilda melpoda* (Vieillot) [20]

Although this species has been listed in the literature among the hosts of the pintail, I have been unable to find a single actual record. Chapin (1954, p. 577) listed it among the Congo birds in whose nests one should look for eggs of the parasite, but gave no instances of any having been reported. Sander (1957, p. 67), in Nigeria, thought the pintail was locally parasitic on the orange-cheeked waxbill, and always found the two species closely associated in the field.

HOSTS RECORDED ONLY IN AVIARIES: When pintails in captivity attempt to breed they are, of necessity, restricted in their choice of hosts to those birds that are present and breeding in the same cage. Two species occurring in the same geographic areas as the parasite have been recorded as what might be termed "avicultural hosts" but have not been so described in a wild state. The ribbon finch, *Amadina fasciata* is one of them. It reared a young pintail in Anningson's aviary (W. T. Page, 1914, p. 39). The other is the rufous sparrow, *Passer rufocinctus*, so recorded in V. G. L. van Someren's aviary near Nairobi (van Someren, 1917, pp. 288–289; Shore-Bailey, 1923, p. 110). Obviously, neither of them can be looked upon as natural hosts of the pintail, but it is also obvious that they could serve in this capacity.

NESTLING STAGE

The most detailed notes on the nestling stage are the following' paraphrased of Skead (1957, pp. 214–216), who made them near King William's Town, Cape Province. These notes are also here augmented slightly by additional information kindly sent me in personal communications.

NEST NO. 1: March 3, 1953: Skead finds a nest of the common waxbill with eight nestlings, each a few days old and still sightless. Their bodies are dark pinkish-mauve, pinker below. Their bills are black and legs gray. The gape edges are peculiar: At the upper edge is a white waxy, comma shaped tubercle, while on the edge of the mandible immediately below and fitting into each side of this tubercle are two smaller white tubercles. The mouth is very pale pink, and on the roof of it are five black dots. At the edges of the tongue are two black dots, and on the base of the mouth under the tongue is one black dot.

When looking into the nest, i.e., up the spout, Skead sees that the white tubercles produce a most peculiar effect. With all the chicks facing the entrance, the effect is of eight pairs of very white eyes looking out—a purely illusory effect as the true eyes are still closed—but the distinct whiteness probably helps the adults find the mouths

---

[20] *Fringilla melpoda* Vieillot, Nouveau dictionnaire d'histoire naturelle, vol. 12, 1817, p. 177 (west coast of Africa).

of the chicks in the dark interior. The down[21] on most of the chicks has probably been rubbed off, but one has enough down left to show that it occurs on supraorbitals, occiput, secondaries, down the back, and on flanks. Small hairs protrude from primaries and tails. An egg tooth is on the maxilla. This chick is probably a pintail because *Estrilda* chicks have no down. The throats of seven of the chicks are bulging with seeds but that of the eighth is empty, even though it is one of the bigger chicks.

March 12: Eight chicks are still in the nest, very cramped, some facing the entrance, some against the back wall, and one on top of the others. As Skead looks in, they all sit dead still and silent. When he touches them with his finger and even when he pushes his fingers under them, they allow themselves to be moved. Their eyes are well open and they look alert. Their feathers are out. Those chicks that he can see are pinkish below, slightly barred, and have a pink breast spot.

March 14: All chicks are now bunched on top of each other for lack of room. Unfortunately all take fright and fly out of the nest. At least three have red faces and black bills and a pinkish color below with a red spot, and gape tubercles are also still present. Others have black bills and no red faces. Skead catches one, whose bill is waxy and black, crown gray brown, back brown, chin whitish, the rest below tawny brown, and legs black. It looks quite different from the others in coloration. It reacts strongly against him, and pecks his fingers viciously. There is no nest sanitation, but the chicks do not seem to suffer at all.

NEST NO. 2: December 10, 1953: Skead finds a nest with four *Estrilda* chicks and a pintail chick already hatched. Three eggs are hatching, and one other egg appears freshly laid (since the previous day). *Estrilda* chicks: The body and mouth of each is pink and the eyes are closed. The bill is dark but not black and the nostrils are flat. The gape spots are the same as of the pintail. No down is present, but there are very fine hairs on the tail. Pintail chick: The body is mauve, head pink, and bill black. Its legs are mauve, feet pink, and nostrils fairly prominent. Pale yellow down is on the secondaries, and white down is on the rump. It has very fine tail hairs, and its eyes are closed.

December 11: Second day: Two more eggs have hatched. Two are still unhatched. Newly hatched chicks look very weak beside others. No food is in their throats, whereas throats of others bulge with seeds.

---

[21] A chick of similar stage of development in a German aviary in 1957 had short mouse gray down from the occiput to the lower back (G. A. Radtke, in litt.).

December 12: Third day: Two weak chicks are being fed. There are still two unhatched eggs.

December 13: Fourth day: Another egg has hatched (the remaining egg does not hatch and a few days later is found outside the nest). The newly hatched chick looks absurdly small beside the others, but it is quite vigorous. No seeds are visible in its throat. The quills of the primaries show in larger birds. Pintail: Quills are emerging on primaries and secondaries.

December 14: Fifth day: Pintail: Quills are out on primary and secondary coverts. Its eyes are half open.

December 16: Seventh day: Pintail: Quills are emerging on the back, rump, tail, breast, flanks, and humerals.

December 17: Eighth day: *Estrilda:* Quills are out on the back, rump, tail, humerals, breast, and flanks. The eyes are half open. Pintail: Crown and throat quills are out. Natal down still adheres.

December 18: Ninth day: *Estrilda:* Quills are out on crown, but not on throat or chin. The eyes are half open. Pintail: Chin quills, frons, superciliaries, and ear coverts are out. Feathers are breaking through on primaries and their coverts, and on secondaries and their coverts. The eyes are open and bright.

December 19: Tenth day: *Estrilda:* Quills are out on chin, superciliaries, and ear coverts. Remiges are breaking out of the quills. Pintail: All feathers are emerging, except on the head.

December 20: Eleventh day: Pintail: Feathers on the head are all out. Body skin is not yet covered by feathers. The squeak of the parasite is unlike that of the young waxbills.

December 22: Thirteenth day: Pintail: Obviously is different from young waxbills. Cannot now handle it for fear of disturbing.

December 30: Twenty-first day: All have left nest.

Summary: The durations of the nestling periods were as follows: One pintail and 1 *Estrilda* about 20 days; 2 *Estrildas* about 19 days. One *Estrilda* died. There was a difference in the vocalisms of the young waxbill and the pintail when both were ready to leave the nest. The waxbill gave a *chewnk* call much like the adult, while the pintail gave a husky, plaintive *wehk-wehk-wehk* call, to which the foster parents responded. The pintail also uttered a harsh, husky screech when picked up and handled. As with the foster parents of all parasitic birds, these foster parents showed no apparent discrimination between their own chicks and those of the parasite. Here, unlike some of the other cases, there is not so great a difference in size and appearance between them.

Chapin (in litt.) found a nest of the common waxbill in the Lwiro region, eastern Belgian Congo that contained a nestling pintail and some young nestlings of the host. He was able to compare the amazingly similar mouth markings and gape wattles of the two. He thought that the young pintail grew more rapidly than the young waxbills, and would have left the nest sooner had it not been collected.

Young Out of the Nest

The data discussed in the previous section indicate that the developing pintail shows no aggressive hostility toward its nest mates, as we find in the comparable stage of many of the cuckoos and honey-guides, and not even the intense competition for food, as we find with cowbirds. The young pintail does not crowd out, kill, or otherwise eliminate its rightful nest mates, and for a short time after leaving the nest they remain together. While I have found what seemed to be fully fledged young pintails in assemblages of young waxbills, they do not remain together very long (how long is not known). Before they begin their postjuvenal molt, the young pintails often form flocks of their own. I have seen as many as 15 to 20 together, sometimes with 1 or more adults of their own species.

Both V. G. L. van Someren (1917, pp. 288–289) and Pope-Ellis (1951, p. 126) tell of seeing two fledgling pintails attended and fed by their foster parents. Skead (in litt.) sent me notes on a fledgling pintail covering 5 days of its postnestling stage. This pintail was first seen on January 5 together with a young common waxbill and the two foster parents. Two days later the pintail joined a flock of about 40 adult waxbills feeding on the ground. On January 9 it was seen alone, feeding at the edge of a path; five adult pintail males and two in striped plumage flew in and fed close to it, but did not pay any special attention to it.

Apparently in captivity the pintail may show some parental behavior toward fledged young of its own species. W. T. Page (1914, p. 39), inspected a reported rearing of a young pintail by a pair of ribbon finches (*Amadina fasciata*) in the aviaries of Anningson. He found that the young bird had already left the nest in which it had been reared, and that the adult pintails in the cage "watched over it and occasionally fed it as also did the ribbon finches." Unfortunately no details of this case were given; we are not informed whether both or only one sex of the pintails fed the young pintail.

Food and Feeding Habits

The food of the pintail comprises primarily small seeds gathered on or near the ground. In about 20 gizzards examined in the course of my field studies, I found no other identifiable food materials. As many as 75 seeds were found in one specimen. The only food items noted in the diet given nestlings by their foster parents were seeds, but it would be surprising if the waxbills and other hosts did not feed the young pintails insects as well. Chapin (1954, p. 577) saw a pintail capture two winged termites in the air, and then eat them. Otherwise he found only seeds to be used as food, usually seeds of wild grasses, "but in one instance of *Eleusine* and in another of meal made from that same kind of millet."

In captivity all pintails are egg eaters, according to James (1938, p. 325), but I know of no such observation about pintails in the wild state.

The predominantly terrestrial feeding habits of this bird may be carried over to aviary life. Buttner (1959) noted that his captive birds tended to scatter the seeds from the food container and then pick them up from the ground of the cage floor, a way of feeding which he assumed was more natural for the birds than for them to pick the seeds out of a cup or dish.

While not contributing to our knowledge of the normal diet of this bird, it should be mentioned that Terroine and Barthelemy (1922) used several examples of this species in their experiments on avitaminosis and inanition. As is to be expected, they found that the pintail showed the same disastrous results from vitamin deficiency as do mice and other, more ordinary laboratory animals. Terroine and Trautmann (1927) also used examples of this species in their studies of caloric production in homoiothermic animals in relation to changes in external temperature. Their results showed that the pintails need approximately twice (3,468) the number of calories per day at 17° C. as compared with their need (1,646) at 40° C. In the southern winter in South Africa the pintails experience significant degrees of cold over considerable periods of time, but we do not have accurate estimates of seasonal variation in the quantity of seeds ingested daily or any analyses of the seeds in terms of their caloric potential to apply this information to the dietary economy of the species in the wild.

PLUMAGES AND MOLTS

The molts and plumages of the pintail are as follows:

MALE: 1. Natal down grayish dusky, generally, tinged with pale yellowish on inner portions of wings, whitish on rump.

2. Juvenal plumage is acquired by a complete postnatal molt.

Above: Head, hind neck, scapulars, interscapulars, back, and rump Tawny-Olive, darker on the head, which is intermediate in color between Tawny-Olive and Saccardo's Umber. Interscapulars and feathers of back with somewhat dusky centers producing faintly streaked appearance. Rump washed with Cinnamon. Upper tail-coverts Fuscous, broadly edged, and tipped with Sayal Brown. Tail feathers fuscous-brown, narrowly edged with Sayal Brown. Lesser and middle wing-coverts like scapulars. Greater wing-coverts, and tertials light fuscous-brown, broadly edged externally with Sayal Brown. Secondaries and primaries fuscous-brown, externally narrowly edged with Sayal Brown, and internally edged with buffy whitish. Sides of head pale Vinaceous-Buff. Lores blackish.

Below: Chin, throat, breast, flanks, abdomen, thighs, and under tail-coverts light buffy washed with Chestnut. Chestnut most pronounced on the breast, flanks, and thighs. Under wing-coverts whitish tinged with light buff. Bill dark brown.

3. First winter plumage is acquired by a partial molt involving feathers of the head, scapulars, and wing coverts.

Above: Head Ochraceous-Tawny, broad black stripe on either side from base of upper mandible to nape. Nape, back, and rump Tawny-Olive. Interscapulars and scapulars black broadly edged with Ochraceous-Tawny. Upper tail-coverts Fuscous, edged and tipped with Olive-Tawny. Lesser, middle, and inner greater-coverts like scapulars. Remiges and rectrices as in juvenal plumage, fuscous-brown, but with tawny edges narrow from wear. Buffy-white inner edges of primaries also narrower than in juvenal plumage. Sides of head pale buffy. Black stripe present through eye from bill to nape; and line of black spots on sides of head, varying considerably in different specimens.

Below: Chin whitish. Throat, breast, abdomen, flanks, thighs, and under tail-coverts as in juvenal plumage but whiter and with few black spots on sides of breast and occasionally on thighs. Bill reddish brown.

4. First nuptial plumage is acquired chiefly by wear and is similar to first winter plumage, but the remiges and retrices are darker, and the entire upper parts are more streaked blackish. The bill is red.

5. Adult winter plumage is acquired by a complete postnuptial molt. It is similar to the first nuptial plumage, but the upper parts are more heavily streaked with black. The remiges and rectrices are dark fuscous-black, margined with tawny. The bill is red. Birds in this plumage may be distinguished from individuals in the first nuptial plumage by the darker remiges and rectrices, which are new and unworn.

6. Adult nuptial plumage is acquired by a partial molt involving feathers of the head, body, and tail, but not the remiges.

Above: Head, scapulars, interscapulars, and back black slightly glossed with greenish. Nuchal collar white. Lower back and rump White with blackish shaft stripes. Lesser and middle wing-coverts White forming a large white wing patch. Greater coverts, primaries and secondaries Black. Some of inner secondaries with remnants of tawny edges of adult winter plumage. Tail feathers Black, four central ones greatly elongated and wholly Black. Other rectrices tipped with Tawny. Inner webs very broadly margined with White. Sides of head white. Lores Black, the black sometimes extending in small specks onto cheeks.

Below: Chin White, sometimes with a black spot (better developed in birds from the northern border of the equatorial forest than elsewhere, but not constant). Throat, breast, abdomen, flanks, thighs, and under tail-coverts whitish. Sides of throat Black, forming a distinct gorget on either side. Bill red. Wings 64.5–75 mm. Tail 44–51.5 mm. Long median rectrices 235–340 mm. Culmen 9–10.5 mm. Tarsus 14.5–17 mm.

FEMALE: 1. Natal down is the same as in the male.

2. Juvenal plumage is acquired by complete postnatal molt and is the same as in the male.

3. First winter plumage is acquired by a partial molt, and is the same as in the male.

4. First nuptial plumage is acquired by wear, and is the same as in the male. The bill is reddish.

5. Adult winter plumage is acquired by complete postnuptial molt, and is similar to the young male's first nuptial plumage. The bill is red.

6. Adult nuptial plumage is acquired by wear. The bill changes from red to dark brown. This plumage is similar to adult winter plumage except that the bill is dark brown. The size is as in the male (with, of course, no elongated median tail feathers).

In the prenuptial molt the four long rectrices come in at about the time that body molt commences. The crown molts first, and then come the sides of the breasts to form the black gorgets of the breeding plumage. The nuchal collar, the scapulars, and the lesser coverts come next. The interscapulars, back, and rump are not molted, but the brown edges wear off and leave the uniform black color. The rectrices and remiges are not changed in the prenuptial molt. The tertials apparently are not molted, but become black through the wearing away of their brownish edges. The postjuvenal molt is usually incomplete, the juvenal rectrices being retained in the first nonbreeding plumage.

The breeding plumage (in the male, at least) may be acquired a considerable time before breeding commences. In South Africa, where the pintails are late summer breeders (late November to April), they come into nuptial dress in September and October, although I saw some molting males as late as early December. Winterbottom (1942, p. 388) similarly noted the early assumption of breeding plumage in Barotseland. In Zanzibar, Vaughan (1930, pp. 47–48) found that the males acquire nuptial feathering in November and retain it until June or July—more than half the year. Still, this species does not wear the breeding plumage as long as the paradise widow bird does.

In their experimental study of the relation of light to molt, F. A. Brown and M. Rollo (1940) used pintails among other birds. They used what they considered to be young pintails (how age was determined is not explained, but apparently they were given this information by the dealer who supplied the pintails, a doubtful source). They reported that in suitably controlled experiments male birds acquire adult nuptial plumage during their first year of life if subjected to daily light periods of 16 hours. If the age of the pintails used was correct, this result is contrary to the picture in the wild. Further studies along the same line are needed to establish this result.

Aside from the accelerating effect of supernormal illumination on plumage cycles, the investigators also described an aspect of the molt that has not otherwise been recorded. "*Vidua* had feathers on its back that were black in the center and brown on the edges. As in many other species, when the bird changed color these feathers did not molt but the edges dropped off leaving a solid color. This phenomenon is usually attributed to wear, but, from these experiments there would seem to be some kind of control in addition to simple wear or age of the feather. The edges of the feathers of *Vidua* dropped off in one week and out of season. The shabby appearance of remiges at the end of the season may be related in the same way to the molt." Examination of museum specimens throws no light on this point, and there are no detailed pertinent field observations. In this connection, I cannot help but think of the peculiar marginal shedding in the elongated rectrices of nuptial male paradise widow birds (see pp. 137–138 for a discussion of this item).

NATIVE NAMES

While I have made no special attempt to gather all known native African names applied to the pintail, the following were noted as I came across them. In a few instances the name of the tribal language was not stated, and I have not been able to fill in this information. As in all compilations of this sort, there are two main sources of error to be kept in mind: The man recording the names may have misheard or poorly transliterated them; the native informant may not have distinguished the bird from other similar species, and may even have invented names to please the inquirer.

Native name	*Tribe*	*Locality*
Abou mous	"Arabicized"	French West Africa
Am faseye	"Arabicized"	French West Africa
Ardo-bicha	Fulani	West Africa
Babewatoto	Bondei	Tanganyika

Native name	*Tribe*	*Locality*
Bendenge-osesan	Bulu	Cameroons
Chemilunda		Zanzibar, eastern Tanganyika
Chinyampimbiri	Chindao	South Africa
Chiunga	Kiyao	Tanganyika
Fumbwe		Tanganyika
Hlakwe	Xhosa	South Africa
Hlekwe	Xhosa	South Africa
Hleko	Xhosa	South Africa
Kalundyondyo	Sangwe	Angola
Kamkwichi	Tumbuku	Northern Rhodesia
Katzuzenchira	Nyungwe	Nyasaland
Kavosi	Kuvangu	Angola
Kijao		Southeastern Tanganyika
Kimakonde		Southeastern Tanganyika
Kwichi	Yao	Nyasaland
Le-Helo ("female" only)	Sesuto	South Africa
Lufite		Zanzibar
Lulangiragira	Lulega	Tanganyika
Lushindishindi	Banya-Bongo	Belgian Congo (Kivu)
Luvungabwasi (female)	Banya-Bongo	Belgian Congo (Kivu)
Manchuja	Chagga	Tanganyika
Mleya	Bisa	Northern Rhodesia
Mmamonoka	Sesuto	South Africa
Mnankwigi		Nyasaland
Mo-Lepe	Sesuto	South Africa
Nalamusweswe	Luvale	Northern Rhodesia
Nandumbe	Kimakonde	Southeastern Tanganyika
Nantjedje	Kimakonde	Southeastern Tanganyika
Ndalangimbu	Tonga	Northern Rhodesia
Nnunochuku	Ibo	Nigeria
Nuzaguhumeka	Banya-Bongo	Belgian Congo (Kivu)
Nyalundshirandshira	Banya-Bongo	Belgian Congo (Kivu)
Nyaluntindi	Banya-Bongo	Belgian Congo (Kivu)
Nyancheche	Mbwere	Mafia Island, Tanganyika
Nziramukindi		West of Lake Edward, Belgian Congo
Ogbodu	Bini	Nigeria
Ologoshe	Yoruba	Nigeria
Ongungu	Bimbi	Angola
Sempia		Upemba Park, Belgian Congo
Shindishindi	Banya-Bongo	Belgian Congo (Kivu)
Sikanimbaanimba	Tonga	Northern Rhodesia
Silicilacila	Lozi	Northern Rhodesia
Tahapietsi	Sechuana	South Africa
U-Hlegwane	Zulu	South Africa
Yiwiri		Nyasaland
Zandi	Hausa	Nigeria
Zulaidu	Hausa	Nigeria

MISCELLANEOUS DATA

LONGEVITY: Fillmer (1904, p. 168) bought a male pintail in 1894 for his aviary. It was still going through its annual molts with regularity at the time of his writing in 1904. It was then 10 to 11 years old. Mitchell (1911, p. 476) recorded a maximum longevity in captivity of 6 years, 9 months, for this species.

PUGNACITY: Aviculturists (Hennig, 1936, for example) have remarked that because the pintail is aggressive and pugnacious in captivity, it is difficult to keep other birds in the same cage. James (1938, p. 325) wrote that the pintail is "a killer, likely to scalp any other inmate from a Waxbill to a Java Sparrow." Parker (1931, p. 52) found it advisable to rid his aviary of pintails because they annoyed (but apparently did not injure) his other birds. That this trait is not confined to captive pintails is suggested by the observations made by E. V. Page (1946, p. 341) in Natal, on a small flock of one male in breeding plumage and several hen-feathered birds. "The cock . . . was seen on several occasions to make unprovoked attacks on Double-collared Sunbirds, as well as on a Bully Seed-eater, which had perched . . . close to him on a large sunflower. These incidents left little doubt in my mind as to who was the self-appointed 'boss' of the . . . grounds."

WINTER FLOCKING: During the nonbreeding season flocks of as many as 100 or even more are not unusual. In South Africa the pintails seem less strictly terrestrial in the winter, and I have often seen flocks perching in trees at heights of from 15 to 50 feet. These winter flocks do not appear to have any observable organization, but are loosely knit aggregations. In agricultural areas the birds come down to the ground in old maize fields and in the short grass near barnyards and cattle pens to feed, but spend the night in the trees. In several places I knew of Eucalyptus trees near such farm yards that seemed to be favorite roosting places, as the flocks came back to them night after night. In South Africa these flocks persist until October or early November, when they break up into small groups, usually consisting of a single male just beginning to get its nuptial feathering, and two to five hen-feathered birds. In the Somerville area of Cape Province, Godfrey (1923, p. 133) recorded similar nocturnal roosting habits.

Straw-Tailed Widow Bird

Vidua fischeri (Reichenow)[22]

PLATE 1

DISTRIBUTION

The straw-tailed widow bird of eastern Africa is very imperfectly known. It inhabits the same type of country and the same geographic range as the blue widow bird. My own experience with it was in the dry thornbush from Taveta to Maktau, Kenya. Its known range is from Ethiopia and British Somaliland south to central Tanganyika. A more detailed statement of its distribution follows:

ETHIOPIA: Chiefly hot, fairly dry lowlands of southern portion of country, Ourso, Shoa, Webi-Schebelli, Ira-Luku, Hariro, Arussi Gallaland (Sheik Hussein, Bali), Abaya Lakes area (Gato River near Gardula), and Boran (Tertale, Yavello).

BRITISH SOMALILAND: Arabsiyo, Gebili, Hargeisa.

SUDAN: Reported seen (not collected) on eastern slope of Dongotona Mountains and at Lolimi and Lodmara, in eastern part of Equatoria Province.

ITALIAN SOMALILAND: Karo-Lola, Djido, Damaso, Wante, Gobwin, Ogodan, Goura, Bussaler, Hallier, Odda.

KENYA: Chiefly to east of Rift Valley, but not entirely so, Meuressi and southeast of Lake Stephanie in Turkanaland, Marsabit, Nguruman near Lake Naivasha, Kendu Bay on Lake Victoria, Kikuyu, Loita, Kitui, Simba, Suk, Tsavo, Ndai, M'toto Andei, Kinani, Tsavo, Voi, Taveta, Maktau, Samburu.

UGANDA: Kapus and Lokosomal, in dry sandy thornbush country of northern Karamoja, not far from Uganda-Sudan border.

TANGANYIKA: Steppes around Kilimanjaro, Moschi, Useguha, Ngare Nairobi, Dodoma, Samumba, Singida, Suna, Useguha, 10 miles north of Iringa, Ugogo, and Unyamwesi.

Customarily I have found this species in somewhat denser growths of bushes and thorny scrub than I have the pintail. In southern Ethiopia, Pease (in Ogilvie-Grant and Reid, 1901, p. 614) found the strawtail in the high trees bordering the marshes of the Errer Gota River, quite a different type of habitat from the essentially terrestrial one or the low vegetation favored in most places farther south. Granvik (1934, pp. 177–178), however, found it frequenting tall Acacias and other trees at small pools or streams in Turkanaland, where he considered it a bird of the steppes and deserts. In Kenya, Jackson (1938, p. 1529) found it in small open spaces in the bushveld where the grass was short and scanty, and also near rock pools at M'toto Andei and Kinani.

The altitudinal range is from less than 1,000 feet up to 5,000 feet.

---

[22] *Linura fischeri* Reichenow, Ornith. Centralbl., vol. 7, 1882, p. 91 (Usegua).

BREEDING SEASON

The following are the known indications of breeding season of the strawtail:

ETHIOPIA: Near Yavallo, eggs presumed to be of this species, June 12.

ITALIAN SOMALILAND: Fledged young birds, May and July.

KENYA: Between Ndai and Kinani, female with a well developed egg in the oviduct, collected April 2. Maktau, adult male with much enlarged gonads collected March 29.

TANGANYIKA: Birds said to be in breeding condition, March to April (Mackworth Praed and Grant, 1955, pp. 1048–1049, but evidence not given).

SONGS AND CALLS

Schuster (1926, p. 728) considers the call note of the strawtail "finch-like" and difficult to describe. The only calls I heard of the strawtail were a series of short, sharp, monosyllabic *tschip* notes, indistinguishable to my ear from those of the pintail.

Mackworth-Praed and Grant (1955, pp. 1048–1049) described the song as a short bunting-like song and also as a small, sweet, rather lisping serinlike song. In my field notes, I described the song as like that of the pintail but more modulated and the notes more run together.

Krabbe (1931, p. 134) described the song of captive strawtails as a series of twittering notes given in rapidly rising tempo.

COURTSHIP, TERRITORIAL BEHAVIOR, AND MATING

In central Tanganyika, Schuster (1926, p. 728) observed the "dance flight" of the strawtail, a courtship performance essentially similar to that of the pintail. The male hovered a little distance above the female, and rose and fell in an undulatory manner while the rapid wing beats made a loud whirring sound. I observed a similar performance near Taveta, Kenya, but was not close enough to hear any whirring noise.

Little is known of territorialism in the strawtail. Once, at Maktau, Kenya, March 29, 1925, I observed a fight between two males of this species. One of the males was perching in a tall bush when suddenly another male flew nearby. The first one immediately gave chase and the two began fighting with their bills and wings in midair, about 20 feet from the ground. As they struggled they slowly fell to the ground, and first one was on top and then the other, as they began rolling over and over like a ball. As they fought they uttered only a few occasional *tschip* notes, and were remarkably silent for birds under the stress of excitement. The fight ended just as suddenly as it started, when one of the birds (it was impossible to distinguish between them) flew off. The other pursued it a few yards and then came back, perched on a bush where it remained for a few seconds, and then flew off too. As it flew I collected it and found it to be a male with much enlarged testes. It seems as though the fight may have been over the acquisition or maintenance of a breeding territory.

There are also no data on mating. While it is true that there are usually a number of female-appearing individuals with each male in breeding plumage, there is no evidence that all of them are really females, and not immature or nonbreeding males. It is therefore not warranted to assume a polygamous state from such observations. In Ethiopia, Erlanger (1907, p. 24) found the species in groups of from 10 to 20 birds, almost always with only a single adult male in breeding plumage. Erlanger noted that it seemed as though the leadership of the flock was vested in the full-plumaged male, as when he flew off the others always followed.

EGGS AND EGG LAYING

No authentically identified eggs of the strawtail have been described. Benson (1947, p. 43) recorded two eggs found in a nest of *Granatina ianthinogaster ugandae*,[23] with four eggs of the waxbill, near Yavello. He reported the two as unmarked white in color, and 15.7 by 12.7 mm. and 15.7 by 12.5 mm. in size. He considered them as probably belonging to a strawtail but his view cannot be accepted as more than a guess. He may well have been influenced by R. Neunzig's earlier assumption (1929b) that the purple grenadier is the "usual" host of the strawtail, an assumption based solely on the general similarity of the juvenal plumages of the two species. Boetticher (1952, p. 51), following Neunzig, listed *Granatina ianthinogaster*[24] as the host, but gave no actual data.

HOSTS

I know of no hosts, although several writers, such as Delacour and Edmond-Blanc (1934, p. 118), Benson (1947, p. 43), and Mackworth-Praed and Grant (1955, pp. 1038, 1048) mentioned *Granatina ianthinogaster* as a victim of the strawtail. These statements seem to be based on R. Neunzig's earlier statement (1929b), which remains only a guess. I note, in passing, that Neunzig postulated the same host for the strawtail as he did for the shafttail of southern and southwestern Africa and on this basis suggested that the two species may be more closely related to each other than to the other members of the genus *Vidua*.

---

[23] *Granatina ianthinogaster ugandae* van Someren, Bull. British Ornith. Club, vol. 40, 1919, p. 53 (Moroto, northern Uganda).

[24] *Uraeginthus ianthinogaster* Reichenow, Ornith. Centralbl., vol. 4, 1879, p. 114 (Massa, Tana River).

Food and Feeding Habits

The gizzard of a strawtail collected at Maktau, Kenya, March 29, 1925, held about 50 small grass seeds, as did another specimen from Iringa, Tanganyika. Other individuals were seen to pick up small objects (probably seeds) from the ground in open grassy spots.

Plumages and Molts

Adult male in breeding plumage: Forehead, crown, upper part of lores, and anterior part of occiput Pale Orange-Yellow to Buff-Yellow. Lower part of lores, cheeks, auriculars, posterolateral portions of occiput, chin, throat, breast, and upper back black with a slight gloss. Upper wing-coverts dark Clove Brown to Fuscous, narrowly edged externally with pale buffy brown. Remiges somewhat pale-dark Olive-Brown to Clove Brown. Feathers of middle and lower back, rump, and upper tail-coverts dark Olive-Brown, broadly edged, and tipped with ashy pale buffy brown. Four median rectrices pale Buff-Yellow in color, very much elongated and very narrow, looking much like long, thin straws. Other rectrices dark Olive-Brown narrowly edged with paler brown. Abdomen, sides, flanks, under tail-coverts, and thighs pale Buff-Yellow, becoming almost white medioventrally. Under wing-coverts pale Olive-Brown, narrowly edged and tipped with paler brown. Bill and feet orange red. Iris brown. Wings 64–71 (68) mm. Tail 44–48 (45.5) mm. Long rectrices up to 190 mm. Culmen 9–10 (9.7) mm. Tarsus 15–16.5 (16) mm.

Adult male in nonbreeding plumage: Feathers of forehead, lores, crown, occiput, and hind neck Ochraceous-Tawny with dusky Fuscous shaft streaks. Hind neck slightly paler. Feathers of upper back and the upper tail-coverts with median streaks broader and much more pronounced, margins narrower and paler, Clay Color to pale Clay Color. Rump and upper tail-coverts like top of head but with lateral portions of feathers paler, less ochraceous. Inner secondaries Fuscous narrowly edged and tipped with pale Clay Color. Outer secondaries and primaries Natal Brown to Olive-Brown. Primaries basally edged with pale Clay Color on their inner webs. Rectrices Natal Brown to Olive-Brown, narrowly edged, when fresh, with pale Clay Color. Lores, cheeks, and breast pale Cinnamon to pale Tawny Olive. Chin more whitish. Feathers of sides and flanks pale Tawny Olive with narrow ashy Natal Brown shaft streaks. Abdomen, thighs, and under tail-coverts whitish tinged with Pale Ochraceous-Salmon. Under wing-coverts dusky Tawny-Olive. Iris brown. Bill pinkish, becoming dusky at the tip of the maxilla. Feet flesh color.

Adult female: Similar to the nonbreeding male.

Juvenal (sexes alike): Forehead, lores, crown, occiput, nape, cheeks, auriculars, chin, throat, and breast Orange-Cinnamon to Ochraceous-Tawny. Feathers of back, rump, and upper wing-coverts with Clove Brown medial streaks and broad edges of Sayal Brown to Snuff Brown. Upper tail-coverts similar but with edges somewhat more rufescent, Mikado Brown. Secondaries Clove Brown edged with Sayal Brown. Primaries Clove Brown externally very narrowly edged with Sayal Brown and internally with pale tawny. Rectrices similar, Clove Brown, with narrow external edges pale Sayal Brown. Abdomen, sides, flanks, and thighs like breast but much paler. Center of abdomen and under tail-coverts white. Under wing-coverts pale Ochraceous-Tawny.

Shaft-Tailed Widow Bird

Vidua regia (Linneus) [25]

PLATES 2, 10

DISTRIBUTION

The shafttail is a bird of southern Africa, except for the eastern portion, where it inhabits the drier bushveld from southern Angola (Benguella, Huilla,[26] Gambos, and near Humbe in the upper Cunene District), southern part of Northern Rhodesia (Katombora, Livingstone), south through Matebeleland in Southern Rhodesia (Kanye, Selenia Pan, Tati, Mangwe, Wankie, Bulawayo District, including Matopos Mountains though not known east to Mashonaland), South-West Africa (Ondonga, Ombujomatemba, Omaruru, Otjoro, Otjimbingue, and Rehoboth, all in Damaraland, and south to Lion River, Namaqualand), Bechuanaland (Kabulabula, Kuke, Kaotwe, Nkate, Maun, Mabeleapudi), eastern Transvaal (Rustenberg, Marico, Moordrift, Bloemhof, "Vaal River to the Zambesi"), to Griqualand West (near Kimberley), the northern fringe of the Orange Free State, and the Colesberg District of northern Cape Province.

My own field acquaintance with the shafttail was in the Transvaal between Potgietersrust and Moorddrift, in 1924–25, and in Southern Rhodesia near Bulawayo in 1950. In neither area was the species very common. In the former area I found the birds on and off during December and early January—single males in breeding plumage in what seemed to be pairs, i.e., one male in full nuptial dress and one "sparrowy" feathered individual. In its general habits the shafttail seemed much like the pintailed widow bird, *V. macroura*, but more nervous, moving more rapidly, and jerking its body when feeding on the ground among the grass. I note that W. T. Page (1907) found the shafttail to frequent marshy ground interspersed with groves of

---

[25] *Emberiza regia* Linnaeus, Systema naturae, ed. 12, vol. 1, 1766, p. 313, (Africa, south Angola).

[26] No recent records. It is not clear if "Benguella" as given generally by authors is different from Anchieta's bird from Huilla. In his work on Angola birds, Monard (1934) did not include the shafttail.

trees and bushes, a moister habitat than where I found it, but he does not say if it stayed and fed in these areas or was merely seen there on its way elsewhere.

Breeding Season

The following are the pertinent data on the breeding season and range of the shafttail:

Southern Rhodesia: Matopos Research Station, February 16, egg. Queen's Mines, Bulawayo District, March 14, egg.

Transvaal: Moordrift, January 1, egg. Warmbath, January 18, 25, February 7, eggs. Andalusia (near Kimberley), April 12, egg. Bloemhof, April 22, egg.

South-West Africa: Okahandja, March 6 and April 27, eggs. Between Etoscha Pan and Ondonga, May 26, eggs.

In other words, eggs, whose identification is not completely certain in all cases but seems reasonably reliable, and young have been taken from January 1 to May 26 from the middle to the latter part of the southern summer. Similar records are true of the pintail from southern Africa; it too is a fairly late breeder. The breeding season appears to begin somewhat earlier in the Transvaal, Bechuanaland, and Southern Rhodesia than in South-West Africa, and apparently depends on the start of the rainy season.

The breeding range is the same as the total range, since the shafttail is not considered to be migratory in most areas of occurrence, but Hoesch and Niethammer (1940, pp. 361–363) inferred that in Damaraland the majority of the local population of this species do not remain to breed. That there may be some seasonal movements in Southern Rhodesia is also indicated by Mouritz (1915, p. 556), who observed little flocks of shafttails around his home for only a few weeks in February and March.

Songs and Calls

In 1924 in the Transvaal, I noted that the ordinary call note of the shafttail was like that of the pintail, but more abrupt and slightly sharper. Otherwise there is little difference in the vocalisms of the shafttail and the better-known pintail. The song of the shafttail seemed to me at the time a little softer and less distinctly broken into syllables. The only published statement about the song is not very informative. Townsend (in W. T. Page, 1907, pp. 5–7) noted that among aviary birds, the male was "very lavish in the morning with his little if not lovely song."

Courtship and Mating

At Moorddrift, Transvaal, in the first half of December, I witnessed the courtship performance of a male shafttail. He was hovering in a somewhat jerky flight a little distance above the female (at least a bird in the "sparrowy" plumage) accompanied by fairly violent undulations of the long flowing rectrices, very similar to the pintail. Its song was also similar to the pintail, but seemed softer and feebler, possibly because I was not very close at the time.

Hoesch and Niethammer (1940, pp. 361–363) in South-West Africa found in the early months of summer small flocks composed of male birds only or mixed flocks with a preponderance of males. At this time the change from off-season to breeding plumage had not yet been completed, and was especially noticeable in the partly grown, long, median tail feathers. The first fully plumaged males were not seen there until February 7–10, at least two months later than in the Transvaal. Hoesch and Niethammer (1940) recorded flocks with only a single male in breeding plumage from March to May, and considered these birds to be mated polygamous groups. They noted that the males in these groups would fly low over the females of their "harems" in a bouncing, undulating flight from time to time. A few actual females (not males in winter plumage) collected from such a flock in March showed undeveloped or only slightly enlarged ovaries, and indicated that the breeding season does not begin immediately after the conclusion of the molt into nuptial plumage. Earlier writers such as Stark (1900, p. 149) and W. T. Page (1907, pp. 5–7) considered the shafttail polygamous, but without critical evidence. Inasmuch as the hens examined by Hoesch and Niethammer were not yet in breeding condition, one cannot say that more than one breeding female is found with one male later in the season. The evidence at present points to polygamy, but only superficially.

Males in breeding plumage have been noted as quite pugnacious among themselves, a trait usually resulting in but one male in each small flock. When two come together, they chase each other energetically until one leaves.

Eggs and Egg Laying

The eggs of the shafttail are, like those of the other long-tailed widow birds, pure white, the dimensions of the most satisfactorily identified example being 16.5 by 12.5 mm. (from the nest of *Prinia flavicans;* see hosts, where the data are given concerning the identification of this egg). Measurements of 10 other eggs justifiably attributed to the shafttail, range from 15.3–17.2 mm. by 11.4–13.3 mm. (average 16.1 by 12.5 mm.). Teschemaker (1910a, p. 90), Hopkinson (1918, pp. 156–157; 1926, p. 25), K. Neunzig (1921, p. 330), and Priest (1948, p. 135) all refer to the shafttail as having been known to lay eggs in captivity. Whatever the basis was for these statements (apparently an instance in an aviary of Mr. Heumann's in Sydney, Australia), however, apparently no measurements or descriptions of the egg or eggs have been recorded.

I discard as erroneous the eggs attributed to the shafttail by Carlisle (1923, p. 122), who reported nests and whole clutches of eggs of this bird.

Nothing is known as to the number of eggs laid by one hen in one season, the interval between eggs, the existence or otherwise of host specificity, the length of the incubation period, or whether or not the laying bird removes one of the host's eggs at the time of depositing her own. Probably only one egg is laid in any one nest.

HOSTS

Mörs, (1925), R. Neunzig (1929b), and A. Roberts (1939) stated that the violet-eared waxbill, *Granatina granatina*, is the main host of the shafttail. It is true that there are more records of this waxbill serving as a victim than there are of any other single host species, but that six other species are also known to be affected and that the records for *Granatina* total less than half of all the cases of host-parasite relations make it unwise to emphasize this one host species unduly. All but one of the recorded hosts are weaverbirds, and it does seem probable that birds of this family are the chief victims of the shafttail; however, with the present state of our knowledge, this generalization is tenuous. The known hosts and the data for each follow.

Black-chested longtail: *Prinia flavicans* (Vieillot) [27]

About sunrise on January 1, 1925, in the bushveldt between Pietpotgietersrust and Moorddrift, Transvaal, I found a nest of this warbler containing three eggs of the owner. About a quarter of an hour later I passed near it and saw a female shafttail fly out from it and go over to a male of its species about 100 feet away. The two then flew off. On examining the nest I found, in addition to the three *Prinia* eggs, a fresh, pure white one, similar in size and shape to the egg of the pintail. I consider that the egg was laid by the shafttail, even though it cannot be ruled out that a female pintail might have laid the egg during the 15 minutes between my visits. The pintail was present in the region. Unfortunately, in the excitement over this discovery, I took the eggs out of the nest to look at them more carefully, and while I was examining them, the host returned and then flew off. I put the eggs back, but she deserted the nest.

The parasitic egg was very slightly larger than those of the host, and measured 16.3 by 12.5 mm., as compared with 16 by 11.5 mm. of the host. The parasitic egg was unmarked white, while those of the host were pale olive green marked with brownish lines and spots.

---

[27] *Sylvia flavicans* Vieillot, Encyclopédie méthodique . . . , vol. 2, 1820, p. 438 (South Africa, Namaqualand ex Levaillant).

Scaly weaver: *Sporopipes squamifrons* (Smith)[28]

Both of the proposed races of the scaly weaver are reported as victims of the shafttail. At Quickborn, near Okahandja, Damaraland, on May 20, 1925, R. D. Bradfield (reported by A. Roberts, 1928, p. 318) collected a young shafttail that was being fed by a pair of scaly weavers. This record involves the Damaraland race of the host, *S. s. damarensis* Reichenow.[29] A record assignable to the nominate race of the host was reported by D. C. H. Plowes, who collected a set of five eggs of the scaly weaver with one of the shafttail 2 miles southeast of Warmbaths, Transvaal, on January 25, 1948.

Another record, possibly pertinent here, is a set of five eggs of the scaly weaver and one of a long-tailed widow bird (possibly the shafttail) taken at Andalusia, Transvaal, on April 12, 1942, by C. H. Jerome, in whose collection the set was when I examined it in 1950. The locality, near Kimberley, is one where both the shafttail and the pintail are said to occur, and therefore the actual parasite cannot be determined. In his published note on these eggs, Jerome (1943, pp. 100–101) had called it "*V. macroura* or *V. regia*," but in 1950, when showing me his egg collection, he came to the conclusion that it was a shafttail egg. In an editorial note on Jerome's paper, A. Roberts (1943, p. 102) called it "probably *V. macroura*," but he admitted lacking accurate data on eggs of the shafttail.

Masked weaver: *Ploceus velatus* Vieillot[30]

The masked weaver was stated to be a host of the shafttail, but corroborative data was not published. Hoesch and Niethammer (1940, pp. 361–363) stated that for several years the greatest number of shafttails met with were seen in close proximity to colonies of masked weavers. During this time hundreds of nests of the masked weaver were examined, but no indication of any parasitism by the shafttail was found; however the authors stated that at Okawaka, in the Waterberg area, the masked weaver was said to be the unquestioned host of the shafttail. They refer to "K. Lorang-Okawaka am Waterberg" as the source of this information, but there are no published data pertaining to this reference. Hoesch and Niethammer cast some doubt on this matter by observing that both the *Ploceus* and the *Vidua* live together in mixed groups as long as they are in the off-season plumage, and that the majority of shafttails seen in the *Ploceus* colonies were birds not yet finished molting. They even question whether the shafttail is a regularly breeding bird of South-

---

[28] *Estrelda squamifrons* A. Smith, Report of the expedition for exploring central Africa . . . , 1836, p. 49 (South Africa).

[29] *Sporopipes squamifrons damarensis* Reichenow, Die Vögel Afrikas, vol. 3, 1905, p. 838 (Rehoboth).

[30] *Ploceus velatus* Vieillot, Nouveau dictionnaire d'histoire naturelle, vol. 34, 1819, p. 132 (Namaqualand).

West Africa, but in this matter they are in error, as there are at least two definite instances (see Breeding Season and Range above).

Quail finch: *Ortygospiza atricollis* (Vieillot)[31]

One record refers to the southern race of the host, *O. a. polyzona* (Temminck).[32] D. C. H. Plowes informed me that on April 22, 1946, 9 miles southwest of Bloemhof, Transvaal, he found a nest of the quail finch containing four somewhat incubated eggs of the owner and one fresh egg of a long-tailed widow bird. Inasmuch as the shafttail was the only parasitic longtail in the area, it probably was the species involved. As the eggs of the quail finch are pure white, like those of the parasitic longtails, it is possible that the fifth egg might have been an abnormal one of the quail finch, though the difference in incubation as well as in size seems to make this alternative unlikely.

Melba finch: *Pytilia melba* (Linnaeus)[33]

There are four records of nests, all unfortunately somewhat uncertain as to the identification of the eggs ascribed to the shafttail. All four were kindly related to me by the collector, D. C. H. Plowes. The records of the nests are:

Matopos Research Station, Southern Rhodesia, February 16, 1950, four eggs attributed to the melba finch and one to the shafttail.

Queens Mine, near Bulawayo, Southern Rhodesia, March 14, 1950, three eggs attributed to the melba finch, one to the paradise widow bird, and one to the shafttail.

Two miles southeast of Warmbaths, Transvaal, January 18, 1942, three eggs attributed to the melba finch, one to the paradise widow bird and one to the shafttail.

Same locality, February 7, 1944, two eggs attributed to the melba finch, two to the violet-eared waxbill, and one to the shafttail. This unfortunately confused instance, probably too uncertain to be of any use, had a still more involved history. When first found a male melba finch was brooding on two eggs. A week later a male violet-eared waxbill was brooding and no sign of the melba finch could be found; the nest then contained the five eggs listed above.

In each of these four nests the eggs were differentiated by size only, as all the species involved lay pure white eggs. The eggs of the paradise widow bird are sufficiently larger to distinguish them but those of the other three species differ by not more than a millimeter in their long axis, and not that much in their transverse axis. Until an identified fledged young shafttail is obtained from a nest of a melba finch, it cannot be looked upon as definitely a host of the shafttail.

---

[31] *Fringilla atricollis* Vieillot, Nouveau dictionnaire d'histoire naturelle, vol. 12, 1817, p. 182 (Senegal.)

[32] *Fringilla polyzona* Temminck, Nouveau recueil de planches coloriees d'oiseaux, vol. 37, 1823, pl. 221, fig. 3 (Gambia=Natal).

[33] *Fringilla melba* Linnaeus, Systema naturae, ed. 10, vol. 1, 1758, p. 180 (China=Angola, ex Zedlitz).

Cordon bleu: *Estrilda angolensis* (Linnaeus)[34]

A. Roberts (1939, pp. 109–110) found a nest of the cordon bleu between Etoscha Pan and Ondonga, South-West Africa, May 26. It contained one egg of the host and one of a long-tailed widow bird. The shafttail was the only longtail observed in the area. The identification of the egg is therefore somewhat probable.

Violet-eared waxbill: *Granatina granatina* (Linnaeus)[35]

The most frequently recorded host, the violet-eared waxbill was first mentioned in this connection by Aldersparre (1922, p. 10) without supporting evidence, and then by Mörs (1925, pp. 299–300), who reported finding eggs and young of the shafttail in nests of this waxbill in the Transvaal, and also noted that the young of the two grew up together in apparent amity. A. Roberts (1930, p. 64; 1935, p. 181) obtained further evidence bearing out what Mörs wrote. At Hamanskraal, near Pretoria, F. O. Noome obtained a fledged young shafttail in a group of young violet-eared waxbills, an observation duplicated by Roberts at Kuke Pan in the Kalahari. Hoesch (1934, p. 338) related that in South-West Africa he noted young long-tailed widow birds, probably shafttails, in groups of violet-eared waxbills, but this report is not wholly certain. In a later paper, Hoesch and Niethammer (1940, pp. 360, 361–363) stated that although numerous nests of the waxbill were examined they failed to find any evidence of parasitism by the shafttail. A. Roberts (1939, pp. 109–110) recorded that in the collections of the Transvaal Museum are two parasitized clutches of eggs of the violet-eared waxbill, both collected at Quickborn, Okahandja, South-West Africa—one with three eggs of the host and one of the shafttail taken on March 6, the other with five eggs of the host and one of the parasite taken on April 27. Gill (1945, p. 32) commented that in the Kalahari, Roberts found that the violet-eared waxbill was frequently parasitized by the shafttail and that the young of the two are almost exactly alike.

NESTLING STAGE

The only data that we have is the statement by Mörs (1925, pp. 229–300) that the young shafttails and the young violet-eared waxbills, in whose nests he found them, grew up together without any recorded mutual difficulties. R. Neunzig (1929b, p. 7), quoting Mörs, wrote that the nestlings of the two species closely resemble each other in plumage and in the corn-flower blue papillae at the corners of the mouth.

---

[34] *Fringilla angolensis* Linnaeus, Systema naturae, ed. 10, vol. 1, 1758, p. 182 (Angola).

[35] *Fringilla granatina* Linnaeus, Systema naturae, ed. 12, vol. 1, 1766, p. 319 (Brazil=Angola, ex Sclater).

Young Out of the Nest

Hoesch (1934, p. 338) A. Roberts (1939, pp. 109–110) reported seeing fledged young shafttails in company with the fledged young *Granatinas*, in whose nests they probably had been raised. How long the young parasites remained with their former nestmates is not known. Roberts wrote that "at later dates young shafttails were seen with flocks of adults of their own species."

Food and Feeding Habits

The shafttail feeds largely upon small seeds mostly of grasses. I have watched them feeding on or near the ground, and have seen the birds pick up bits of gravel as well as seeds. The stomach contents of two birds examined contained only small grass seeds. Holub (in Holub and Pelzeln, 1882, p. 123) recorded this species as eating small insects as well as seeds, but did not give any details.

Plumages and Molts

Adult male in breeding plumage: Forehead, lores, small subocular area, crown, occiput, back, upper wing-coverts, inner secondaries, and upper tail-coverts Black. Broad band across the hind neck between Light Ochraceous-Buff and Pale Ochraceous-Buff. Primaries and outer secondaries Natal Brown to Olive-Brown. All but four median rectrices blackish. (I have yet to see an individual with all the lateral rectrices like this. In most birds examined, apparently in full nuptial plumage, some, not always the same ones, of the lateral rectrices are Natal Brown, fairly broadly tipped, and lateroterminally edged with white. Possibly the black lateral rectrices are the last feathers of the nuptial plumage to be acquired and the first to be shed, and thus the time of their presence is reduced.) Four median rectrices very elongated and, except for their terminal 50 mm., reduced to mere shafts, blackish. Terminal "flags" also blackish, and becoming as much as 12 to 15 mm. broad. Chin, cheeks, throat, breast, sides, and anterior abdomen Pale Ochraceous-Buff tinged, especially posteriorly and laterally with Ochraceous-Buff. Thighs, extreme posterior abdomen, and under tail-coverts black. Under wing-coverts whitish tinged with Light Ochraceous-Buff. Iris dark hazel. Bill and feet Coral Red. Wing 69–76 (73.5) mm. Tail 44–47 (45.5) mm. Long rectrices 180–235 mm. Culmen 9–10.5 (10) mm. Tarsus 15–16.5 (16) mm.

There may be some geographic variation in this plumage. Four specimens from Bulawayo (in the American Museum of Natural History) are much more intensely colored below and on the cheeks and the nuchal collar than a long series from Angola, Bechuanaland, and South Africa—almost Ochraceous Orange as opposed to Ochraceous Buff in the latter group. One Bulawayo example, however, is like the Bechuanaland Angola birds.

ADULT MALE IN NONBREEDING PLUMAGE: Very different from the above. Forehead, lores, crown, occiput, nape, back, upper tail-coverts, and upper wing-coverts, very pale Wood Brown to very pale Tawny-Olive, with each feather having a broad median shaft streak of Fuscous. Streaks narrower on the crown and occiput, broadest on the upper back and sometimes almost disappearing in upper tail-coverts, or at least paling there to ashy Benzo Brown. Median streaks on head tending to be less pronounced on feathers of the mid-dorsal area, producing an ill-defined appearance of darker superciliary bands on either side. Inner secondaries dark Fuscous, broadly edged and tipped with very pale Tawny-Olive. Other secondaries Fuscous with no paler margins. Primaries paler, Benzo Brown, basally margined on their inner webs with pale ashy to whitish. Four median rectrices Fuscous-Black, narrowly edged and tipped with buffy white and slightly longer than more lateral ones, which are Natal Brown, broadly tipped and lateroterminally edged with white. Chin, cheeks, throat, breast, sides, and flanks ashy Pinkish Cinnamon, palest on chin, tinged with Ochraceous-Tawny on cheeks, lower breast and sides. Abdomen, under tail-coverts, and thighs white. Bill pale pinkish brown. Feet light brown.

ADULT FEMALE: Similar to male in nonbreeding plumage, but usually with chin, throat, cheeks, breast, and sides whiter, less tinged with very pale Ochraceous Tawny, and (in limited material examined) usually with pale margins of feathers of upper parts somewhat narrower. Rectrices Natal Brown. Lateral ones tipped and lateroterminally edged with whitish (in a single example one new inner rectrix coming in is Fuscous-Black narrowly edged and tipped with white; either the sex of this specimen is wrongly given, or the tail of the female may become like that of the nonbreeding male).

JUVENAL (SEXES PROBABLY ALIKE, BUT ONLY 1 OF EACH SEX EXAMINED): Forehead, crown, occiput Cinnamon-Drab to Tawny-Olive, unstreaked. Hind neck paler, forming an indistinct nuchal collar of ashy pale Tawny Olive. Upper back and upper tail-coverts dusky Tawny Olive, feathers with wide shaft streaks of dark Benzo Brown to pale Fuscous. Rump and upper tail-coverts similar but without dark median streaks. Remiges and rectrices dark Olive Brown to Fuscous, externally edged with pale Tawny-Olive. Primaries internally edged basally with buffy white. Lores slightly duskier than crown. Chin, cheeks, throat, breast, sides, flanks, and thighs pale Tawny-Olive, more intense on breast and upper sides. Anterior abdomen paler, more whitish. Posterior abdomen and under tail-coverts white. Under wing-coverts whitish, tinged with tawny.[36]

MISCELLANEOUS DATA

LONGEVITY: According to Russ (1878, p. 97), individuals of this species may live as long as 8 to 10 years in captivity.

Paradise Widow Bird: Genus *Steganura*

Several authors (Delacour and Edmond-Blanc, 1934; Winterbottom, 1939a; and others) considered the paradise widow bird (*Steganura*) congeneric with the long-tailed widow birds (*Vidua* proper). But while I have reduced the combassous (*Hypochera*) to the rank of a subgenus in this paper, I consider *Steganura* to be a valid generic entity. Some writers may claim that *Steganura* is only an extreme development of the tendency shown by *Vidua* proper in its divergence from *Hypochera*, and that to recognize *Steganura* but not *Hypochera* is inconsistent. I find, however, that there are sufficient numbers of ethological and morphological characters to warrant the judgment that *Steganura* is more different from *Vidua* than *Vidua* proper is from *Hypochera*.

ETHOLOGICAL CHARACTERS: In its aereal courtship performance, *Steganura* differs markedly from all the other viduines. As may be seen in our account of this part of its life history, the male paradise widow bird may rise hundreds of feet in the air and then plummet down toward the female, a very different display from the usual viduine hovering performance. Also aviculturists reported that the paradise widow bird is much less aggressive or pugnacious with other birds in an aviary. By itself this last "character" is not very impressive, but it is something to consider in the sum total of differences, which, in passerine genera, is never very great.

MORPHOLOGICAL CHARACTERS: In size, which by itself is not a generic character, *Steganura* is much larger than any of the other viduines, which are all about the same size. More importantly, *Steganura* differs in the pattern of the mouth markings of the nestling and in the very peculiar type of rectricial growth in the nuptial plumage of the male. The newly hatched *Steganura* differs from all species of *Vidua* in having no spots on the tongue or the floor of the mouth, and only a single anteromedian one on the roof of the mouth, whereas the *Vidua* have two spots on the tongue, five spots on the roof of the mouth, and a band either complete or interrupted

---

[36] In single young female examined, top of head, breast, and back were slightly darker than in one young male seen; it is doubtful, however, that there is anything more than purely individual variation involved. In the male (dried skin), the bill was pale yellowish brown; in the female (equally dried) it was blackish (both maxilla and mandible); in the young the feet are dark brown.

on the floor of the mouth. The peculiar rectricial growth appears to be a significant character, especially because rectricial elongation has developed in parallel but different ways independently in widely dissimilar genera of the family. So unusual is this development in *Steganura* that it is given in detail in the following paragraphs.

In *Steganura* the median pair of rectrices not only have the webs greatly broadened, but their shafts are twisted 90 degrees so that the lower surfaces of the webs are opposed to each other. These broadened plumes are comparatively short and end in a filamentous prolongation of the shaft. The next pair are much longer and have their webs widened all along, narrowing somewhat terminally, and hang down in a crescentic curve. Furthermore, each of these feathers has, springing from near its base, a hairlike filament of the same length as the feather. This filament, first described by Brisson (1760, p. 123) and later more fully by Strickland (1850, pp. 88–91, 149), originally adheres to and runs along the margin of the outer web, and detaches and is shed only when the feather has attained its full growth.

Since Strickland's description and illustration (see my fig. 3) seems to have been generally overlooked (his publication is not widely available), I quote from it in some detail. Speaking of the long, submedial rectrices he noted:

> They differ from all the other tail-feathers in presenting a serrated appearance at their margins. In the other feathers the barbs end in fine points, so that the webs which they compose terminate in an acute margin. But in this particular pair of rectrices, the barbs terminate abruptly, with an obliquely flattened disk at the extremity of each, and the webs composed of those barbs are consequently both blunt and serrated at the margin.
>
> On examining these feathers when in a half-grown state, a singular hair-like filament is seen to spring from their base, which explains the cause of these marginal serrations. This filament is narrow, flat, and thin, much resembling in appearance the barbs of the feathers, but reaching to three or four inches in length. Its distal extremity is free; but toward the base of the half formed feather it is seen to adhere to the extremities of all the barbs on one . . . side of the feather, forming a conspicuous margin or "selvage" to the web. Toward the base of the feather, where the imperfectly formed barbs are collected, as in all young feathers, into a cylindrical bundle, and inserted into a membranous sheath, the barbs belonging to both webs of the feather are seen to be connected at their extremities to the opposite sides of this intermediate filament. As the feather grows and the barbs become mature, their tips are gradually released from this connecting filament, those of the lower or exterior web first, and those of the interior one subsequently. Hence the distal portion of the filament becomes free and waves loosely in the air. It is probable, that when the whole feather reaches maturity, the filament is shed altogether.
>
> The cicatrices, or points of junction between the tips of the barbs and the flat surface of the filament, produce a succession of slight indentations on both sides of the latter, and give it a serrated appearance, which is further increased by the

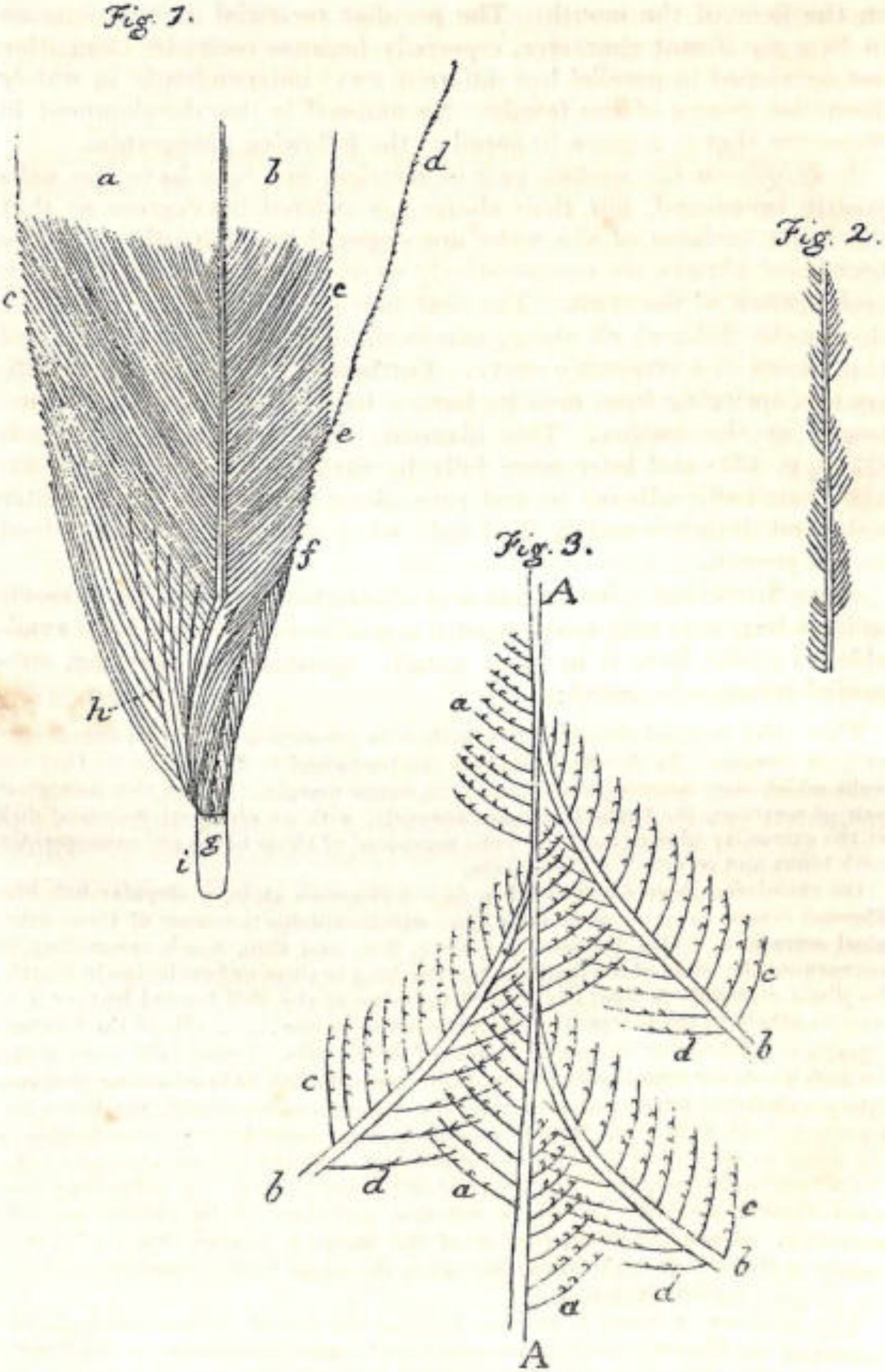


FIGURE 3.—Structure of elongated rectrices of *Steganura* (after Strickland, 1850, figs. 1–3): Fig. 1, ventral view of basal portion of one of the submedian rectrices in a partly grown

> alternate tufts of barbules which fringe its margin. Hence also arise the corresponding serrations on the margins of the feather. . . .
>
> It is remarkable that these filaments, though apparently formed for some temporary purpose in the development of the feather, should exhibit a structure as highly complex as that of the feather-barbs themselves. I allude to the double row of barbules . . . which fringe the outer margin of the filament; they are not continuous as on the barbs . . . , but in little tufts, alternating with the surfaces of attachment of the barb-tips. . . . These barbules further exhibit those ultimate fringes to which the name *barbicels* has been given.
>
> In ordinary feathers, the barbules on the distal side of the barb are, as is well known, furnished with hooked barbicels . . . while those on the proximal side are simple. But it is remarkable, that in these deciduous filaments . . . both series of barbules are furnished with hooked barbicels. The object of these is obviously to embrace the barbules of the feather barbs, during the attachment of the latter to the filament, and as these barbules are attached to both sides of the filament, it is requisite that the filament should be provided with a double series of hooks.

It would be of interest to learn if some similar type of growth also operates in the development of the primaries of the saw-winged swallows of the genera *Stelgidopteryx* and *Psalidoprocne,* but as yet no information is available.

There is some difference of opinion among informed taxonomists whether *Steganura* comprises one or two species. I tentatively consider it comprises one species, but discuss this matter, which is of very considerable biological interest, as fully as current data and understanding permit under the account of the species.

Paradise Widow Bird

Steganura paradisaea (Linnaeus)[37]

PLATES 4, 10–12, 16

Although favorite cage birds for a long time and common, wide-ranging, and conspicuous in the fauna of the open country of Africa, the paradise widow birds, unfortunately, are still inadequately understood. I treat all recognized forms of them here as one specific aggregate, but with further data they may prove to be divisible into

---

[37] *Emberiza paradisaea* Linnaeus, Systema naturae, ed. 10, p. 178, 1758 (Africa, restricted to Angola, Linnaeus).

state: *a*, Inner web; *b*, outer web; *c*, serrated margin; *d*, free portion of filament; *e*, *f*, portion attached to both webs; *h*, barbs of outer web recently detached from the filament and not yet incorporated into the web; *i*, membranous sheath surrounding the immature barbs. Fig. 2, part of filament magnified to show alternating tufts of barbules on each side. Fig. 3, part of filament highly magnified, with portions of barbs attached as in fig. 1, *f*–*g*: *a*, Filament barbules forming two series of tufts, both furnished with hooked barbicels; *b*, feather barbs belonging to the opposite webs of the feather, connected at their distal extremities to opposite sides of the filament; *c*, barbules of the proximal sides of the barb devoid of barbicels, or furnished with only a very few simple ones.

two distinct species. The elongated tail feathers are noticeably tapered toward the tip in one race of eastern and southern Africa, while these feathers remain broad to their ends in six other forms inhabiting mainly western Africa. Birds of both types, however, occur together in northeastern Africa, in Kenya, and in the area from Mozambique to Angola. As Chapin (1954, p. 579) has put it, geographic overlapping by birds of the tapered, narrow-tailed type with at least two of the broad-tailed races is definitely known. If it could be demonstrated that certain kinds of males mated with certain kinds of females, the tapered, narrow-tailed form would merit specific status, but no one has been able to distinguish forms among the females (only the breeding males have the elongated rectrices). "It has been suggested that the tail form of males is a mutational character, determined by a single pair of genes and thus to be compared with color phases among other birds and especially with *Coliuspasser ardens*. Pairing would be indiscriminate, no intermediates would result, and were it not that each form does occupy an area mainly its own, they should not even be dignified with trinomials. Such a view is reasonable but will not be easy to prove by either field observation or breeding experiments."

On the other hand, we may have two closely similar species—*paradisaea* with tapered elongated rectrices in the adult male, and *aucupum* (six races) with broad elongated rectrices. In an earlier paper, Chapin (1922) favored this view and postulated that *paradisaea* originated in southern Africa and that *aucupum* became differentiated north of the Cameroons-Congo forest, which, being then much more extensive to the east, formed an effective barrier between these two bush and grassland birds. When the forest became reduced in East Africa with the drying up of that area (there is both botanical and geological evidence linking these two facts), the two forms of paradise widow bird were by then supposedly sufficiently differentiated so that as *paradisaea* spread northward and *aucupum* eastward and southward they presumably did not interbreed where they came together. In a subsequent discussion (1932, pp. 277–278) Chapin further remarked upon the influence of the equatorial forest, which "once extended farther over East Africa cutting the ancestral *Steganura* into two distinct populations." How the *aucupum* stock became isolated from *paradisaea*, however, is unclear, as there is no evidence suggesting that *Steganura* as a group is older than the equatorial forest, and that the group could as a result have once been fractionated by this forest and then subsequently allowed to merge again.

Aside from the purely taxonomic problem presented, the paradise widow birds appear to be essentially alike in their habits. Unfortunately, what is known of them is still extremely fragmentary, as will be apparent from the following account. Here is another opportunity for resident naturalists to help clarify a very difficult situation.

DISTRIBUTION

The paradise widow bird occurs throughout the greater part of Africa south of the Sahara, except for the heavily forested areas and the area extending south of Damaraland, Bechuanaland, the Transvaal, and Natal. It has been recorded from Senegal (Diourbel, Dakar, St. Louis), Gambia (Bathurst), Casamance, Sierra Leone (Bendugu, Kamaron), Ivory Coast (Bandama), Upper Volta (Wagadugu), French Sudan (Beledugu, Ansongo, Fiko, north to latitude 16° N.), Ghana (Tumu, Northern Territory), Togoland, Nigeria, Cameroons, French Equatorial Africa, Sudan, (Darfur to Sennar), Ethiopia (north to northern Ethiopia, up to 7,000 feet elevation, Bogosland, Eritrea), and British Somaliland, south through the Belgian Congo, Uganda, Kenya, Italian Somaliland, Tanganyika, Mozambique, Angola, the Rhodesias, Nyasaland, and Bechuanaland (Lake Ngami), to Damaraland (Ombujomatemba, Erongo Plateau, Omaloko), Transvaal (Rustenberg), extreme northeastern Cape Province (Kimberley), Natal (Zululand), Port Natal and extreme eastern Cape Province (King William's Town). It is not found in the Orange Free State or most of Cape Province, and has not yet been recorded in Liberia, where it probably occurs.

Throughout its range it is a bird of fairly dry types of country, the thorny bushveldt, and the more open savannas, but not grasslands devoid of trees or shrubs. It has been recorded from about sea level to as much as 7,000 feet elevation, but appears to be most numerous below elevations of 5,000 feet.

In the literature, I came across frequent statements that the species is locally present for only part of the year and that suggest, if not regular migration, a good deal of seasonal movement. Probably some of these statements arose because the paradise widow birds go unobserved or at least unidentified from other "off season" weavers when not in breeding plumage. I cannot, however, rule out the possibility that the breeding range may not be wholly coincidental with the total recorded range of the species. Thus, in Gambia, Hokinson (*in* Bannerman, 1949, p. 394) noted that the paradise widow birds increased in numbers in the rainy season. Priest (1936, p. 368) failed to find a male in nonbreeding plumage or any females after June in the Salisbury-Marandellas area of Southern Rhodesia, and suggested that the paradise widow bird might be migratory to some extent. In northeastern Africa Heuglin (1869, pp. 584–585) doubted that it was resident through the year, as he saw none except from May to December. I cannot find any real evidence by which to limit the breeding range as different from the total geographic distribution of the species.

Ranges of the races are as follows:

Steganura paradisaea paradisaea: Eritrea and Ethiopia south across eastern Africa to eastern Cape Province; west across Rhodesia and the southern Belgian Congo to Angola; absent in southwestern Africa south of Damaraland, Bechuanaland, and Transvaal.

Steganura paradisaea aucupum:[38] Senegal and French Sudan east to Lake Chad and Shari River, south to the northern limits of the forests of the Upper Guinea coast and the Cameroons.

Steganura paradisaea togoensis:[39] Togoland, probably Ghana and Upper Guinea coastal area where not forested.

Steganura paradisaea kaduglicnsis:[40] Southern Kordofan Province, and probably northern Bahr-el-Ghazal, Sudan.

Steganura paradisaea interjecta:[41] Eastern Cameroons, east to the Upper Uele District, Belgian Congo, and Mongalla Province of the Sudan.

Steganura paradisaea orientalis:[42] Valley of the Blue and White Niles, west to Darfur, and possibly to Lake Chad, where it intergrades with *aucupum*.

Steganura paradisaea obtusa:[43] Eastern Belgian Congo east to western Kenya, south to Nyasaland, Gazaland, Mozambique, Northern Rhodesia, and Angola.

There appears to be no essential difference in the ecological habitats of the various races.

Breeding Season

The following data, culled from the labels of museum specimens, the published notes of many observers, and a number of unpublished observations, give a résumé of definite evidence for the breeding time of the paradise widow bird in the various parts of its range. The picture is still incomplete, and will undoubtedly be added to as new data become available. The dates of first appearance of nuptial plumage in adult males and the beginning of postnuptial molt are not by themselves invariably reliable indices of breeding, but have been used in connection with other evidence. As Chapin noted (1954, p. 584), throughout its range the paradise widow bird retains the nuptial plumage much longer than does the pintail, and this fact may have some connection with the fact that the main group of known host species of the paradise widow birds, the members of the genus *Pytilia*, are late breeders.

GAMBIA: July to November (given as the breeding season by Hopkinson, 1909, p. 7).

SIERRA LEONE: Bendugu and Kamaron, November 16 and 17, males with swollen testes collected.

---

[38] *Steganura paradisaea aucupum* Neumann, Bull. British Ornith. Club, vol. 21, 1908, p. 43 (Diourbel, near Dakar).

[39] *Steganura paradisaea togoensis* Grote, Ornith. Monatsb., vol. 31, 1923, p. 43 (Kete, Togoland).

[40] *Steganura paradisaea kadugliensis* Bowen, Proc. Acad. Nat. Sci. Philadelphia, vol. 83, 1931, p. 230 (Kadugli, southern Kordofan, Sudan).

[41] *Steganura paradisaea interjecta* Grote, Journ. Ornith., vol. 70, 1922, p. 402 (Weg Nola, eastern Cameroons).

[42] *Vidua paradisaea orientalis* Heuglin, Ornithologie Nordost-Afrika's . . ., vol. 1, 1871, p. 583 (Bogosland, type from Keren).

[43] *Steganura aucupum obtusa* Chapin, Amer. Mus. Nov., No. 43, 1922, p. 6 (Luchenza, Nyasaland).

FRENCH SUDAN: Fiko, December, males in breeding condition.

GHANA: 30 miles east of Tumu, January 19, male with swollen testes collected.

NIGERIA: Pategi, Koton Karafi, and Lokoja, December and January, breeding males.

SUDAN: Said to be in breeding condition in September.

ETHIOPIA, ERITREA, AND BRITISH SOMALILAND: Chapin (1954, p. 581) noted that fully plumaged males were recorded from May to December, and some even in February and March. "It would seem that the breeding season must vary somewhat according to the district and its particular seasons of rain. In British Somaliland the breeding season may end in September," but males in full nuptial feathering were taken in Eritrea on January 9 and March 5.

ITALIAN SOMALILAND: Absona, May 26, egg. Solole, June 11, egg.

BELGIAN CONGO: Marungu, April 13 to 23, specimens in breeding condition collected. Savannas of southeastern Congo, February to July, males in nuptial plumage. Near Elisabethville, late April, egg. Upper Uelle, northeastern Congo, breeds November to December, possibly to January (Chapin).

KENYA: Northern part, Turkana, July, male with swollen gonads. Marsabit, July, young birds. Ngong, no date, eggs.

TANGANYIKA: Northern part, March to August and October to December. Western part, March to June and November to December. Central and southern part, January to April and October to December (ex Mackworth-Praed and Grant, 1955, p. 1050).

NYASALAND: April and May, eggs.

MOZAMBIQUE: February to July, birds in breeding condition. Gorongoza, October 3, egg.

SOUTHERN RHODESIA: Vumba, Umtali, Urungwe, December, eggs. Male seen in courtship display in full breeding plumage in June (Beit Bridge).

DAMARALAND: Okhandja, April 15, egg.

TRANSVAAL: Mokeetsi, February 15, March 17, eggs.

NATAL: Umhloti Beach, November 21, egg.

SONGS AND CALLS

The only notes I ever heard from the paradise widow bird were monosyllabic chirping sounds that seemed more mellow, less strident, than the corresponding note of the pintail. Many years ago Heuglin (1869, p. 585) described the paradise widow bird's notes as having a flutelike quality, apparently because of the same mellowness that I noted many years later. Priest (1936, p. 369) also stated that the call is flutelike, but it is not clear whether his report is based on personal observation or on Heuglin's statement. Priest went on to state that "a love song" may be heard before and during the breeding season, but he gave no description of it. Apparently he distinguished it from the flutelike call note. Heuglin, also called what he considered the true song "monotonous," but gave no description. Russ (quoted in Butler, 1899, p. 272) wrote that the song is a "little harmonious chirping of monosyllabic longdrawn sounds, partly shrill, partly euphonious."

Considering how frequently naturalists met with and collected the paradise widow bird, it is surprising how few comments are available as to its vocalisms—so few as to make me wonder if the species is silent a good part of the time. Thus, Chapin (1954, p. 583) described the display flight of the males in some detail but added that he heard no vocal note from them.

Schütze (1929, p. 614) received a male paradise widow bird in a shipment of live birds from Ethiopia. He kept it in his aviary and found it to have a song like that of the common waxbill, *Estrilda astrild*.

COURTSHIP, TERRITORIAL BEHAVIOR, AND MATING

The courtship display of the paradise widow bird is quite different from that of the other long-tailed widow birds. Whereas in the latter the male hovers in a bouncing undulatory flight a few feet above the females, in the paradise widow bird the displaying male soars up to a very considerable height (said by Belcher, Bannerman, and others to be as much as 300 feet), and then catapults down to a few feet from the females. I never saw a cock go more than 50 or 60 feet up in the air, and then descend rapidly. My observations agree with those of Priest (1936, pp. 370–371), who observed a male in full nuptial plumage apparently displaying to a number of females (or at least, birds in "sparrowy" plumage) perched in a thorn bush near Beit Bridge, Southern Rhodesia, on June 6. The male—

> flew to some 60 feet from the ground, and then commenced to progress with small wing-beats, covering very little ground whilst these antics were being performed. He would circle round in ever increasing rings, remaining at the same altitude, and in the distance his flight might be compared to that of an aeroplane. After a number of these evolutions had been made the bird descended rapidly to the ground by a series of prolonged undulations, and finally alighted on a thorn bush near the females.
>
> After a short pause the same display was again commenced, and the bird went to an even higher altitude, in fact, to such a height that its small body was only just visible, and if it were not for the long knife-bladed tail it possessed, and the decided "bustle" near the base of the tail, one might easily lose sight of such a small object. It was after 4 o'clock in the afternoon . . . [and] finally the male, and either his wives or the combined broods of the last season, dispersed.

Bannerman (1953, p. 1505) bore out the "even higher altitudes" involved in this display, when he wrote that males may be "observed to soar to a height of 300 feet or so and to hover in the air with flapping wings, presently to descend with great velocity. They have a habit, too, of flying from one bush to another, perching for a while on the topmost twig. The elongated tail makes the male a very conspicuous creature when indulging in these nuptial antics."

Schuster (1926, p. 728) gave a somewhat different account—writing that the male flies from an elevated perch, slowly rises with rapid wing beats, and then swoops down in a similarly slow descending flight, in an oblique course to another elevated perch, in the vicinity of which he lets himself down in a great arch flight.

According to Russ (*in* A. G. Butler, 1899, p. 273), in captivity, possibly because of the impossibility of rising to heights, the male gives a "jumping love-dance" many times a day. Unfortunately no description is given of this behavior, which does not appear to have been recorded in wild birds, but which makes me think of the courtship behavior of the combassous (pp. 71, 76, 82). In fact, Russ (1884, p. 180) actually made this very comparison, and stated further that when the change into breeding condition begins (usually first noticeable with the darkening of the tip of the bill and the appearance of a few feathers of the nuptial plumage on the head, neck, and breast), the male becomes more lively and begins to sing. He then flies hour after hour in the flight space of the bird room, but comes back to alight each time on the same perch. As the nuptial plumage becomes more complete, the bird's movements become more and more lively, until he indulges in the hopping or bouncing courtship dance many times every day.

One unusual courtship pattern was recorded for a captive bird. In the aviary of T. Lloyd (1955), a pair of fire finches reared a young paradise widow bird. As soon as the chick left the nest, the adult male paradise widow bird "seemed to pay attention to the chick immediately and started displaying in front of it, even while the foster parents were feeding it, and then he became very aggressive, so for the safety of the chick the parent whydah cock was removed."

In a recent book Gilliard (1958, p. 386) erroneously described a very different courtship display for the paradise widow bird. The behavior that he described is that of Jackson's whydah (*Drepanoplectes jacksoni*).

There is still little evidence for or against the existence of territorialism in the paradise widow bird. In Northern Rhodesia, Jones (1945, p. 182) noted six or seven fully plumaged males together with attendant females—a condition which does not suggest the exclusiveness usually associated with territorialism. On the other hand, in Uganda, Stoneham (1929, p. 276) wrote that "each male seemed to have occupied his territory and doubtless the many females were busy building or brooding." While this report involves the false assumption of nesting by the paradise widowbirds, it suggests a spatial separation of the males, the only birds Stoneham appeared to have actually seen.

Chapin (1954, pp. 580–581) noted that the paradise widow bird lives in small flocks "which may include several adult males until the prenuptial molt is complete. Later the males separate and display in sustained flights over the treetops." Jackson gave further evidence of the spatial isolation of breeding males inherent in the concept of territoriality, when he noted (1938, pp. 1530–1531) that on Manda Island "single cock birds in full breeding dress were frequently seen . . . and I have no note of more than one full-plumaged cock with half a dozen or so of females and immature birds being met with until February 1910, when there were five beautiful cocks in a flock of twenty at a spot between Voi and Tsavo." Unfortunately he gave no indication that the February birds were really in breeding plumage. Bannerman (1949, p. 394), apparently using notes made by Col. W. R. Thompson in Sierra Leone, noted that the males are occasionally pugnacious and "territorial minded," and drive away intruders from their favorite perches. However, no actual data were given. Obviously, much more actual data is needed to determine the extent of territorial behavior in the paradise widowbird.

Many writers reported the paradise widow bird to be polygamous because usually there are several females (or female-like birds) with each nuptial-plumaged male. This evidence is by no means sufficient as many of these "sparrowy" individuals may be year-old birds of either sex not yet in breeding condition. Lynes (1924, p. 678) suspected, from his notes, specimens, and the observations of Chapin, V. G. L. van Someren, and others that the supposed harems and even the assumed polygamous habit are due to the appearance created by the adherence to the group of the young of the previous season, as was found to be the case among pintails and, with less evidence, among shafttails. On the other hand, polygamy does occur as the normal picture in some species of *Euplectes* and *Ploceus*. Mouritz (1915, p. 556) found near Bulawayo that while single full-plumaged male paradise widow birds were often seen with as many as 50 brown "sparrowy" birds, elsewhere he found each male followed by only two or three females (or female appearing birds). Hoesch and Niethammer (1940, pp. 363–365) wrote that the paradise widow bird lives polygamously, but they recorded no actual evidence in this matter.

Eggs and Egg Laying

The eggs of the paradise widow bird are pure white and measure from 17.7–19.5 by 13–14 mm. These facts are known from a completely shelled oviduct egg from a wild, killed bird recorded by J. Vincent (1936, p. 115) and from eggs laid in aviaries.

Nothing is known of the number of eggs laid in one season. Vincent found one bird had already laid one or more eggs and had two more well developed ova, one almost ready to lay. In captivity one hen laid 10 eggs between early May and mid-July (Lloyd, 1955), some in a nest of a fire finch, and some on the floor of the cage.

The behavior of paradise widow birds breeding in captivity is by no means a reliable index of their normal habits, but it is known that such birds have laid eggs in nests of melba finches, fire finches, and zebra finches, facts which suggest that more than one kind of nest is acceptable to a hen of the parasite. In the wild, we have as yet no indication either of host specificity or of its absence.

The interval between eggs and their incubation period are also still to be discovered.

A. R. Robertson (1949) reported that in captivity the paradise widow birds breeding in Prinsloo's aviary (discussed below in our account of the melba finch, *Pytilia melba* as a host) showed no attempt to destroy the eggs of the hosts in whose nests they had been laid. On the other hand, Lloyd (1955) felt that he had sufficient evidence to the contrary to cause him to suspect the female paradise widow bird of deliberate egg destruction. He reported that on one day a fire finch's nest in his aviary contained four eggs of its own and two of the paradise widow bird, and that the next day three of the fire finch's eggs were gone. The female paradise widow bird was suspected and was removed from this cage to a smaller solitary one. Some weeks later, when the fire finches had nested again and had several eggs in the nest, the hen paradise widow bird was brought back into the cage and it laid another egg in the nest, "destroying a Fire Finch's egg as before." The destruction of three eggs in one day without any egg laying by the parasite points more to ordinary egg robbing than to the usual parasitic "replacement" behavior. The subsequent instance listed gives the impression of egg removal to make room for a parasitic substitute.

Although the paradise widow bird is wholly parasitic in its breeding, there is an old avicultural observation that is difficult to fit in with the more recently learned facts. A. G. Butler (1899, p. 273) cited Russ, who, after trying for years to breed this bird in captivity, had one partial success, which he related as follows:

> I . . . turned loose three females with one male in the bird-room. During the first year these did not exhibit the slightest inclination to nest. Only towards the autumn of the second year all three began to drag straws hither and thither, and in November, whilst the male was still exhibiting full ornamental plumage, they collected bents, threads of bast, tufts of cotton-wool and the like, into an apparently disordered heap on the wire bottom of a high hanging cage. I could, however, never make sure of an approach between male and female. When, after a considerable time, I at length investigated, I found an extraordinary double nest within the large tower, of all possible materials. One nest cavity was shaped like a baker's oven. . . . In the first were three, unfortunately dead, young ones, in the second a living one. . . . The living youngster was fed by two females, but I never noticed that the old male troubled himself about the nest or the young one. The latter in its young clothing was very like the old

female, only much paler whitish-grey. After its flight it proved itself a lazy, thoroughly voracious bird.

At this late date, it is impossible to learn if any other kinds of birds that might have acted as foster parents were present in the same cage, though it appears that there probably were some. Aviculturists would hardly refer to a "bird-room" unless it were a sizeable enclosure with many small birds in it. Probably an aviculturist as experienced as Russ would have known his birds well, and hence it may be inferred that a certain amount of nestling feeding was done by the paradise widow hens. Unfortunately this brief statement remains as the only evidence of "attentive behavior" for this parasitic species.

Boosey (1956, p. 74) noted with justifiable skepticism that Reve in Germany was said to have bred the paradise widow bird in his "bird room," but Boosey gave no details.

That more than one egg of a paradise widow bird may be laid in the same nest of a host is indicated by a case reported by Belcher (1930b, pp. 74–75), who found a nest of *Pytilia afra* at Nyambadwe, Nyasaland, June 25, 1924, containing seven eggs, four of which he considered attributable to the paradise widow bird. This set, less one egg which was broken before Belcher took the picture, is shown on plate 12. It is impossible to say how many individuals were responsible for these eggs.

HOSTS

The known hosts of the paradise widow bird are all weaverbirds. Our data are still too meager to enable us to say that only species of this family are regularly parasitized, but the evidence available indicates that members of one genus of this family, *Pytilia*, are the most frequently used hosts. Of all host records, including some that are not too definite, but on which I have some data, three quarters relate to two species of *Pytilia*. In the following list of hosts I have included only those records that appear to be fairly clear with respect to the identification of the parasitic eggs; however, even some of these records are far from satisfactory.

Cape sparrow: *Passer melanurus* (Müller)[44]

This record is hardly more than a guess. Jerome (1943, p. 100) found a nest of a Cape sparrow in an old nest of a lesser striped swallow (*Hirundo abyssinica unitatis* Sclater and Mackworth-Praed[45]) containing four eggs of the host, one of a didric cuckoo, and one pure white egg. The pure white egg measured 18.5 by 12 mm. Jerome thought that it was a shaft-tailed widow bird's egg, but A. Roberts

---

[44] *Loxia melanura* P. L. S. Müller, Des Ritters Carl von Linné . . . vollständiges Natursystem . . ., Supplement, 1776, p. 153 (Cape of Good Hope).

[45] *Hirundo puella unitatis* Sclater and Mackworth-Praed, Ibis, ser. 10, vol. 6, 1918, p. 718 (Pinetown, Natal).

(1943, p. 103) suggested that both from the standpoint of size and of geography, the egg was probably that of a paradise widow bird. The nest was found near Umhloti Beach, Natal, on November 21, 1941. I think that while Roberts may have been correct in his reidentification of the parasite, the nest is not of a sort that one would expect a paradise widow bird to enter. The egg is certainly small for a lesser honey-guide (*Indicator minor* [46]), but that is a possibility that cannot be ruled out.

Gray-headed sparrow: *Passer griseus* (Vieillot) [47]

Adlersparre (1922, p. 10) wrote that the paradise widow bird is parasitic on the gray-headed sparrow, but gave no supporting evidence. No one else appears to have found this sparrow to be a host of the paradise widow bird, although Adlersparre seemed to have based his statement on field observations of someone else in Africa.

Cardinal dioch: *Quela cardinalis* (Hartlaub) [48]

V. G. L. van Someren (1956, p. 464) wrote that he found eggs of the paradise widow bird in nests of the cardinal dioch, but unfortunately gave no details as to dates, exact localities, or number of such instances observed.

Red bishop: *Euplectes orix* (Linnaeus) [49]

H. M. Miles wrote me that P. Cooke once found an egg of a paradise widow bird in a nest of a red bishop bird in Southern Rhodesia.

Yellow-rumped bishop: *Euplectes capensis* (Linnaeus) [50]

I know of two records, both merely based on eggs attributed to the paradise widow bird, taken from nests of this host, and deposited in the collections of the Victoria Memorial Museum, Salisbury, Southern Rhodesia: At Vumba, Umtali, Southern Rhodesia, on December 27, 1957, J. L. Walker collected three paradise widow bird eggs from a nest of this host. At Urungwe, also in Southern Rhodesia, on December 30, 1926, C. Myers obtained two such eggs from another nest of this bishop bird (race *E. c. zambesiensis* (Roberts)).

Cut-throat finch: *Amadina fasciata* (Gmelin) [51]

I know of only one uncertain record. The van Somerens (1945, p. 42) found a nest of the cutthroat in an old nest of a Speke's weaver

---

[46] *Indicator minor* Stephens, *in* Shaw, General zoology, vol. 9, 1815, p. 140 (Cape of Good Hope).

[47] *Pringilla grisea* Vieillot, Nouveau dictionnaire d'histoire naturelle, vol. 12, 1817, p. 198 (United States=Senegal, ex Lafresnaye).

[48] *Hyphantica cardinalis* Hartlaub, Journ. Ornith., vol. 28, 1880, p. 325 (Lado).

[49] *Emberiza orix* Linnaeus, Systema naturae, ed. 10, vol. 1, 1758, p. 177 (Africa=Angola, ex Edwards).

[50] *Loxia capensis* Linnaeus, Systema naturae, ed. 12, vol. 1, 1766, p. 306 (Cape of Good Hope).

[51] *Loxia fasciata* Gmelin, Caroli a Linné . . . systema naturae, ed. 13, vol. 2, 1789, p. 859 (Senegal, ex Vieillot).

(*Ploceus spekei* (Heuglin))[52] containing a most unusual assortment of eggs—1 infertile egg of Speke's weaver, 11 cutthroat eggs (5 slightly incubated, 5 fresh, and 1 runt), and 3 white eggs attributed to the paradise widow bird. No date or locality were given.

Yellow-backed pytilia: *Pytilia afra* (Gmelin)[53]

A. W. Vincent (1949, p. 696) found a nest of a yellow-backed pytilia near Elisabethville, southern Belgian Congo, late in May. It contained four eggs of the owner and two which Vincent distinguished by their larger size and attributed to the paradise widow bird (race *S. p. obtusa*), this bird being fairly common in the vicinity. The 4 eggs of the host measured 15.5–16.9 by 11.7–12.0 mm; the 2 of the parasite measured 18.2 by 13.1 and 17.9 by 13.0 mm. This inferred identification is probably correct, but until a completely certain record becomes known, this pytilia cannot be looked upon as a proven host. Chapin (1954, p. 513) cited Vincent's record without raising any questions as to its probability. Belcher (1930a, p. 330) wrote that in Nyasaland nests of this pytilia and the melba finch often contain larger eggs, "almost certainly those of the Paradise Whydah, though this is not yet definitely established." In another paper (1930b, pp. 73–75) he cited two instances of the yellow backed pytilia serving as a host and illustrated the parasitized sets of eggs.

Melba finch: *Pytilia melba* (Linnaeus)[54]

The most authenticated host of the paradise widow bird is the melba finch, but of even this host most of the records are inferential rather than positive.

Impressed by the coincidence of the ranges, both geographical and ecological, and by the similarity of the mouth markings and plumage of the young of the paradise widow bird and the melba finch, R. Neunzig (1929b, pp. 12–13) suggested that the former was parasitic on the latter. He had, however, no proof. Hoesch (1939, p. 208), on the contrary, found that a fledgling paradise widow bird did not show the correspondence in gullet markings with young melba finches, that it had only a black speck near the end of the palate and had none of the blue dots on the sides of back of the palate, a characteristic said to be common of young melba finches. Possibly the young paradise widow bird was already old enough to have lost these markings, which are of relatively short duration. Hoesch and Niethammer (1940, pp. 363–365) noted that the blue spots of the young melba finches remain visible for a fairly long time after the birds leave the nest.

---

[52] *Hyphantornis spekei* Heuglin, *in* Petermann's Geographische Mittheilungen, 1861, p. 24 (Somali).

[53] *Fringilla afra* Gmelin, Caroli a Linné . . . systema naturae, ed. 13, vol. 2, 1789, p. 905 (Angola).

[54] *Fringilla melba* Linnaeus, Systema natuae, ed. 10, vol. 1, 1758, p. 180 (China=Angola, ex Zedlitz).

In spite of the lack of evidence behind his conclusions, however, Neunzig may have been correct when he decided that the melba finch was the regular host of the paradise widow bird. A. Roberts (1939, pp. 110–112), commenting on Neuzig's statement, added that he—

> was long ago informed by Mr. F. E. O. Mörs, of de Krom, that the Melba Finch was the host of the Paradise Widow Bird, and Mr. Melville Carlisle of Onderstepoort Veterinary Laboratories also stated the same thing, upon the last occasion, in March last, telephoning to inform me that he had just seen two young Paradise Widow Birds in company with a party of young Melba Finches. In April last, when I was in Bulawayo, Captain R. H. R. Stevenson presented the Museum with a clutch of Melba Finch eggs and one of the Paradise Widow Bird, taken in his garden in Hillside, Bulawayo. The birds had been under observation from the time when the Melba Finches had started building their nest, and the large egg was noted but not removed until one day a hen Paradise Widow Bird was observed to drive away the Melba Finches and to sit on the nest, though it did not enter it.

The larger egg of the parasite was broken and permitted measurement only of its width, which was 14 mm. as compared with 13 mm. in the melba finch eggs. On his return to the Transvaal Museum, Roberts examined the sets of melba finch eggs preserved there, and found three of them to contain eggs of the paradise widow bird. One of these sets was taken at Okahandja, South West Africa, April 15, 1928, by R. D. Bradfield, and contained three eggs of the parasite and two of the host. Two other sets were collected at Mokeetsi, Transvaal, by F. Streeter, on February 15 and March 17, each of these sets having one egg of the parasite and two eggs of the host. Roberts listed a fourth set taken at Gorongoza, Mozambique, October 3, 1903, by Harry Miller, but the date seems early, especially in view of the fact that J. Vincent (1936, p. 115) found paradise widow birds to be in breeding condition in Mozambique in March, May, and July. Plowes (in litt.) found one egg of the paradise widow bird with two of the melba finch in a nest of the latter at Matopos Research Station, Southern Rhodesia, on February 16, 1952.

Neunzig tentatively identified paradise widow bird eggs in two sets of melba finch eggs collected in southern Somaliland by von Erlanger (1907, p. 18). These identifications, it must be remembered, are only inferred, but I think that they are probably correct. One set of five eggs of the host and one of the parasite was taken near Bardera on May 26. The other had four eggs of the melba finch and one of the paradise widow bird and was collected at Solole on June 11.

Other writers also accept the melba finch as the host of the paradise widow bird. In Nyasaland, Belcher (1930a, pp. 338–339) concluded that larger eggs found with ordinary ones in nests of melba finches were probably laid by paradise widow birds. In another publication (1930b, pp. 73–75), he devoted himself explicitly to this question, and gave details and photographs of several parasitized sets of melba finch and of yellow-backed pytilia eggs, all taken in Nyasaland. In his account of the birds of the Belgian Congo, Chapin (1954, p. 510) agreed that there "is good reason to believe that the eggs of *Steganura paradisaea* are frequently deposited in the nests of *Pytilia melba*, where they can be distinguished by their larger dimensions." Probably on the basis of these still far from certain records, Mackworth-Praed and Grant (1955, pp. 1049–1050) merely stated that the paradise widow bird is parasitic on species of the genus *Pytilia*.

Despite all these statements, we still lack conclusive proof that the melba finch is a host of the paradise widow bird. In captivity aviculturists have recorded incontrovertible instances of this actually happening, but in these cases the paradise widow bird was necessarily limited to the birds breeding in the same cages. A. L. Robertson (1946, p. 209), gave the following information: "In captivity this bird has parasitized the nest of Melba finches and in 1943 and 1944 they were successfully bred by two independent people. . . . After the first nest of Melba finches had been successfully reared along with two paradise whydahs, I examined other nests of Melba finches and found eggs white in colour and slightly larger than the Melba finch eggs. The Paradise Widow hens not only parasitized Melba finch nests but also deposited eggs in Australian Zebra Finch nests as well. [This parasitism, of course, could only happen in an aviary.] In all, in one breeding season, four young Paradise Widow Birds were bred. The following year in Pretoria they were again successfully bred and the host again was a Melba finch." In a later paper, A. R. Robertson (1949, pp. 158–159) gave details that transpired in an aviary of Prinsloo at Evaton, Transvaal. In a cage about 24 by 12 by 8 feet, there were among other birds three pairs of melba finches, and two male and one female paradise widow birds. The three pairs of melba finches nested at different times during the season, but each time the nest was parasitized by the female paradise widow bird.

> During the course of the incubation period by the first Melba hen it was noticed that the Paradise hen paid visits to the . . . nest. . . . Three young ones left the nest, two were Melbas . . . but the third . . . was not. . . . As it grew older and was able to fend for itself it left the Melbas and was to be found only with the Paradise Whydahs which it now resembled very closely. When the second Melba Finch went to . . . nest I examined the eggs; there were six in all. Five were almost identical and white, and, I presumed, Melba eggs, the sixth egg white as well, but larger and longer than the other eggs. From this nest eventually one Paradise Whydah was reared. The Paradise Whydah did not only confine her marauding to the nest of Melba Finches, but laid eggs in the nests of every Australian Zebra Finch she could find.

> Her eggs were larger than the infertile eggs of Melba Finches which were kept for comparison. In a third nest of Melbas a third Paradise Whydah . . . was hatched out. When they moulted out into the first summer plumage, there were two hens and one cock. Mrs. Prinsloo watched the Paradise hen going into the Zebra Finch nests. There was, as far as she was able to see, no attempt at destroying the eggs of the host.

Yellow-winged pytilia: *Pytilia hypogrammica* Sharpe[55]

Serle (1957, p. 679) found a nest at Enugu, eastern Nigeria, on January 18, 1955. It contained three eggs of the yellow-winged pytilia and one of the paradise widow bird (of the race *S. p. interjecta*). The parasite's egg measured 17.2 by 13.3 mm., as compared with 14.8–15.2 by 11.5–11.9 mm., the measurements of the host's eggs.

Another closely related species not yet definitely recorded as a host but which was suspected of being one, is the red-winged pytilia, *Pytilia phoenicoptera*.[56] Writing of the race *P. h. emini* in the Uelle District of northeastern Belgian Congo, Chapin (1954, pp. 514, 584) considered it as probably a fosterer of the paradise widow bird (race *S. p. interjecta*), on the grounds that the breeding seasons of the two appear to be synchronized in that area.

In addition to the birds discussed above, one other species was suggested as a victim of the paradise widow bird. Hoesch (1936, p. 10) noted two kinds of eggs in a nest of a masked weaver, *Ploceus velatus*,[57] in Damaraland; the unusual egg, he suggested, might have been laid by a paradise widow bird. However, it is described as being pale gray with brownish speckles and measuring 22 by 15 mm. Neither in coloration nor in size does it agree with the eggs of the paradise widow bird, and this suggested identification must be rejected. Apparently Hoesch himself later doubted that it was a paradise widow bird's egg, as no reference is made to it in his later report (Hoesch and Niethammer, 1940).

NESTLING STAGE

R. Neunzig (1929b, p. 5) pointed out, and indicated diagrammatically, the close similarity in mouth markings between the nestlings of the paradise widow bird and of its most frequently recorded host, the melba finch (*Pytilia melba*). The nestling parasite was said to have a single black spot on the roof of the mouth (palate) and black marks on each side on both the maxilla and the mandible inside the gape wattles—this pattern agreeing exactly with that of the melba finch. Chapin (1954, p. 579) remarked that while the young of the yellow back (*P. afra*) may also show this arrangement, the nestling of

---

[55] *Pytilia hypogrammica* Sharpe, Ibis, n.s., vol. 6, 1870, p. 56 (Fantee, Gold Coast).

[56] *Pytilia phoenicoptera* Swainson, Birds of western Africa, vol. 1, 1837, p. 203, pl. xvi (Senegal).

[57] *Ploceus velatus* Vieillot, Nouveau dictionnaire d'histoire naturelle, vol. 34, 1819, p. 132 (Namaqualand).

the redwing, *P. phoenicoptera* lacks the black palatal spot, and that consequently, if Neunzig was correct about the exactness of this apparent mimicry between parasite and victim, the young of *S. p. interjecta* (the race of paradise widow birds occurring within the range of *P. phoenicoptera*) may turn out to have an unspotted palate. I cannot, however, find any definite evidence that Neunzig actually examined a young paradise widow bird. He may possibly have intended to describe the condition in the melba finch as the presumed pattern for its parasite. Hoesch and Niethammer (1940, pp. 363–365) wrote that while the young melba finch has a black spot on the roof of the mouth and dark spots on the sides at the gape, the young paradise widow bird has only the palatal spot and not the ones at the corners of the mouth. They further described one young paradise widow bird as having bluish red edgings on the fissure of the palate, a condition not described in *Pytilia*. Apparently the resemblance between the host and the parasite is not as extreme as Neunzig's account suggests.

There are no observations on the growth or behavior of the nestling paradise widow bird in the wild state.

In captivity, with fire finches as the host, duration of the nestling stage was given by Lloyd (1955) as 16 days. The paradise widow bird egg hatched on June 14, and the chick "left the nest on June 30th when sixteen days old, and even then it was quite strong on the wing and fully feathered. It was actually out of the nest on the two previous days, but each time I returned it. On the 30th, however, the foster-parents, the Fire Finches, followed it right outside into the flight [cage]. It was then quite as big as the Fire Finches, and fawn in color, with dark feathers in the wings, and a lighter shade of fawn on the underparts. Nowit is about eight weeks old, and it has the prominent striped markings of the whydah on the head, is very pale fawn on the breast, and almost white at the vent."

YOUNG OUT OF THE NEST

Hoesch and Niethammer (1940, pp. 363–365) found in Damaraland a few young paradise widow birds still with the greenish, or at least partly greenish, juvenal feathers, in a mixed flock of adults of their own species, red-billed weavers *Quelea quelea* [58]), and finch larks (*Eremopteryx verticalis* [59]). This find occurred on August 24, and later on, these reporters noted still other young of the same year in other similarly mixed flocks. Inasmuch as neither the red-billed weavers nor the finch larks are known to be victims of the paradise widow birds, it

---

[58] *Emberiza quelea* Linnaeus, Systema naturae, ed. 10, vol. 1, 1758, p. 177 (India=Senegal).

[59] *Megalotis verticalis* A. Smith, Report of the expedition for exploring central Africa . . ., 1836, p. 48 (country both sides of Orange River).

appears that the young parasites upon leaving their foster parents join with adults of their own kind, and with them join with other unrelated species. There is no reason for assuming that these young birds seen by Hoesch and Niethammer were associated with their nest mates or their foster parents.

Lloyd (1955) wrote that a newly fledged paradise widow bird reared by a pair of fire finches in his aviary readily found its way around the cage, but often liked to sit just inside a coconut shell placed there as a possible nesting site for the birds, and from this perch it watched everything about it. After it had been out of the nest two weeks its foster parents began to nest again. "Although by then the baby Whydah was feeding himself, the cock Fire Finch stayed with him quite a lot and still occasionally fed him."

Food and Feeding Habits

The gizzards of specimens examined in Southern Rhodesia contained only small seeds, probably of grasses. Chapin recorded similar findings in birds shot in the Belgian Congo, and others also commented on the almost exclusive seed diet of the paradise widow bird. Chubb (1909, p. 166) wrote, however, that in Southern Rhodesia Mennell saw several individuals eating flying termites as the insects swarmed from a hole in the ground.

I also note Freyberg's (1879) report that a captive paradise widow bird once coughed up what he identified as a portion of its stomach lining. This occurrence has since never again been reported to my knowledge, and it would be strange indeed if this bird actually coughed up a part of the lining of its alimentary canal. Such a habit is known in hornbills but not in passerine birds.

Plumages and Molts

Lynes (1924, p. 678) and others suggested that the paradise widow bird, like the species of *Vidua*, does not acquire fully adult plumage in the first year, and does not breed until at least the second year. As far as the study of specimens is concerned, there is no discernible subadult plumage, even though there may be one in reality that is identical in appearance with the juvenal one, or with the nonbreeding plumage of male birds. The question is one that cannot be solved with museum specimens, but must be worked out in the field or in the aviary with marked, living birds. Until such information is available, I can only describe a juvenal and an adult plumage (in the males two seasonal adult plumages).

Brown and Rollo (1940) studied the effect of light on the molt in weaverbirds, and, among other examples, used two paradise widow birds. In the normal daylight periods at Chicago, where the studies were carried out, these birds did not assume nuptial plumage for nearly 2 years, but in suitably controlled experiments they were induced to acquire breeding plumage during their first year of life by being subjected to daily light periods of 16 hours. *Steganura* proved less resistant to the effect of increased light than did *Vidua* and *Euplectes*. In a subsequent report, Rollo (1941, p. 162) noted that paradise widow birds assumed nuptial plumage in a 12-hour period, but went into eclipse plumage in both a 10- and a 16-hour period. In other words, a daily light period above or below the optimum actually retarded the appearance of breeding plumage. Autopsy revealed a correlation between the state of the gonads and the onset of nuptial feathering, so it becomes wholly proper to utilize breeding plumage as an indication of gonadal activity in this bird, even though the duration of the plumage is greater than the actual breeding season.

As stated in the opening paragraphs of our account of the paradise widow bird, all the recognized forms are considered conspecific. The differences between the races are presented immediately after the description of the plumages.

ADULT MALE IN BREEDING PLUMAGE: Forehead, lores, crown, most of occiput, cheeks, auriculars, chin, and throat Black with faint purplish-blue gloss. Broad nuchal collar from posterior part of occiput and hind neck extending to sides of neck posterior to sides of head varying from shining golden Light Yellow Orange to pale Mars Yellow to Orange-Buff in some races (*S. p. paradisaea, obtusa, orientalis, kaduglìensis*), and deep Orange-Buff to bright Sanford's Brown in others (*S. p. aucupum, interjecta, togoensis*). Back, rump, upper wing coverts, upper tail coverts, long inner secondaries, and long median rectrices Black with slight velvety purplish-blue sheen. Other secondaries, primaries, and lateral rectrices Fuscous, narrowly edged with white when first acquired, but these edgings and tips quickly worn off. Primaries internally edged to varying extent with whitish. Black of throat extending posteriorly in a V on middle of breast. Rest of breast bright Sanford's Brown to rufous Chestnut, paling somewhat laterally and posteriorly. Abdomen, sides, and flanks bright Ochraceous-Buff to Pale Ochraceous Buff. Tuft of white feathers on flanks on either side. Abdomen paling on midventral area to buffer whitish. Thighs buffy whitish. Under tail-coverts dull blackish tipped with white. Iris dark brown. Bill black. Feet dark brown. Wings 76–83 (79) mm. Long rectrices 245–345 (300) mm. Shorter rectrices 60–65 (63) mm. Culmen 11–12 (11.7) mm. Tarsus 16–17.5 (17) mm. Length and terminal breadth of long tail feathers vary greatly in different subspecies.

ADULT MALE IN NONBREEDING PLUMAGE: Forehead, lores, crown, and occiput Pale Pinkish Buff to Cartridge Buff. Broad band from top of lores to sides of occiput Chaetura Black. Few of pale feathers in center of occiput with narrow terminal shaft streaks of Chaetura Black. Feathers of hind neck Avellaneous to light Wood Brown, with terminally widening blackish shaft streaks. Upper back, back, and upper wing-coverts bright Tawny-Olive to Sayal Brown. Each feather with broad blackish or Chaetura Black shaft streak. Brownish edges becoming paler on middle and greater upper wing-coverts where they pale to Cinnamon-Buff terminally. Innermost secondaries deep Buffy Brown to Clove Brown, edged externally with Tawny-Olive. Rest of secondaries and primaries Olive-Brown to Clove Brown, externally edged with Tawny-Olive. Rectrices Fuscous, narrowly margined with Tawny-Olive, and tipped with whitish. Sides of head, cheeks, auriculars, chin, and upper throat Pale Pinkish Buff to Cartridge Buff. Blackish line from commisure of bill to eye and broadening somewhat behind eye. In some birds black margin extends around auriculars. Lower throat, breast, sides of throat, sides, flanks, and thighs Honey Yellow to Isabella Color, becoming palest and somewhat grayish on thighs. Feathers of sides of throat with small, terminally broadening blackish medioterminal streaks. Center of abdomen, vent, and under tail-coverts whitish very lightly tinged with buffy. Under wing-coverts buffy to pale Isabella Color. Iris, bill, and feet brown.

MALE IN FIRST WINTER (IMMATURE) PLUMAGE: Similar to adult male in nonbreeding plumage, but often with some of juvenal remiges and rectrices, which are paler, Buffy Brown, as compared with deep Buffy Brown to Clove Brown in older birds, and also often with tinge of ashy gray on midoccipital area and nape. These differences may be due to incomplete postjuvenal molt and might have disappeared in the specimens exhibiting them had they lived a week or two longer.

JUVENAL MALE: Lores, crown, occiput, nape, chin, throat, cheeks, and auriculars pale grayish Hair Brown. Auriculars and circumocular area tinged with Tawny-Olive. Upper back similar to nape but slightly more tawny. Back, lower back, rump, upper wing-coverts, and upper tail-coverts grayish Buffy Brown. Remiges Olive Brown, externally edged with Tawny-Olive. Rectrices similar but with less Tawny-Olive edgings. Breast, sides and flanks Hair Brown tinged with Tawny-Olive. Center of abdomen, vent, and under tail-coverts whitish. Under wing-coverts pale tawny grayish buffy. Iris brown. Bill and feet light brown. This plumage appears to be replaced by the first winter plumage by the time the bird is 8 weeks old (at least in captivity, as described by Lloyd, 1955).

NATAL DOWN: Unknown.

ADULT FEMALE: Not distinguishable with certainty from males in nonbreeding plumage, but frequently with dark head stripes less blackish, more brownish. Also rectrices somewhat paler. Size as in adult male.

JUVENAL FEMALE: None seen, but probably like corresponding male plumage.

The various races of this species are distinguishable only in the nuptial plumage of the adult male. This condition may be the actual state of affairs or it may be merely a reflection of the imcompleteness of museum collections when it comes to "winter" males, females, and young birds. There is some reason to think that completer, more fully documented material may reveal some racial differences at least in adult males in nonbreeding plumage. Years ago, Chapin noted that typical *S. p. paradisaea* differed from *S. p. aucupum* in this stage in the following particulars: *S. p. paradisaea* appeared to be darker above, with heavier, coarser, blackish streaks on the back, to have the breast more streaked and spotted with blackish (these spots barely present in *aucupum*), and to have the pale median coronal stripe narrower than in *aucupum*. More material is needed before we can say whether these distinctions are constant.

The breeding adult males of races of *Steganura paradisaea* may be identified by the following key:

- 1*a*. Elongated rectrices tapering noticeably terminally . . . **S. p. paradisaea**
- 1*b*. Elongated rectrices tapering terminally.
  - 2*a*. Hind neck pale yellow without any orange golden brown.
    - 3*a*. Wing 75–80 mm. Breadth of long rectrices 24–30 mm. **S. p. orientalis**
    - 3*b*. Wing 80–89 mm. Breadth of long rectrices 35–37 mm. . **S. p. obtusa**
  - 2*b*. Hind neck golden orange brown or darker.
    - 4*a*. Breast not noticeably darker than hind neck.
      - 5*a*. Long rectrices very long, over 275 mm.
        - 6*a*. Long rectrices 290–360 mm . . . . **S. p. togoensis**
        - 6*b*. Long rectrices 284–298 mm . . . . **S. p. interjecta**
      - 5*b*. Long rectrices shorter, under 275 mm . . . . **S. p. aucupum**
    - 4*b*. Breast definitely darker, more brownish, than hind neck. **S. p. kadugliensis**

NATIVE NAMES

The following names have been noted in the literature as native names for the paradise widow birds. In all probability many of them apply only to males in breeding plumage.

Native name	*Tribe*	*Locality*
Abu mus	Arabicized	Sudan
Chirinundu		Nyasaland
Cilimundu	Nyanja	Northern Rhodesia
Doutoulou	Baya	French West Africa

Native name	*Tribe*	*Locality*
Fumbwe	Nyanja	Nyasaland
Futumpe		Upemba Park, Belgian Congo
Jonkhála	Ouolof	Senegal
Kanyatindilimfundo	Nsenga	Northern Rhodesia
Kijao		southeastern Tanganyika
Kimakonde		southeastern Tanganyika
Kipili	Lunda	Northern Rhodesia
Lidialenga		southeastern Tanganyika
Lipingwe	Nyanja	Northern Rhodesia
Malaali	Bornou	French West Africa
Masikaghacha		Nyasaland
Mbembela		Angola
Zuzi	Nyungwe	Nyasaland

Miscellaneous Data

Flocking in nonbreeding season: A number of observers in various parts of Africa noted the tendency of paradise widow birds to form larger flocks in the "off" season than have been reported for the species of *Vidua*. Thus, Hoesch and Niethammer (1940, pp. 363–365) wrote that in the southern part of Damaraland, great swarms of these birds in winter plumage were seen. Over 100 were seen in one group at Ombujomatemba on January 11. As the breeding season approached and the males advanced in their prenuptial molt, these flocks quickly shrank in size to about 4 males and 20 "females" on January 20, and 1 male and 2 "females" by March 3. The first male in complete breeding plumage was seen on February 7. At the end of the breeding season, the first large flocks of birds in postnuptial molt were seen on June 29. Most of the paradise widow birds met with in July, August, and September on the Erongo Plateau were in mixed flocks with great numbers of red-billed weavers (*Quelea quelea*) feeding near water. In many cases finch larks (*Eremopteryx verticalis*) were also present in these flocks.

Longevity: Many years ago Bennett (1835, p. 307) noted that paradise widow birds had been said to live 12 to 15 years in captivity. Since then additional observations have been published, in which Mitchell (1911, p. 476) gave a maximum longevity in aviary conditions of 16 years, 7 months; A. G. Butler (1910b, p. 186) noted a female living for 14 years; and Prinsloo (1944, p. 146) recorded a male that was kept in a cage for 9 years. Prinsloo's and Butler's birds were apparently adult when obtained, and so it seems justifiable to add at least a year to the age accredited to each. The experience of many aviculturists seems to be that males generally live 3 or 4 years in confinement. About the male that lived for 9 years, Prinsloo noted that the prenuptial molt seemed to be a very severe strain on the bird, so much so that in his 9th year (when the note was written) he was unable to fly up the side of the cage, but worked his way up the wire netting much as a parrot does. He took longer to attain full plumage than in earlier years.

Disposition: A. G. Butler (1899, p. 274) found that captive adult paradise widow birds are usually peaceful in contrast with the pin-tailed widow birds, and are even timid at times. On one occasion however, a male became aggressive and entered the nests of some zebra finches breeding in the same cage, and killed the young. In Sierra Leone, Thompson (1925, p. 50) considered the paradise widow bird pugnacious as he saw it driving away other small birds. Unfortunately, this statement has no supporting details indicating from what the paradise widow bird was repelling other birds.

Many years ago Teschemaker (1907, p. 27) mentioned a hen paradise widow bird in his aviary sitting for sometime on a nest. It is not clear, however, whether there was anything in the nest, or if the bird was using an old partial nest structure as a temporary roost. Teschemaker was unaware of the fact that this bird is parasitic, and presumed it was nesting.

References

ABRAHAMS, C. N.

1939. A supposed hybrid whydah. Avicultural Mag., ser. 5, vol. 4, pp. 203–204.

ADLERSPARRE, AXEL

1922. Zur Kenntnis einiger seltenen exotischen Vogerlarten. Gefiederte Welt, vol. 51, pp. 10–11.

1925. Zu den Ausführungen des Herrn Krabbe über die Gattung *Vidua*. Gefiederte Welt, vol. 54, p. 25.

1931. Einiges über *Spermestes nigriceps* (Braunrücken Esterchen). Journ. Ornith., vol. 79, pp. 370–374.

ALEXANDER, BOYD

1902. On the birds of the Gold Coast Colony and its hinterland. Ibis, ser. 8, vol. 2, pp. 355–377.

1908. Exhibition and description of new species of African birds. Bull. British Ornith. Club, vol. 23, pp. 15–16.

ALI, SALIM

1931. The nesting habits of the baya (*Ploceus philippinus*). Journ. Bombay Nat. Hist. Soc., vol. 34, pp. 947–964.

1958. The breeding biology of some Indian weaver birds (Ploceidae: Ploceinae), Abstracts of Papers, Centenary and Bicentenary Congress, Singapore, Univ. of Malaya, p. 29.

ALI, SALIM, AND AMBEDKAR, V. C.

1956. Notes on the baya weaver bird (*Ploceus philippinus* Linn.). Journ. Bombay Nat. Hist. Soc., vol. 53, pp. 381–389.

ALLEN, GLOVER M.

1930. The birds of Liberia. Report of the Harvard African Expedition to the African Republic of Liberia and the Belgian Congo, vol. 2, pp. 636–748.

ALSTON, MADELINE

1951. Sunbirds and jacarandas. A bird-lover in Rhodesia, Cape Town and Johannesburg, Juta, 178 pp.

ALTINI, GUISEPPE

1939. *In* Voliera. Ploceidi, Fringillidi and Embirizidi della regione Etiopica. Riv. Avicultura, vol. 17, pp. 1–52, esp. pp. 1–16.

ANDERSSON, CARL JOHAN

1872. Notes on the birds of Damara Land and the adjacent countries of South-West Africa, London, xlviii+394 pp., 4 pls.

ANONYMOUS

1909. Breeding pin-tailed whydahs. Bird Notes, Nov., p. 267.

1925. Brutparasitismus der Konigswitwe. Ornith. Monatsb., vol. 33, p. 153.

1932. Birds of the eastern Cape Province. Widow birds. Blythswood Rev., vol. 9, pl. 96.

1937. Note. Gefiederte Welt, vol. 66, p. 276.

ARMSTRONG, EDWARD ALLWORTHY
1942. Bird display, 381 pp., 22 pls.

AUBER, L.
1957. The distribution of structural colours and unusual pigments in the class aves. Ibis, vol. 99, pp. 463–476.

AURELIEN, R. F.
1954. *Spermestes cuculatus.* Zooleo, No. 26, pp. 367–39.

"AVICULTURIST"
1925. *Amadina fasciata.* Bird Notes, vol. 7, pp. 118–120.

BAER, JEAN GEORGES
1951. Ecology of animal parasites, Urbana, Univ. Illinois Press, 224 pp.

BAKER, EDWARD CHARLES STUART
1934. Nidification of the birds of the Indian Empire, vol. 3 (Ploceidae—Asionidae), London, Taylor and Francis, 568 pp.

BANNERMAN, DAVID ARMITAGE
1922. Description of two new African birds; *Hypochera chalybeata sharii* and *Euprinodes rufigularis angolensis.* Bull. British Ornith. Club, vol. 43, pp. 29–30.
1923. Report on the birds collected during the British Museum expedition to the Ivory Coast (French West Africa). Ibis, ser. 11, vol. 5, pp. 667–748.
1932. Account of the birds collected by Mr. G. L. Bates on behalf of the British Museum in Sierra Leone and French Guinea; (ii) by Lt. Col. G. G. Hougton, R.A.M.C. in Sierra Leone, recently acquired by the British Museum, III. Ibis, ser. 13, vol. 2, pp. 217–261.
1949. The birds of tropical West Africa, vol. 7, London, Oliver and Boyd, 413 pp., 14 pls.
1953. The birds of West and Equatorial Africa, 2 vols., London, Oliver and Boyd, 1526 pp., 37 pls.

BANNERMAN, DAVID ARMITAGE, AND BATES, GEORGE LATIMER
1924. On the birds collected in northwestern and northern Cameroon and parts of northern Nigeria. II. Systematic Notes. Ibis, ser. 11, vol. 6, pp. 199–277.

BATES, GEORGE LATIMER
1909. Field-notes on the birds of southern Kamerun, West Africa. Ibis, ser. 9, vol. 3, pp. 1–74, 3 figs., 2 pls.
1930. Handbook of the birds of West Africa, London, John Bale, Sons and Danielsson, xxiii + 572 pp., 2 maps.
1933. Descriptions of two new subspecies . . . also remarks on the races of *Dicrurus adsimilis, Hypochera chalybeata* and *Hypocheraa mauropteryx*, and *Steganura paradisaea.* Bull. British Ornith. Club, vol. 53, pp. 175–181.
1934. Birds of the southern Sahara and adjoining countries in French West Africa, V. Ibis, ser. 13, vol. 4, pp. 685–717.

BEACH, FRANK AMBROSE
1948. Hormones and behavior, New York, Paul Hoeber, 368 pp.

BEECHER, WILLIAM JOHN
1953. A phylogeny of the oscines. Auk, vol. 70, pp. 270–333.

BELCHER, CHARLES FRANCIS
1930a. The birds of Nyasaland, London, Crosby Lockwood and Son, xii+356 pp., 1 map.
1930b. Brutparasitismus bei den Webervögeln. Beitr. Fortpflanz. Vögel, vol. 6, pp. 73–75.
1949. Review of "Parasitic Cuckoos of Africa." Nature in East Africa, vol. 2, pp. 14–20.

BENNETT, EDWARD TURNER
1835. The gardens and menagerie of the Zoological Society delineated, vol. 2, Birds, 328 pp.

BENSON, CONSTANTINE WALTER
1940. Further notes on Nyasaland birds (with particular reference to those of the Northern Province), I. Ibis, ser. 14, pp. 257–298.
1941. Further notes on Naysaland birds, IV. Ibis, ser. 14, vol. 5, pp. 1–55.
1942. Additional notes on Nyasaland birds. Ibis, ser. 14, vol. 6, pp. 299–337.
1945. Observations from Kenya Colony, Uganda, and Tanganyika Territory. Ibis, vol. 87, pp. 90–95.
1947. Notes on the birds of southern Abyssinia. Ibis, vol. 89, pp. 29–50.
1953. A check list of the birds of Nyasaland, Blantyre, Nyasaland Society and The Publications Bureau, 116 pp., map.
1956. A contribution to the ornithology of Northern Rhodesia. Occas. Pap., Nat. Mus. Southern Rhodesia, No. 21B, 51 pp.

BENSON, CONSTANTINE WALTER AND WHITE, CHARLES MATTHEW NEWTON
1957. Check-list of the birds of Northern Rhodesia, Government Printer, Lusaka, 166 pp., 8 col. pls., 20 black and white pls., 1 map.

BLANCOU, LUCIEN
1948. Contribution a l'etude des oiseaux de l'Oubangui-Chari oriental (Haut Mbomou). Oiseaux Rev. Française Ornith., n.s., vol. 18, pp. 33–77.

BLANFORD, WILLIAM THOMAS
1870. Observations on the geology and zoology of Abyssinia made . . . in 1867–68, London xii+487 pp., 13 pls.

BOETTICHER, HANS VON
1935. Aus der Vogelleben Ugandas. Gefiederte Welt, vol. 64, pp. 445–446.
1951. Zur Klassification der Stahl-oder Atlasvögel, *Hypochera* Bp. Anz. Ornith. Gesellsch. Bayern, vol. 4, pp. 16–22.
1952. Die Widahvögel und Witwen, Leipzig, Geist and Portig, 88 pp., 3 pls.

BOLUS, FRANK
1909. The pin-tailed whydah (*Vidua serena*). Journ. South African Ornith. Union, vol. 5, p. 113.

BOOSEY, EDWARD J.
1956. Foreign bird keeping, London, 342 pp., 149 illus.

BOUET, GEORGES
1945. Revision des collection d'oiseaux recueillis au Congo et dans l'Oubangui par la Mission J. Dybowski (Avril 1891–Mai 1892). Oiseaux Rev. Française Ornith., n.s., vol. 14, pp. 44–88.

BOWEN, W. WEDGWOOD
1931. Two new subspecies of Sudanese birds. Proc. Acad. Nat. Sci. Philadelphia, vol. 83, pp. 229–231.

BOXBERGER, L. VON
1924. Neuere Forschungen über Brutparasitismus. Beitr. Fortpflanz. Vögel, vol. 1, pp. 17–18.

BOYD, M.
1914. Breeding of combassous. Bird Notes, vol. 5, p. 338.

BRANDES, GUSTAV
1901. Ueber Leuchtorgane am Vogelschnabel. Zeitschr. Naturw. vol. 74, pp. 458–460.

BRELSFORD, VICTOR
1941. Field-notes on some Northern Rhodesian birds. Ibis, ser. 14, vol. 5, pp. 161–172.

BRISSON, MATHURIN J.
1760. Ornithologie . . . , vol. 3, xci +734 pp., 37 pls., esp. pp. 120–131.

BROWN, FRANK A., JR., AND ROLLO, MARIE
1940. Light and molt in weaver finches. Auk, vol. 57, pp. 485–498.

BROWN, LESLIE H.
1948. Notes on birds of the Kabba, Ilorin, and N. Benin Provinces of Nigeria. Ibis, vol. 90, pp. 525–538.

BULLOCK, E.
1938. Orange bishop bird. Avicultural Mag., ser. 5, vol. 3, pp. 15–16.

BULLOUGH, W. S.
1945. Endocrinological aspects of bird behavior. Biol. Rev., vol. 20, pp. 89–99.

BUTLER, ARTHUR GARDINER.
1898. On the ornamentation of the mouth in the young Gouldian finch. Avicultural Mag., vol. 5, pp. 25–27.
1899. Foreign finches in captivity, ed. 2, Hull and London, Brumby and Clarke Ltd., 317 pp., 59 pls.
1908. Is the pintailed whydah parasitic? Avicultural Mag., n.s., vol. 6, pp. 121–122.
1910a. Breeding whydahs. Avicultural Mag., ser. 3, vol. 1, p. 134.
1910b. Duration of life in captivity. Avicultural Mag., ser. 3, vol. 1, pp. 181–191.
1914a. Egg-laying and nesting experiences. Avicultural Mag., ser. 3, vol. 5, pp. 179–185.
1914b. Thirty-two years of aviculture. Avicultural Mag., ser. 3, vol. 5, pp. 272–278.

BUTLER, ARTHUR LENNOX
1905. A contribution to the ornithology of the Egyptian Sudan. Ibis, ser. 8, vol. 5, pp. 301–401.

BUTTNER, E. E.
1959. The pin-tailed whydah at home. Birds Illustrated, vol. 4, p. 407.

Calder, David

1944. Skimmer on Karkloof River, eggs of pin-tailed widow-bird in nest of thick-billed weaver, and white storks seen on 12th August. Ostrich, vol. 15, pp. 76–77.

Carlisle, J. S.

1923. Rare South African eggs. South African Journ. Nat. Hist., vol. 4, pp. 115–126.

Carter, G. S.

1951. Animal evolution, London, Sidgwick and Jackson, 368 pp.

Cave, Francis O., and MacDonald, James D.

1955. The birds of the Sudan, Edinburgh, Oliver and Boyd, 442 pp., 24 pls., 2 maps.

Chapin, James Paul

1917. The classification of the weaver-birds. Bull. Amer. Mus. Nat. Hist., vol. 37, art. 9, pp. 243–280, 5 pls.

1922. The species and geographic races of *Steganura*. Amer. Mus. Nat. Hist. Nov., No. 43, 12 pp.

1923. Ecological aspects of bird distribution in tropical Africa. Amer. Nat., vol. 57, pp. 106–125.

1929a. The races of the paradise whydah. Ibis, ser. 12, vol. 5, pp. 392–393.

1929b. Nomenclature and systematic position of the paradise whydahs. Auk, vol. 46, pp. 474–484.

1932. The birds of the Belgian Congo, I. Bull. Amer. Mus. Nat. Hist., vol. 65, 756 pp., 10 pls., 208 text figs, 10 pls., map.

1954. The birds of the Belgian Congo, IV. Bull. Amer. Mus. Nat. Hist., vol. 75B, 846 pp., 27 pls., 45 text figs.

Cheesman, Robert Ernest, and Sclater, William Lutley

1935–36. On a collection of birds from north-western Abyssinia, III, IV. Ibis, ser. 13, vol. 5, pp. 594–622; vol. 6, pp. 163–197.

Child, Charles Manning

1924. Physiological foundations of behavior, New York, Henry Holt, 330 pp.

Chubb, E. C.

1909. On the birds of Bulawayo, Southern Rhodesia. Ibis, ser. 9, vol. 3, pp. 140–172.

1914. A descriptive list of the Millar collection of South African birds' eggs. Ann. Durban Mus., vol. 1, pt 1, pp. 29–106, 1 pl. (pl. vii).

Chun, Carl

1902. Ueber eigenthümliche Schnabelbildung bei Nesthockern, speciell Leuchtorgane bei Prachtfinken. Verh. Gesellsch. Deutscher Naturf. Aerzte, vol. 73, t. 2, hälfte 1, p. 274.

1903. Ueber die sogenannten Leuchtorgane australischer Prachtfinken. Zool. Anz., vol. 27, No. 2, pp. 61–64.

Clay, Gervas

1953. Some notes on the birds of the Isoka District of the Northern Province of Northern Rhodesia. Ostrich, vol. 24, pp. 76–97.

Collias Nicholas E.

1944. Aggressive behavior among vertebrate animals. Physiological Zool., vol. 17, pp. 83–123.

CRASS, R. S.

1944. The birds of Sulenkama, Qumbu District, Cape Province. Ostrich, vol. 15, pp. 10–20.

CROMBIE, A. C.

1947. Interspecific competition. Journ. Animal Ecol., vol. 16, pp. 44–73.

CROOK, JOHN HURRELL

1958. Etudes sur le comportement social de *Bubalornis a. albirostris*. Alauda, vol. 26, pp. 161–195.

DE KLERK, W. DE K.

1942. Notes on nests of birds in Adelaide, C. P. Ostrich, vol. 13, pp. 57–63.

DELACOUR, JEAN

1943. A revision of the subfamily Estrildinae of the family Ploceidae. Zoologica (New York City), vol. 28, pp. 69–86.

1951. Review of Bannerman's "The birds of tropical West Africa." Auk, vol. 68, pp. 123–125.

DELACOUR, JEAN, AND EDMUND-BLANC, F.

1934. Monographie des veuves (Revision des genres *Euplectes* et *Vidua*): II Les veuves-combassous. Oiseau Rev. Française Ornith., n.s., vol. 4, no. 1, pp. 52–110.

DISNEY, H. J. DE S., AND MARSHALL, A. J.

1956. A contribution to the breeding biology of the weaver finch (*Quelea quelea*) in East Africa. Proc. Zool. Soc. London, vol. 127, pp. 379–387.

DISTANT, W. L.

1892. A naturalist in the Transvaal, xvi+277 pp., 6 pls.

DOBZHANSKY, THEODOSIUS

1951. Genetics and the origin of species, ed. 3, New York, Columbia University Press, 364 pp.

DUBOIS, ALPHONSE

1886. Liste des oiseaux recueillis par le capitaine Em. Storms dans la région du lac Tanganyka (1882–1884). Bull. Mus. Hist. Nat. Belgique, vol. 4, pp. 147–150.

1905. Remarques sur l'ornithologie de l'état indépendant du Congo suivies d'une liste des espèces recueillies jusqu'ici dans cet état. Ann. Mus. Congo Belge., zool. ser. 4, vol. 1, pp. 1–36, 12 pls.

EMIN PASCHA (EDOUARD SCHNITZER)

1894. Bruchstücke aus Emin Paschas letztem Tagebuch. Journ. Ornith., vol. 42, pp. 162–171.

EMLEN, JOHN T., JR.

1956. Display and mate selection in the widow-bishop birds. Anat. Record, vol. 125, p. 605.

1957. Display and mate selection in the whydahs and bishop birds. Ostrich, vol. 28, pp. 202–213.

ERLANGER, CARLO VON

1907. Beiträge zur Vogelfauna Nordostafrikas, V. Journ. Ornith., vol. 55, No. 1, pp. 1–58.

EVERITT, C.

1959. The purple whydah. Avicultural Mag., vol. 65, p. 96.

Feo, M.
1910. Vogelbilder aus Transvaal. Gefiederte Welt, vol. 39, No. 19, pp. 145–146.

Fillmer, Horatio R.
1904. [Note]. Bird Notes, vol. 8, p. 168.

Finsch, Otto, and Hartlaub, Carl Johann Gustave
1870. Die Vögel Ost-Afrikas, *in* Baron C. C. von der Decken's Reisen in Ost Afrika in 1859–61, vol. 4, viii+897 pp., 11 pls.

Forbes, W. A.
1880. On two rare Ploceine birds now or lately living in the Society's Menagerie. Proc. Zool. Soc. London, pp. 475–476.

Freyberg, Baron von
1879. Ueber das Ausstossen der Magenhaut eines kärnerfressenden Vogels. Zoologishe Garten (Frankfurt), vol. 20, pp. 58–59.

Friedmann, Herbert
1929. The cowbirds, a study in the biology of social parasitism, Springfield, Illinois, Charles C. Thomas, 421 pp., 28 pls., 12 text figs.
1930. Birds collected in the Belgian Congo, *in* R. P. Strong, The African Republic of Liberia and the Belgian Congo, vol. 2, Cambridge, Harvard Univ. Press, pp. 749–768.
1937. Birds collected by the Childs Frick expedition to Ethiopia and Kenya Colony, II. Passeres, U.S. Nat. Mus. Bull. 153, xii+506 pp., 14 pls., 30 text figs.
1948. The parasitic cuckoos of Africa. Washington Acad. Sci. Monogr. No. 1, xii +204 pp., illus.
1950. The breeding habits of the weaverbirds. A study in the biology of behavior patterns. Annual Report of the Smithsonian Institution for 1949, pp. 293–316.
1955. The honey-guides. U.S. Nat. Mus. Bull. 208, 292 pp., 25 pls.
1957. Aviculture and our knowledge of the parasitic weaverbirds. Avicultural Mag., vol. 63, pp. 158–160.

Friedmann, Herbert, and Loveridge, Arthur
1937. Notes on the ornithology of tropical East Africa. Bull. Mus. Comp. Zool., vol. 81, pp. 1–413.

Gause, George Francis
1934. The struggle for existence, Baltimore, Williams and Wilkins, 163 pp.

Gil Lletget, Augusto
1935. Aves del Congo Belga. I. Fam. Ploceidae. Bol. Soc. Española Hist. Nat., vol. 35, pp. 69–82.

Gill, Edwin Leonard
1945. A first guide to South African birds, Cape Town, Maskew Miller, 224 pp., 20 pls.

Gilliard, E. Thomas
1958. Living birds of the world, New York, Doubleday, 400 pp., 400 illus.

Godfrey, Robert
1923. Birds of Somerville. South African Journ. Nat. Hist., vol. 4, pp. 127–138.
1929. The birds of Blythswood. Blythswood Rev., vol. 6, pp. 117–118.

GOOD, ALBERT I.
1953. The birds of French Cameroon, II. Mem. Inst. Français Afrique Noire., ser. sci. Nat., No. 3, 269 pp.

GRANT, CLAUDE HENRY BAXTER, AND MACKWORTH-PRAED, CYRIL WINTHROP
1945. Notes on Eastern African birds. Bull. British Ornith. Club, vol. 65, pp. 42–45.

GRANVIK, HUGO
1923. Contributions to the knowledge of the East African ornithology. Journ. Ornith., vol. 71, supp., 280 pp., 11 pls.
1934. The ornithology of north western Kenya Colony with special regard to the Suk and Turkana District. Rev. Zool. Bot. Africaines, vol. 25, fasc. 1, pp. 1–190, 4 pls.

GROEBBELS, FRANZ
1937. Der Vogel, vol. 2, Berlin, Gebrüder Borntraeger, 547 pp.

GROTE, HERMANN.
1922. Bemerkungen über einige neue afrikanische Formen. Journ. Ornith., vol. 70, pp. 397–404, 482–487.
1923. [Review of J. P. Chapin's paper on *Steganura*.] Ornith. Monatsb., vol. 31, pp. 41–43.
1924. Beiträg zur Kenntnis der Vogelfauna des Graslandes von Neukamerun. Journ. Ornith., vol. 72, pp. 479–517.
1925. Zum Brutparasitismus von *Vidua serena*. Beitr. Fortpflanz. Vögel, vol. 1, pp. 34–35.

GRZIMEK, B.
1952. Zum Balzverhalten des westafrikanischen Textor-Webers, *Hyphanthornis* (*Ploceus*) *cucullatus*. Zeitschr. Tierpsychol., vol. 9, pp. 289–294.

GUICHARD, K. M.
1950. A note on weaver birds of the genus *Ploceus* in the inundation zone of the River Niger, Soudan Français. Comptes Rendus Premiere Conference Internat. de Africanistes de l'Ouest., vol. 1, pp. 194–198.

GYLDENSTOLPE, NILS
1924. Zoological results of the Swedish expedition to central Africa. 1921. Vertebrata. I. Birds. Svenska Vetensk. Akad. Handl., ser. 3, vol. 1, No. 3, 326 pp., 2 pls.

HAAGNER, ALWIN KARL, AND IVY, ROBERT H.
1907a. The birds of Albany Division, Cape Colony. Journ. South African Ornith. Union, vol. 3, pp. 76–116.
1907b. Sketches of South African bird-life, Cape Town, T. Maskew Miller, 316 pp., 158 figs.

HAMLING, H. H.
1944. A field naturalist's peregrinations. Bird notes from a northern sector of Southern Rhodesia, III. Ostrich, vol. 15, pp. 30–43.
1953. Observations on the behaviour of birds in Southern Rhodesia. Ostrich, vol. 24, pp. 9–16.

HARRISON, B. G.

1933. A few remarks on the factors governing the development of parasitic habits in passerine birds (troupials and weavers) and in particular the American cowbirds. Bull. British Ornith. Club, vol. 53, pp. 102–107.

HARRISON, C. J. O.

1956. Some fire-finches and their behaviour. Avicultural Mag., vol. 62, pp. 128–141.

HARTERT, ERNST

1901. Verzeichniss der bisher bekannten Vogel des eigentlichen Haussalandes. Nov. Zool., vol. 8, pp. 338–355.

HARTLAUB, CARL JOHANN GUSTAV

1857. System der Ornithologie Westafrika's, lxvi+ 280 pp.

HAWKER, RICHARD M.

1899. On the results of a collecting-tour of three months in Somaliland. Ibis, ser. 7, vol. 5, pp. 52–81.

HENNIG, ERWIN

1936. Erfahrungen in der Vogelliebhaberei. Gefiederte Welt, vol. 65, pp. 133–135.

HEUGLIN, MARTIN THEODOR VON

1862. Beitrage zur Ornithologie Nord-Ost-Afrika's. Journ. Ornith., vol. 10, pp. 24–42.

1867. Synopsis der Vogel Nord-Ost-Afrika's, des Nilquellengebietes und der Kustenlander des Rothen Meeres. Journ. Ornith., vol. 15, pp. 361–398.

1869–1873. Ornithologie Nordost-Afrika's der Nilquellen und Kusten-Gebiete des Rothen Meeres und des nordlichen Somal-Landes, 2 vols., cccxxv+ 1512 pp., 51 pls.

HOESCH, WALTER

1934. Nester und Gelege aus dem Damaraland. Journ. Ornith., vol. 82, pp. 325–339.

1936. Nester und Gelege aus dem Damaraland II, Journ. Ornith., vol. 84, pp. 3–20.

1939. Kritische Betrachtungen zum Problem des Brutparasitismus bei den afrikanischer Viduinen. Beitr. Fortpflanz. Vogel, vol. 15, pp. 200–214.

1955. Der Vogelwelt sudwestafrikas. Windhoek, John Meinert, Ltd., 300 pp.

HOESCH, WALTER, AND NIETHAMMER, G.

1940. Die Vogelwelt Deutsch-Südwestafrikas. Journ. Ornith., vol. 88, Sonderheft, 404 pp., 1 pl., 76 figs.

HOLUB, EMIL, AND PELZELN, AUGUST VON

1882. Beiträge zur Ornithologie Südafrikas . . ., 384 pp., illus., map.

HOPKINSON, EMILIUS

1905. On the nesting of some Gambian birds. Bird Notes, vol. 4, p. 258.

1909. The birds of Gambia. Bird Notes, vol. 8, pp. 5-9.

1917. Whydahs. Bird Notes, n.s., vol. 8, pp. 183–186, 210–214, 237–243, 259–264.

HOPKINSON, EMILIUS—Continued
1918. Records of birds which have bred in captivity. Bird Notes, ser. 3, vol. 1, pp. 153–157.
1926. Records of birds bred in captivity, London, Witherby, xii + 330 pp.

IRWIN, MICHAEL P. STUART
1952. Notes on some passerine birds from Mashonaland, Southern Rhodesia. Ostrich, vol. 23, pp. 109–115.

JACKSON, FREDERICK JOHN
1899. List of birds obtained in British East Africa, I. Ibis, ser. 7, vol. 5, pp. 587–640.
1938. The birds of Kenya Colony and the Uganda Protectorate, London, Gurney and Jackson, 3 vols., 1592 pp., 24 pls.

JAMES, RICHARD
1938. Aviary management. Avicultural Mag., ser. 5, vol. 3, pp. 323–326.

JAMESON, JAMES S.
1890. The story of the rear column of the Emin Pasha relief expedition. Natural history appendix by R. B. Sharpe, pp. 392–422.

JEROME, C. H.
1943. Difficulties of amateur ornithologists in identifying the eggs of parasitic birds. Ostrich, vol. 14, pp. 99–102.

JOHNSTON, HARRY HAMILTON
1884. The River Congo, from its mouth to Bólóbó . . ., ed. 2, 470 pp., 68 illus., 2 maps.

JONES, HUMPHREY
1945. Notes on some birds of the Northern Rhodesia copperbelt. Ostrich., vol. 16, pp. 176–183.

JOURDAIN, FRANCIS CHARLES ROBERT, AND SHUEL, RONALD
1935. Notes on a collection of eggs and breeding habits of birds near Lokoja, Nigeria. Ibis, ser. 13, vol. 5. pp. 623–663.

KELSALL, HARRY JOSEPH
1914. Notes on a collection of birds from Sierra Leone. Ibis, ser. 10, vol. 2, pp. 192–228, 1 pl., 2 figs.

KENDEIGH, SAMUEL CHARLES
1952. Parental care and its evolution in birds. Illinois Biol. Monogr., vol. 22, Nos. 1–3, 356 pp.

KNAUER, FRIEDRICH
1889. Mittheilungen aus dem Wiener Vivarium. Schwalbe, vol. 13, pp. 366–371.

KRABBE, A.
1926. Webervögel and Widafinken. Gefiederte Welt, vol. 55, pp. 2–4, 26–27, 38–40, 50–52, 62–65.
1931. Webervögel and Widafinken. Gefiederte Welt, vol. 60, pp. 121–123, 133–136.

LACK, DAVID LAMBERT

1935. Territory and polygamy in a bishop-bird, *Euplectes hordeacea hordeacea* (Linn.). Ibis, ser. 13, vol. 5, pp. 817–836.

1940. Pair-formation in birds. Condor, vol. 42, pp. 269–286.

1941. Some aspects of instinctive behaviour and display in birds. Ibis, ser. 14, vol. 5, pp. 407–441.

1947. Darwin's finches, Cambridge, Univ. Press, 218 pp., 9 pls., 27 figs.

1954. The natural regulation of animal numbers, Oxford, Clarendon Press, 343 pp.

LANYON, WESLEY EDWIN.

1957. The comparative biology of the meadowlarks (*Sturnella*) in Wisconsin. Publ. Nuttall Ornith. Club, No. 1, 67 pp., 31 figs.

LEWEK, THEODORE

1901. Ueber leuchtende Schnabel-Papillen bei Goulds-Amandinen. Gefiederte Welt, vol. 30, pp. 169–170.

LLOYD, T.

1955. First breeding of the paradise whydah. Foreign Birds, vol. 21, pp. 156–160.

LONG, R. C.

1958. The least honeyguide, *Indicator exilis* from Chididi and the green indigo-bird, *Hypochera aena codringtoni* from the Malawi escarpment. Ostrich, vol. 29, p. 49.

LÖNNBERG, EINAR

1907. Notes on birds collected in the Congo Free State by the Swedish missionary, K. E. Laman. Arkiv. Zool., vol. 3, No. 21, pp. 1–18.

1911. Birds collected by the Swedish Zoological Expedition to British East Africa 1911. Svenska Vetensk. Akad. Handl., vol. 47, No. 5, 131 pp., 5 pls.

LORENZ, KONRAD ZACHARIAS

1935. Der Kumpan in der Umwelt des Vogels. Journ. Ornith., vol. 83, pt. 2, pp. 137–213; pt. 3, pp. 289–413.

1937. Über den Begriff der Instinkthandlung. Folia Biotheoretica, ser. B, vol. 2, No. 2, pp. 17–50.

1950. The comparative method in studying innate behaviour patterns. Physiological mechanisms in animal behaviour. Symposia Soc. Exp. Biol., No. 4, pp. 221–268.

LOWE, WILLOUGHBY P.

1937. Report on the Lowe-Waldron expedition to the Ashanti forests and Northern Territories of the Gold Coast, Ibis, ser. 14, vol. 1, pp. 830–864.

LYNES, HUBERT

1924. On the birds of north and central Darfur, with notes on the west central Kordofan and north Nuba provinces of the British Sudan. Ibis, ser. 11, vol. 6, pp. 648–719.

1926. On the birds of north and central Darfur. Taxonomic appendix, I. Ibis, ser. 12, vol. 2, pp. 346–405, 3 pls.

1930. Review of the genus *Cisticola*. Ibis, ser. 12, special supplement, 673 pp., 20 pls.

LYNES, HUBERT—Continued

1934. Contribution to the ornithology of southern Tanganyika Territory. Journ. Ornith., vol. 82, supp., 147 pp., 15 pls.

1938. Contribution to the ornithology of the southern Congo Basin. Rev. Zool. Bot. Africaines, vol. 31, pp. 1–128, pls, 1–13.

MACKWORTH-PRAED, CYRIL WINTHROP, AND GRANT, CLAUDE HENRY BAXTER

1948. On the plumages and races of *Anomalospiza imberbis* (Cabanis). Ibis, vol. 90, pp. 322–324.

1949. On the indigo birds of Africa. Ibis, vol. pp. 98–109.

1955. Birds of Eastern and North Eastern Africa, vol. 2, 1099 pp., 56 pls., 43 in color.

MACLAUD, C.

1906. Notes sur les mammifères et les oiseaux de l'Afrique occidentale, Paris—Vendôme, G. Vilette, xiv + 532 pp , 15 pls., map.

MADDEN, J. F.

1945. Some common birds of Torit District, Equatoria Province. Sudan Notes and Records, vol. 26, pp. 283–300.

MAINARDI, DANILO

1958. La filogenesi nei fringillidi basata sui rapporti immunologici. Rendiconti, Sci. (B), Instituto Lombardo di Scienze e Lettere, vol. 92, pp. 336–356.

MAKATSCH, WOLFGANG

1937. Der Brutparasitismus der Kuckucksvögel . . ., Leipzig, Quelle and Meyer, 152 pp., 9 pls.

1956. Der Brutparasitismus in der Vogelwelt, Berlin, Neumann, 236 pp., 28 pls.

MANUEL, CANUTO G.

1930. Observations on the Philippine weaver, *Munia jagori* Martens. I: Breeding and associational habits. Philippine Agric. vol. 19, pp. 427–437.

MARCHANT, STEPHEN

1942. Some birds of the Owerri Province, Southern Nigeria. Ibis, ser. 14, vol. 6, pp. 137–196.

MARSHALL, WILLIAM, HEMPELMANN, F., AND STRASSEN, O. ZUR.

1913. Brehm's Tierleben, Vögel, Bd. 4, Sperlingsvögel, Leipzig and Vienna, Bibliographische Institut, 568 pp., 40 pls., 3 maps.

MASTERSON, B. A.

1916. Observations on the birds of the district of Humansdorp, Cape Province. Journ. South African Ornith. Union, vol. 11, pp. 119–142.

MAYAUD, NOËL

1950. Biologie de la reproduction, *in* P. P. Grassé, Traité de zoologie, anatomie, systematique, biologie, vol. 15, Paris, Masson, pp. 539–653.

MAYR, ERNST

1947. Ecological factors in speciation. Evolution, vol. 1, pp. 263–288.

1948. The bearing of the new systematics on genetical studies. The nature of species. Advances in Genetics, vol. 2, pp. 205–237.

1955. Comments on some recent studies of song bird phylogeny. Wilson Bull., vol. 67, pp. 33–44.

MAYR, ERNST, AND AMADON, DEAN

1951. A classification of recent birds. Amer. Mus. Nov., No. 1496, 42 pp.

MCATEE, WALDO LEE

1947. Luminosity in birds. Amer. Midl. Nat., vol. 38, pp. 207–213.

MEISE, WILHELM

1930. Zur Problem der Brutschmarotzertums. Beitr. Fortpflanz. Vögel, vol. 6, pp. 119–131.

1937. Zur Vogelwelt des Matengo-Hochlandes nahe dem Nordende des Njassasees. Mitt. Zool. Mus. Berlin, vol. 22, pp. 86–160, 4 pls.

1956. Über Nestokkupation durch fremde Vogelarten. Beitr. Vogelkunde, vol. 5, pp. 117–137.

MEYER DE SCHAUENSEE, RODOLPH

1951. Northern Rhodesian birds. Proc. Nat. Sci. Philadelphia, vol. 103, pp. 23–63.

MILLER, ALDEN H.

1946. Social parasites among birds. Scientific Monthly, vol. 62, pp. 238–246.

MILLET-HORSIN, H.

1921. Guide de l'amateur d'oiseaux débarquant sur la terre d'Afrique. Oiseau Rev. Française Ornith., 13th yr., pp. 134–137, 167–171, 180–182.

MITCHELL, PETER CHALMERS

1911. On longevity and relative viability in mammals and birds; with a note on the theory of longevity. Proc. Zool. Soc. London, pp. 425–549, 868.

MOLTONI, EDGARDO

1925. Un nuova ploceide abissino: *Hypochera ignestii* n.sp. Att. Soc. Italiana Sci. Nat., vol. 64, pp. 46–48.

MONARD, ALBERT

1934. Ornithologie de l'Angola. Arquivos do Museu Bocage, vol. 5, pp. 1–110.

1951. Resultats de la Mission Zoologique Suisse au Cameroun. Mem. Inst. Français Afrique Noire, Centre du Cameroun, ser. sci. nat., No. 1.

MOREAU, HENRI

1891. L'amateur d'oiseaux de voliere, Paris, J. B. Bailliere, 455 pp.

MOREAU, REGINALD ERNEST

1940. Contributions to the ornithology of the East African Islands. Ibis, ser. 14, vol. 4, pp. 48–91.

1957. Variations in the western Zosteropidae (Aves). Bull. British Mus. (Nat. Hist.), Zool., No. 4, pp. 309–433, 11 figs., 14 maps.

MOREAU, REGINALD ERNEST, AND MOREAU, WINIFRED M.

1938. The comparative breeding ecology of two species of *Euplectes* (bishop birds) in Usambara. Journ. Animal Ecol., vol. 7, pp. 314–327.

1939. Observations on some East African birds. Ibis, ser. 14, vol. 3, pp. 296–323.

1940. Incubation and fledgling periods of African birds. Auk, vol. 57, pp. 313–325.

Morel, G.

1959. Le Parasitisme de *Lagonosticta senegalla* (L.) par *Hypochera chalybeata* (Müller). Proc. First Pan-African Ornith. Congress, pp. 157–159.

Morel, G., and Bourliere, F.

1955. Recherches ecologiques sur *Quelea quelea quelea* (L.) de la basse vallee du Senegal. I. Donnes quantitatives sur le cycle annuel. Bull. Inst. Française Afrique Noire, vol. 17, ser. A., No. 2, pp. 617–663.

1956. Recherches ecologiques sur les *Quelea quelea quelea* (L.) de la basse vallee der Senegal. I. La reproduction. Alauda, vol. 24, pp. 97–122.

Morel, G., and Morel, M. Y.

1955. Au sujet du parasitisme de *Lagonosticta senegala* L. par *Hypochera chalybeata* Muller. Alauda, vol. 23, pp. 281–282.

Morris, Desmond

1954a. The courtship behaviour of the cutthroat finch. Avicultural Mag., vol. 60, pp. 165–177.

1954b. The reproductive behaviour of the zebra finch (*Poephila guttata*) with special reference to pseudofemale behaviour and displacement activities. Behaviour, vol. 6, pp. 271–322, 12 figs.

1955. The markings of the cutthroat finch. Birds Illus., vol. 1, pp. 182–183.

1957. The reproductive behaviour of the bronze mannikin, *Lonchura cucullata*. Behaviour, vol. 11, pp. 156–201.

1958. The comparative ethology of grassfinches (*Erythrurae*) and mannikins (*Amadinae*). Proc. Zool. Soc. London, vol. 131, pp. 389–439.

Mörs, F. E. O.

1910. Vogelbilder aus Transvaal. Gefiederte Welt, vol 39, p. 146.

1925. Vogelbilder aus Transvaal. Gefiederte Welt, vol. 54, pp. 168, 299–300.

Mouritz, G. Beresford

1914. Notes on birds observed in Katanga, Belgian Congo. Ibis, ser. 10, vol. 2, pp. 26–38.

1915. Notes on the ornithology of the Matopo District, Southern Rhodesia, II. Ibis, ser. 10, vol. 3, pp. 534–571.

Moynihan, Martin and Hall, M. F.

1954. Hostile, sexual, and other social behaviour patterns of the spice finch (*Lonchura punctulata*) in capitivity. Behaviour, vol. 7, pp. 33–76, 6 figs.

Neave, Sheffield Airey

1907. On a collection of birds from N. E. Rhodesia. Mem. Proc. Manchester Lit. Phil. Soc., vol. 51, No. 10, pp. 1–104.

1910. On the birds of Northern Rhodesia and the Katanga District of Congoland. Ibis, ser. 9, vol. 4, pp. 78–155, 225–262.

Neuby-Varty, Brian V.

1950. Some oological notes. Ostrich, vol. 21, pp. 37–38.

Neumann, Oscar

1905. Vögel von Schoa und Süd-Äthiopien. Ploceidae. Journ. Ornith., vol. 53, pp. 335–360.

1908. Description of new African birds from Senegambia. Bull. British Ornith. Club., vol. 21, pp. 43–44.

NEUNZIG, KARL

1921. Die fremdländischen Stubenvögel, Magdeburg, 895 pp., 42 col. pls., 400 figs.

NEUNZIG, RUDOLF

1926. Zur Biologie brutschmarotzender Webervögel. Gefiederte Welt, vol. 55, No. 11, pp. 547–548.

1927. Vogelpflege und Vogelzucht. *in* E. Abderhalden, Handbuch der biologischen Arbeitsmethoden, Abt. IX, I, Berlin, Urban und Schwarzenberg, pp. 703–850.

1928a. Beiträge zur Kenntniss der Ploceiden. VI. Neue Rassen. Zool. Anz., vol. 78, pp. 107–118.

1928b. Beiträge zur Kenntniss der Ploceiden. VII, Revision der Gattung *Steganura*. Zool. Anz., vol. 78, pp. 177–190.

1929a. Beiträge zur Kenntniss der Ploceiden. I. Rachenzeichnungen und Reflexionspapillen der Nestjungen der Spermestinen, ihr systematische Bedeutung und ihr biologischer Wert bei dem Fütterungsvorgang. Beitr. Fortpflanz. Vögel., vol. 5, No. 1, pp. 7–17.

1929b. Zum Brutparasitismus der Viduinen. Journ. Ornith., vol. 77, pp. 1–21, 2 pls.

1930. Welche Folgerungen sind aus dem Freileben der Weber und Widafinken für ihre Haltung und Zürchtung zu ziehen? Gefiederte Welt, vol. 59, pp. 292–294, 304–306.

1931. Bemerkungen über den Atlasfinken mit verlängerten Schwanzfedern. Gefiederte Welt, vol. 60, pp. 545–546.

NIELSEN, A. R.

1951. Atlasfinke, *Hypochera chalybeata* (S. Müll.). Stuekultur, vol. 49, p. 16.

NIELSEN, KARL

1952. Atlasfinke, *Vidua chalybeata chalybeata* (S. Müll.) Et nyt dansk opdret. Stuekultur, vol. 52, p. 146.

1956. A new Danish breeding result—breeding of the combasou (*Hypochera chalybeata chalybeata*). Avicultural Mag., vol. 62, pp. 11–13.

NISSEN, HENRY W.

1951. Phylogenetic comparisons, *in* Handbook of experimental psychology, ed. S. S. Stevens, New York, John Wiley, pp. 347–386.

OGILVIE-GRANT, WILLIAM ROBERT

1910. Ruwenzori expedition reports: 16. Aves. Trans. Zool. Soc. London, vol. 19, pp. 253–480, 10 pls.

1912. On the birds of Ngamiland. Ibis, ser. 9, vol. 6, pp. 355–404.

1917. Remarks on some recent collections of birds made by Mr. G. L. Bates in Cameroon. Ibis, ser. 10, vol. 5, pp. 79–90.

OGILVIE-GRANT, WILLIAM ROBERT, AND REID, R. J.

1901. On the birds collected during an expedition through Somaliland and Southern Abyssinia to Lake Zwai (with field notes by the collector, Mr. Alfred E. Pease). Ibis, ser. 8, vol. 1, pp. 607–699, 1 pl.

OHNESORGE, KURT

1924. Bericht über die Führung durch den Berliner zoologischen Garten am 25 Juni 1924, nachm. 5 Uhr. Journ. Ornith., vol. 72, pp. 577–579.

OLSEN, H.
1958. Opdraet af atlasfinken. Stuefuglene, vol. 33, pp. 125–128.

OUSTALET, EMILE
1905. Catalogue des oiseaux rapportes par la mission Chari-Lac Tchad, III. Bull. Mus. Hist. Nat. Paris, vol. 11, pp. 10–16.

PAGE, ERNIE V.
1946. Some notes on birds about Cathedral Peak. Ostrich, vol. 17, pp. 337–342.

PAGE, WESLEY THEODORE
1907. The queen whydah. Bird Notes, vol. 6, pp. 5–7.
1909. Visits to members aviaries. Bird Notes, vol. 8, p. 257.
1914. Species which have reared young and hybrids which have been bred in captivity in Great Britain, Ashbourne, Airan Press, viii + 55 pp.

PAGET-WILKES, A. H.
1924. Brevities. Oologists' Record, vol. 4, pp. 22–23.
1938. Notes on the breeding of some species in northeastern Uganda. Ibis, ser. 14, vol. 2, pp. 118-129.

PAKENHAM, RICHARD H. W.
1936. Field-notes on the birds of Zanzibar and Pemba. Ibis, ser. 13, vol. 6, pp. 249-272.
1939. Field notes on the birds of Zanzibar and Pemba. Ibis, ser. 14, vol. 3, pp. 522–554.

PARKER, H. HAMBLY
1931. Aviculture as a hobby. Ostrich, vol. 2, pp. 47–52.

PAYNE, OLIVER
1944. Egg of the cuckoo finch. Ostrich, vol. 15, p. 235.

PETERS, JAMES LEE, AND LOVERIDGE, ARTHUR.
1942. Scientific results of a fourth expedition to forested areas in East and Central Africa. Bull. Mus. Comp. Zool, vol. 85, pp. 217–275.
1953. Zoological results of a fifth expedition to East Africa. Bull. Mus. Comp. Zool., vol. 110, pp. 87–139.

PLOWES, DARRELL CHARLES HERBERT
1945. Data of birds' eggs collected. Ostrich, vol. 16, pp. 109–117.
1947. The birds of Ladysmith, Natal. Ostrich, vol. 18, pp. 134–154.

POPE-ELLIS, P. C.
1951. Points from letters. Ostrich, vol. 22, p. 126.

POULSEN, HOLGER
1953. A study of incubation responses and some other behaviour patterns in birds. Videnskabelige Meddelelser, vol. 115, pp. 1–131.
1956. Breeding of the Senegal combassou (*Hypochera chalybeata* Müll.) in captivity. Avicultural Mag., vol. 62, pp. 177–181.

PRESTWICH, A. A.
1956. [Comment on Karl Nielsen's note.] Avicultural Mag., vol. 62, No. 1, p. 13.

Priest, Cecil Damer

1936. The birds of Southern Rhodesia, vol. 4, London, William Clowes & Sons, Ltd., 420 pp., 10 pls., 122 text figs.

1948. Eggs of birds breeding in Southern Africa, Glasgow, Robert Madehose and Co., 180 pp., 20 pls.

Prigogine, Alexandre

1953. Contribution a l'etude de la faune ornithologique de la region a l'ouest du Lac Edouard. Ann. Mus. Congo Belge, ser. zool., vol. 24, pp. 1–117.

Prinsloo, Hein F.

1944. Correspondence. Ostrich, vol. 15, pp. 146-147.

Rand, Austin Loomer

1951. Birds from Liberia. Fieldiana Zool., vol. 32, no. 9, pp. 561–653.

Reichenow, Anton

1883. Zwei neue Arten. Journ. Ornith., vol. 31, p. 221.

1887. Ueber eine Vogelsammlung aus dem Kongo-Gebiet. Journ. Ornith., vol. 35, pp. 299–309.

1894. Die Vögel Deutsch-Ost-Afrikas. 250 pp.

1904. Die Vögel Afrikas, vol. 3, 880 pp.

1911. Die Vogelfauna des mittelafrikanischen Seengebietes auf Grund der Sammlung Seiner Hoheit des Herzogs Adolf Friedrich zu Mecklenburg, Wissenschaftliche Ergebnisse Deutschen Zentral-Afrika Expedition, vol. 3, pp. 231–274.

1923. Ueber eine Vogelsammlung vom oberen Kongo, und eine neue Würgerart von der Insel Nossibé. Mitt. Zool. Staatsinst-Zool. Mus. Hamburg, vol. 40, pp. 61–65.

Reimann, M.

1937. Aus dem Vogelhaus 1936. Gefiederte Welt, vol. 66, pp. 159–161.

Rensch, Bernard

1924. Zur Enstehung der Mimikry der Kuckuckseier. Journ. Ornith., vol. 72, No. 4, pp. 461–472.

1925. Das Problem des Brutparasitismus bei Vögeln. Sitz.-Ber. Ges. Naturf. Freunde Berlin, pp. 55–69.

Retchie, W. D.

1951. Unusual nesting of the spotted Munia, *Uroloncha punctulata*. Journ. Bengal Nat. Hist. Soc., vol. 25, pp. 63–64.

Rey, Eugen

1901. Rätselhafte Organe bei Vögeln. Ornith. Monatsb., vol. 9, pp. 97–98.

Riddle, Oscar

1937. Physiological responses to prolactin, Cold Spring Harbor symposia on quantitative biology, vol. 5, pp. 218–228.

Ridgway, Robert

1912. Color standards and color nomenclature, 43 pp., 53 pls.

Risdon, D. H. S.

1946. Reminiscences, VI. Avicultural Mag., vol. 52, p. 100.

ROBERTS, AUSTIN
1907. Remarks on the breeding-habits of the pin-tailed widow bird (*Vidua principalis*). Journ. South African Ornith. Union, vol. 3, pp. 9–11.
1909. Pyromelana oryx and its nesting parasites. Journ. South African Ornith. Union, vol. 5, pp. 22–24.
1912. Notes on a collection of birds in the Transvaal Museum from [illegible], Portuguese East Africa, pt. II. Journ. South Africa Ornith. Union, vol. 8, pp. 22–61.
1913. Egg collecting in the bushveld. Journ. South African Ornith. Union, vol. 9, pp. 1–45.
1917. Parasitism amongst finches. Ann. Transvaal Mus., vol. 5, pp. 259–262.
1926. Some changes in nomenclature, new records of migrants and new forms of S. African Birds. Ann. Transvaal Mus., vol. XI, pt. IV, pp. 217–225.
1928. Birds and mammals from South West Africa. Ann. Transvaal Mus., IV, vol. 12, pp. 289–329.
1930. Some recent important records of South African birds. Ostrich, vol. 1, pp. 61–68.
1931. The classification of the higher vertebrates. South African Biol. Soc. Pamphlet No. 3., pp. 12–14.
1935. Scientific results of the Vernay-Lang Kalahari expedition, March to September, 1930. Birds Ann. Transvaal Mus., vol. 16, pp. 1–185, 1 pl., 1 map.
1939. Notes on the eggs of parasitic birds in South Africa. Ostrich, vol. 10, pp. 100–117.
1940. The birds of South Africa, London, Witherby, xxxii+463 pp., 41 pls.
1943. [Editorial comment on C. H. Jerome's paper.] Ostrich, vol. 14, p. 102.

ROBERTS, NOEL
1909. Pyromelana oryx and its nesting parasites. Journ. South African Ornith. Union, vol. 5, pp. 22–24.

ROBERTSON, A. L.
1946. Parasitism of paradise widow bird. Ostrich, vol. 17, No. 3, p. 209.

ROBERTSON, A. R.
1949. Breeding successes in South Africa. Avicultural Mag., vol. 55, No. 5, pp. 158–159.

ROBERTSON, P. R.
1934. [Notes.] Ostrich, vol. 5, pp. 25–26.

ROLLO, MARIE
1941. Photoperiodism and migration. Bird-banding, vol. 12, pp. 161–164.

ROLLO, MARIE, AND DOMM, LINCOLN V.
1943. Light requirements of the weaver finch. I. Light period and intensity. Auk, vol. 60, pp. 357–367.

ROSS, HERBERT H.
1957. Principles of natural coexistence indicated by leafhopper populations. Evolution, vol. 11, pp. 113–129.

ROTHSCHILD, MIRIAM, AND CLAY, THERESA
1957. Fleas, flukes and cuckoos, ed. 3, London, Williams Collins, 305 pp., 40 pls.

Row, C. H.
1908. Zebra finches. Bird Notes, vol. 7, pp. 44–45.

Russ, Karl Friedrich Otto
1878. Handbuch für Vogelliebhaber, -Züchter und -Händler, 482 pp.
1879–1899. Die fremdländischen Stubenvögel, ihre Naturgeschichte, Pflege und Zucht, 4 vols., cv+3,679 pp., 36 pls.
1880. Reproductions d'oiseaux exotiques. Bull. Mens. Soc. Acclimatation, ser. 3, vol. 7, pp. 680–682.
1884. Die Webervögel und Widafinken; ihre Naturgeschichte, Pflege und Zucht, 218 pp., esp. pp. 172–196.
1913–1921. Handbuch für Vogelliebhaber . . ., 2 vols. 895 pp., 42 col. pls.

Salvadori, Tommaso
1912a. Missione per la frontiera Italo-Etiopica sotto il comando del capitan Carlo Citerni. Risultati zoologici. Uccelli. Ann. Mus. Civ. Storia Nat. Genova, ser. 3, vol. 5, pp. 304–327.
1912b. Secondo contributo all'ornitologia del Congo. Ann. Mus. Civ. Storia Nat. Genova, ser. 3, vol. 5, pp. 444–456.

Sander, F.
1957. A list of the birds of Lagos, III. Nigerian Field, vol. 22, No. 2, pp. 55–69.

Sarasin, Carl Fredrich Fritz
1913. Ueber die "Reflexionsperlen" der Nestjungen von *Erythrura psittacea* (Gmelin). Verh. Schweiz. Naturf. Ges., vol. 96, pt. 2, pp. 243–245.

Sassi, Moriz
1924. Wissenschaftliche Ergebnisse der Expedition R. Grauer nach Zentralafrika, Dezember 1909 bis Februar 1911. Beitrag zur Ornis Zentralafrikas, III. Ann. Naturhist. Mus. Wien, vol. 38, pp. 20–81.

Sassi, Moriz, and Zimmer, Franz
1941. Beiträge zur Kenntniss der Vogelwelt des Songea-Distriktes mit besonderer Berücksichtigung des Matengo-Hochlandes (D.O.A.). Ann. Naturh. Mus. Wien, vol. 51, pp. 236–346.

Schalow, Hermann
1886. Der ornithologische Nachlass Dr. Richard Böhm's. Gesichtet und herausgegeben. I. Das Tagebücher Dr. R. Böhm's. Journ. Ornith., vol. 34, pp. 409–436.

Schlegel, F.
1868. Die überseeischen Stubenvogel. Witwen *Vidua*. Zoologische Garten (Frankfurt), vol. 9, pp. 289–294.

Schorkopf, T.
1937. Über Atlasfinken. Gefiederte Welt, vol. 66, p. 455.

Schouteden, Henri
1914. Liste des oiseaux recueillis a Kilo par M. Thelie. Rev. Zool. Bot. Africaines, vol. 3, pp. 260–272.
1918. Contribution a la faune ornithologique de la region des lac de l'Afrique centrale. Rev. Zool. Bot. Africaines, vol. 5, pp. 209–297.
1920. Contribution a la faune ornithologique du Bas-Congo. Rev. Zool. Bot. Africaines, vol. 7, pp. 188–192.
1923. Contribution a la faune ornithologique du Congo Belge. I and II. Rev. Zool. Bot. Africaines, vol. 11, pp. 308–352, 384–405.

Schouteden, Henri—Continued

1924. Contributions a la faune ornithologique der Congo Belge. IV. Mes recoltes ornithologiques a l'equateur. Rev. Zool. Bot. Africaines, vol. 12, pp. 405–425.

1926. Contributions a la faune ornithologique du Congo Belge. VI. Mes recoltes ornithologiques dans le Bas-Congo. Rev. Zool. Bot. Africaines, vol. 13, pp. 182–206.

1930. Mes recoltes ornithologiques au Katanga. I. Environs l'Elisabethville. Rev. Zool. Bot. Africaines, vol. 18, pp. 277–290.

1932. Contributions a la faune ornithologique du Congo Belge. VIII. Mes recoltes ornithologiques au Parc Albert (N. Kivu). Rev. Zool. Bot. Africaines, vol. 21, pp. 268–283, 306–318; vol. 22, pp. 121–131, 245–258.

1933. Contributions a la faune ornithologique du Congo Belge. IX. Recoltes de M. M. Bastiaens, Douce et van Saceghem au nord du Lac Kivu. Rev. Zool. Bot. Africanus, vol. 22, pp. 370–385.

1936. Contribution a la faune ornithologique du nord-est du Congo Belge. Ann. Mus. Congo Belge, zool. ser. 4, vol. 1, fasc. 2, pp. 41–156.

1938. Exploration du Parc National Albert, Mission de Witte, fasc. 9, Oiseaux, Brussels, Inst. Parcs Nat. Congo Belge, pp. 1–198, 11 pls.

1940a. Notes sur la faune ornithologique du Mont Wago (ouest du Lac Albert). Rev. Zool. Bot. Africaines, vol. 33, pp. 282–288.

1940b. Notes sur la faune ornithologique de la foret de Kawa. Rev. Zool. Bot. Africaines, vol. 34, pp. 58–61.

1941. Oiseaux de Kasengi (Lac Albert). Rev. Zool. Bot. Africaines, vol. 34, pp. 264–267, 363, 365.

1942. Contributions a la faune ornithologique du Ruanda-Urundi. I. Collection J. A. Lestrade. Rev. Zool. Bot. Africaines, vol. 36, pp. 329–342.

1943. Contributions a la faune ornithologique du Ruanda-Urundi. II. Collections Verhulst. Rev. Zool. Bot. Africaines, vol. 37, pp. 263–274.

1949. Contribution a l'etude de la faune ornithologique du Katanga (Congo Belge). Rev. Zool. Bot. Africaines, vol. 42, pp. 158–174, 323–342.

1958. Oiseaux du Congo Belge et Ruanda-Urundi. IX. Passeriformes. Ann. Mus. Congo Belge, Zool., ser. 4, vol. 2, fasc. 2, pp. 237–503.

Schubotz, Hermann

1921. Die Tagebücher von Dr. Emin Pascha, vol. 6. Zoologische Aufzeichnungen Emin's und seine Briefe au Dr. G. Hartlaub. II. Vogel. III. Briefe au Dr. G. Hartlaub-Bremen aus den Jahren 1881–1891, pp. 41–295.

Schuster, Ludwig von

1925. Ist Coliuspasser ardens (Bodd.) Brutschmarotzer? Beitr. Fortpflanz. Vögel, vol. 1, No. 3, pp. 55–56.

1926. Beiträge zur Verbreitung und Biologie der Vogel Deutsch-Ostafrikas, III. Journ. Ornith., vol. 74, pp. 709–742.

Schütze, Eduard

1929. Aus dem Vogelhause. Gefiederte Welt, vol. 58, pp. 614–618.

Sclater, William Lutley

1930. Systema avium aethiopicarum . . . II, London, Taylor and Francis, pp. 305–922.

Sclater, William Lutley, and Mackworth-Praed, Cyril Winthrop

1918. A list of the birds of the Anglo-Egyptian Sudan, I. Ibis, ser. 10, vol. 6, pp. 416–476, 1 pl.; pp. 602–721, 1 pl.

Sclater, William Lutley, and Moreau, Reginald Ernest

1933. Taxonomic and field notes on some birds of north-eastern Tanganyika Territory, V. Ibis, ser. 13, vol. 3, pp. 399–440, 2 pls.

Serle, William

1940. Field observations on some Northern Nigerian birds, II. Ibis, ser. 14, vol. 4, pp. 1–47.

1943. Notes on East African birds. Ibis, vol. 85, pp. 55–82.

1949. Birds of Sierra Leone. Ostrich, vol. 20, pp. 114–126.

1951. On the nesting of the red-headed dioch. Oologists Record, vol. 25, pp. 23–24.

1957. A Contribution to the ornithology of the eastern region of Nigeria. Ibis, vol. 99, pp. 628–685.

Sharpe, Richard Bowdler

1871. On the birds of Angola, III. Proc. Zool. Soc. London, pp. 130–135.

1890. Catalogue of the birds in the British Museum, vol. 13, 701 pp., 15 pls.

Shelley, George Ernest

1882. On a collection of birds made by Mr. J. S. Jameson in southeastern Africa, with notes by Mr. T. Ayres. Ibis, ser. 4, vol. 6, pp. 349–368.

1888. On a collection of birds made by Emin Pasha in equatorial Africa. Proc. Zool. Soc. London, pp. 17–50.

1905. The birds of Africa . . ., vol. 4, pt. I, pp. 287, 7 pls., London, R. H. Porter.

Shore-Baily, W.

1923. Whydahs. Avicultural Mag., ser. 4, vol. 1, No. 5, pp. 108-118.

Sich, H. L.

1926. Nesting of *Anomalospiza butleri*. Avicultural Mag., ser. 4, vol. 4, pp. 323–324.

Simpson, George Gaylord

1944. Tempo and mode in evolution, New York, Columbia Univ. Press, 237 pp.

Skead, C. J.

1947 A study of the Cape weaver. Ostrich, vol. 18, pp. 1–42.

1953. A study of the spectacled weaver (*Ploceus ocularius* Smith). Ostrich, vol. 24, pp. 103–110.

1956. A study of the red bishop bird. Ostrich, vol. 27, pp. 112–125.

1957. Parasitism of the common waxbill, *Estrilda astrild*, by the pin-tailed widow-bird, *Vidua macroura*. Ostrich, vol. 28, pp. 214–216.

Skinner, Kenneth L.

1923a. Some scarce finch eggs. Oologists' Record, vol. 3, pp. 22–23.

1923b. Brevities. Oologists' Record, vol. 3, p. 40.

Smithers, Reay H. N., Irwin, M. P. Stuart, and Paterson, Mary L.

1957. A check list of the birds of Southern Rhodesia, Cambridge, Univ. Press, 175 pp.

SNOW, D. W.
1950. The birds of São Tomé and Principe in the Gulf of Guinea. Ibis, vol. 92, pp. 579–595.

SOUSA, JOSÉ AUGUSTO DE
1886. Lista das aves colligidas em Africa de 1884 a 1885 pelos Srs. Capello e Ivens. Journ. Sci. Math. Fysicas e Naturaes, Lisbon, vol. 11, pp. 76–81.

SOUTHERN, H. N.
1954. Mimicry in cuckoos' eggs, *in* Evolution as a process, ed. J. Huxley, A. C. Hardy, and E. B. Ford, pp. 219–232.

SPARROW, RICHARD
1936. Exhibition of eggs of South African parasitic birds. Bull. British Ool. Assoc., vol. 5, pp. 5–7.

STALLCUP, WILLIAM B.
1954. Myology and serology of the avian family Fringillidae. A taxonomic study. Univ. Kansas Publ., Mus. Nat. Hist., vol. 8, pp. 157–211, 23 figs., 4 tables.

STARK, ARTHUR C.
1900. The birds of South Africa, vol. 1, London, R. H. Porter. 322 pp., 81 text figs.

STEFANI, HANS
1931. Der Atlasfink mit verlängerten Schwanzfedern. Gefiederte Welt, vol. 60, pp. 544–545.

STEINBACHER, JOACHIM, AND WOLTERS, H. E.
1952. Vogel in Käfig und Voliere, pt. 1, Die Prachtfinken, 12 pp.

STEINER, H.
1955. Das Brutverhalten der Prachtfinken, Spermestidae, als Ausdruck ihres selbständingen Familiencharakters. Acta XI Congr. Int. Ornith., 1954, pp. 350–355.

STEINMETZ, H.
1937. Brut und Zuchtbericht aus dem Zoologischen Garten Berlin 1936. Gefiederte Welt, vol. 66, pp. 352–354.

STEVENSON-HAMILTON, JAMES
1947. Wild life in South Africa, London, Cassell, 364 pp.

STONE, WITMER
1936. Zoological results of the George Vanderbilt African expedition of 1934. VI. Birds. Proc. Acad. Nat. Sci. Philadelphia, vol. 88, pp. 529–598.

STONEHAM, HUGH FREDERIC
1929. Field notes on a collection of birds from Uganda, III. Ibis, ser. 12, vol. 5, pp. 267–292.

STRESEMANN, ERWIN
1925. Zum Brutparasitismus der Dominikanerwitwe (*Vidua serena*). Ornith. Monatsb., vol. 33, p. 128.
1927–1934. Aves—Vögel, *in* Kückenthal und Krumbach, Handbuch der Zoologie, vol. 7, Berlin und Leipzig, Walter de Gruyter, 899 pp., 944 figs.

STRICKLAND, HUGH EDWIN

1850. On a peculiar structure in the submedial pair rectrices of *Vidua paradisea*, in Jardine, Contributions to ornithology, pp. 88–91.

1850. Note on the rectrices of *Vidua paradisea*, in Jardine, Contributions to ornithology, p. 149.

STUHLMANN, FRANZ

1922. Die Tagebücher von Dr. Emin Pascha, vol. 3, 451 pp.

SUSHKIN, PETER PETROVICH

1927. On the anatomy and classification of the weaver birds. Bull. Amer. Mus. Nat. Hist., vol. 57, pp. 1–32, text figs. 1–18.

SWAINSON, WILLIAM

1837. Birds of Western Africa. The naturalists library, vol. 7, Ornithology, 286 pp. 32 pls.

SWYNNERTON, CHARLES FRANCIS MASSY

1907. On the birds of Gazaland, Southern Rhodesia. Ibis, ser. 9, vol. 1, pp. 279–310.

1908. Further notes on the birds of Gazaland. Ibis, ser. 9, vol. 2, pp. 1–107.

1916. On the colouration of the mouths and eggs of birds. I. The mouths of birds. II. On the coloration of eggs. Ibis, ser. 10, vol. 4, pp. 264–294, 529–606.

SYMONS, RODIN E.

1919. Bird life in the Drakensberg, Natal and Basutoland. South African Journ. Nat. Hist., vol. 1, pp. 224–238.

TAYLOR, J. SNEYD

1946. Notes on the masked weaver (*Hyphantornis velatus mariquensis*). Ostrich, vol. 17, pp. 145–155.

TERROINE, EMILE F., AND BARTHELEMY, H.

1922. Avitaminose et inanition. Comptes Rend. Acad Sci., Paris, vol. 175, pp. 721–724.

TERROINE, EMILE F., AND TRAUTMANN, SIMONE

1927. Influence de la temperature exterieure sur la production calorique des Homeothermes et loi des surfaces. Ann. Physiologie Physicochimie Biol. vol. 3, pp. 422–457.

TESCHEMAKER, W. E.

1907. Nesting of the Chingolo song sparrow. Avicultural Mag. n.s., vol. 6, No. 1, pp. 26–30.

1910a. The nesting of the giant whydah, *Chera procne*. Avicultural Mag., ser. 3, vol. 1, pp. 81–90.

1910b. Nesting of the pintailed whydah. Avicultural Mag., ser. 3, vol. 1, p. 254.

THESIGER, W., AND MEYNELL, M.

1935. On a collection of birds from Danakil, Abyssinia. Ibis, ser. 13, vol. 5, pp. 774–807.

THOMPSON, WILLIAM RALPH

1925. Field notes on the birds of Sierra Leone. Ibis, ser. 12, vol. 1, pp. 47–70.

Tinbergen, Nikolaas

1951. The study of instinct, Oxford, Univ. Press, 228 pp., 130 figs.

1953. Social behaviour in animals . . ., London, Methuen, 150 pp., 8 pls., 67 figs.

Tomlinson, A. F.

1935. African finches. Aviculture, ser. 3, vol. 5., No. 4, pp. 40–41.

Tordoff, Harrison B.

1954. A systematic study of the avian family Fringillidae based on the structure of the skull. Misc. Publ. Mus. Zool. Univ. Michigan, No. 81, 42 pp., 77 figs.

van Someren, Vernon D.

1958. A bird watcher in Kenya, Edinburgh, Oliver and Boyd, 270 pp., 32 illus.

van Someren, Victor Gurnet Logan

1916. A list of birds collected in Uganda and British East Africa with notes on their nesting and other habits, II. Ibis, ser. 10, vol. 4, pp. 373–472.

1917. Whydahs. Avicultural Mag., ser. 3, vol. 8, pp. 288–289.

1918. A further contribution to the ornithology of Uganda (West Elgon and district). Nov. Zool., vol. 25, pp. 263–290.

1919. Notes of interest on some East African birds. Journ. East Africa and Uganda Nat. Hist. Soc., No. 14, pp. 414.

1921. On a collection of birds from Turkanaland. Journ. East Africa and Uganda Nat. Hist. Soc., No. 16, pp. 3–38.

1922. Notes on the birds of East Africa. Nov. Zool., vol. 29, pp. 1–246, pls. 1–7.

1932 Birds of Kenya and Uganda, being addenda and corrigenda to my previous paper in "Novitates Zoologicae," 1922. Nov. Zool., vol. 37, pp. 252–380, 4 pls.

1939. Reports on the Coryndon Museum expedition to the Chyulu Hills. II. The birds of the Chyulu Hills. Journ. East Africa and Uganda Nat. Hist. Soc., vol. 14, pp. 15–129.

1956 Days with birds. Studies of habits of some East African species. Fieldiana, Zool., vol. 38, 502 pp.

van Someren, Victor Gurnet Logan, and van Someren, G. R. C.

1945. Evacuated weaver colonies and notes on the breeding ecology of *Euodice cantans* Gmelin and *Amadina fasciata* Gmelin. Ibis, vol. 87, pp. 33–44.

1949. The birds of Bwamba. Uganda Journ., vol. 13, special supp. 111 pp., 23 figs., map.

Vaughan, John Henry

1930. The birds of Zanzibar and Pemba, II. Ibis, ser 12, vol. 6, pp. 1–48, 3 pls.

Verheyen, Rene

1947a. Notes sur la faune ornitholigique de l'Afrique centrale. VIII. Releve systematique d'une collection d'oiseaux reunie a la frontera Congo Belge-Rhodesie du Nord est description d'un nouveau ploceide. Bull. Mus. Hist. Nat. Belgique, vol. 23, No. 10, pp. 1–4.

1947b. Exploration du Parc National Albert, Mission Frechkop, fasc. 2., Brussels, Institut des Parcs Nationaux du Congo Belge, pp. 1–87.

VERHEYEN, RENE—Continued

1953. Oiseau, *in* Exploration du Parc National de l'Upemba, Mission G. F. De Witte, fasc. 19, Brussels, Institut des Parcs Nationaux du Congo Belge, 687 pp., 5 pls.

1955. La polygamie chez le tisserin noir *Textor nigerrimus* (Vieillot). Gerfaut, vol. 45, pp. 185–196.

VERNON, E. WARREN

1906. Combassous. Bird Notes, vol. 5, p. 148.

VERREAUX, JULES P., AND VERREAUX, EDOUARD

1856. Description d'une espece nouvelle de Veuve. Rev. Mag. Zool. ser. 2, vol. 8, pp. 260–262.

VINCENT, ALFRED WILLIAM

1949. On the breeding habits of some African birds. Ibis, vol. 91, pp. 660–688.

VINCENT, JACK

1936. The birds of northern Portuguese East Africa . . ., X. Ibis, ser. 13, vol. 6, pp. 48–125.

1952. A check list of the birds of South Africa, Cape Town, South African Ornith. Society, 122 pp.

VRYDAGH, J. M.

1949. Observations ornithologiques en region occidentale du Lac Albert et principalement de la Plaine d'Ishwa. Gerfaut, vol. 39, pp. 1–115.

WALKER, ROBERSTON M.

1932. Notes from Cofimvaba. Blythswood Rev. vol. 9, p. 29.

WHITE, CHARLES MATTHEW NEWTON

1943. Notes on the birds of the Lusaka District, Northern Rhodesia. Ibis, vol. 85, pp. 257–264.

1946. The ornithology of the Kaonde-Lunda Province, Northern Rhodesia, IV. Ibis, vol. 88, pp. 206–224.

WHITE, CHARLES MATTHEW NEWTON, AND WINTERBOTTOM, JOHN MIALL

1946. A check list of the birds of Northern Rhodesia, Lusaka, Government Printer, 168 pp., map.

WINTERBOTTOM, JOHN MIALL

1936. Notes sur quelques veuves du nord de la Rhodesie. Oiseaux Rev. Française Ornith., n.s. vol. 6, pp. 77–85.

1937. The birds of the dams in the eastern province of Northern Rhodesia. Ostrich. vol. 8, pp. 68–83.

1939a. A note on the paradise whydahs. Ostrich, vol. 10, pp. 125–128.

1939b. Miscellaneous notes on some birds of Northern Rhodesia. Ibis, ser. 14, vol. 3, pp. 712–734.

1942. A contribution to the ornithology of Barotseland. Ibis, ser. 14, vol. 6, pp. 337–389.

1951. Common birds of the bush, Cape Town, Longmans Green, 40 pp., 4 pls.

1952. Bird notes. Northern Rhodesia Journ., vol. 1, No. 6, p. 40.

WOLTERS, HANS E.
1939. Zur Systematik der Astrilde (Gattung Estrilda). Ornith. Monatsb., vol. 47, pp. 33–37.
1943. Zur Kenntnis von *Hypochera*. Ornith. Monatsb., vol. 51, pp. 99–100.
1944. Uber den taxonomischen Wert der weissen 'Tropfenfleckung' bei den Estrildinen. Ornith. Monatsb. vol. 52, pp. 27–29.
1949. Beiträge zur Gattungssystematik der Finkenvogel, *in* Beiträge zur Gattungssystematik der Vögel II, Krefeld, Goecke und Evers, pp. 3–17.
1950. Uber einige Gattungen der Estrildinae. Bonner Zool. Beitr., vol. 1, pp. 31–38.
1957. Die Klassifikation der Weberfinken (*Estrildidae*). Bonner Zool. Beitr., vol. 2, pp. 90–129.

YAMASHINA, Y.
1930. On a new subspecies of *Prosteganura haagneri*. Tori, vol. 6, No. 30, pp. 113–115, pl. 7.

YEALLAND, J. J.
1959. The national exhibition of cage birds. Avicultural Mag., vol. 65, pp. 49–51.

ZEDLITZ, OTTO VON
1911. Meine ornithologische Ausbeute in Nordost-Africa. Journ. Ornith., vol. 59, pp. 1–92.
1916. Das Süd-Somaliland als zoogeographisches Gebiet, III. Journ. Ornith., vol. 64, pp. 1–120.

ZUCKERMAN, S,
1955. Chairman's closing remarks, *in* The comparative endocrinology of vertebrates, I. Mem. Soc. Endocrin., vol. 4, 253 pp.

INDEX