

## THE BIOGEOGRAPHIC EVIDENCE SUPPORTING THE PLEISTOCENE FOREST REFUGE HYPOTHESIS

ERNST MAYR AND ROBERT J. O'HARA

*Museum of Comparative Zoology, Harvard University, Cambridge, MA 02138*

*Abstract.*—The prevailing explanation for the observed distributional patterns and areas of endemism of tropical forest organisms is the Pleistocene refuge hypothesis, which proposes that wide-ranging ancestral taxa were isolated into forest refuges during certain glacial periods, and that this isolation provided them with the opportunity to speciate. John Endler has recently argued that two predictions of the refuge hypothesis—that contact zones between vicars should be between refuges and that contact zones of rapidly reproducing butterflies should be wider than those of more slowly reproducing birds—are not borne out by the evidence. Endler therefore rejects the refuge hypothesis. We show that the data available are far too imprecise to permit any conclusions regarding contact zone widths and that, according to our reanalysis of the African bird data used by Endler, all the contact zones between vicars do indeed occur between refuges, exactly where they are expected. Additional strong support for the refuge hypothesis comes from the existence of many taxa endemic to the particular forest areas which have been postulated as refuges and from fragmented taxa which are still allopatric, never having come into secondary contact.

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The hypothesis that climatic and vegetational upheavals during the Pleistocene fragmented the previously continuous ranges of many species into isolated refuges curiously antedates the publication of Darwin's *Origin*. It was first proposed by Edward Forbes in 1846 to account for disjunctions in the distributions of plants in Europe. Darwin reached the same conclusion independently (Darwin, 1958 pp. 124-125) but strangely never made use of this refuge hypothesis when, at a later period, he tried to explain speciation on continents. Ultimately, Darwin favored a theory of sympatric speciation for speciation on continents. Moritz Wagner (1868) objected to this solution and suggested that rivers and mountains had provided all the needed isolation for continental speciation. Later authors, however, revived the refuge theory, pointing out that during the Pleistocene the advancing ice sheets could have provided isolation for speciating temperate zone populations surviving in isolated pockets of suitable habitat (Mayr, 1963 p. 561). As it became clear that the Pleistocene produced drastic changes in the distribution of vegetation in the tropics and subtropics, as well as in the temperate

region, various authors argued that isolation by vegetational barriers could have been as effective there as isolation by vegetational and physical barriers had been in cooler regions. Among the analyses which established these ideas were those of Chapin (1932), Moreau (1952), Hall and Moreau (1970), and Snow (1978), for the birds of Africa; Keast (1961) for the birds of Australia; and Haffer (1974) for the birds of South America. Vanzolini and Williams (1970), Hamilton (1976), and Brown et al. (1974), among others, have presented similar analyses for other taxa. Periods of reduced rainfall, all these authors argued, led to the temporary fractionation of previously continuous rainforests into forest islands separated by wide belts of savanna. The fauna of the tropical lowland forests was isolated in these forest refuges and given the opportunity to speciate. With the return of more mesic conditions, the forest islands expanded, simultaneously with the shrinking of the savannas, and in many cases contact zones between previously isolated forest taxa became established. Five possible outcomes of the secondary contact of such isolates are traditionally recognized:

- A. Speciation not completed
1. Smooth fusion if the populations had not diverged appreciably during the period of isolation
  2. Development of a conventional subspecies border if morphological (e.g., color) differences had evolved, but not isolating mechanisms or ecological differences
  3. Development of a hybrid zone along the line of contact
- B. Speciation largely or fully completed
4. Parapatry, with minimal overlap or hybridization
  5. Invasion (unidirectional or mutual) and overlap of the previously allopatric populations.

The most detailed documentation for the occurrence of these five possibilities has been given by Haffer (1974) for the birds of the Amazonian rainforest, and very recently by Prigogine (1984) for the region considered in this paper, tropical Africa. Intensive studies of individual contact zones (possibilities 3 and 4 above), so far as we know, have not been made in any of the tropical lowland forest cases, although numerous such studies may be cited for temperate species (Meise, 1928; Dixon, 1955; Short, 1965; Selander et al., 1969; Huntington, 1952; Barrowclough, 1980; Johnson and Johnson, 1985), and Prigogine and Louette (1983) have recently analyzed the case of a tropical woodland (not lowland forest) taxon. These analyses of contact zones show that they have two characteristics which one would expect to find in zones of secondary hybridization: 1) populations in the hybrid zone have greatly increased variability and contain individuals which may range from the phenotype of one of the adjacent taxa to that of the other; and 2) outside the hybrid zone, the two forms are, over wide areas, relatively uniform, at most varying clinally.

This interpretation of the stages of speciation in Pleistocene forest refuges is in all its details consistent with the theory of allopatric speciation and has been adopted almost unanimously in all evo-

lutionary treatments. Rather than providing additional documentation for the refuge theory, we shall here attempt to refute an alternative theory, recently proposed by John Endler (1982a, 1982b), which is based on the postulated occurrence of parapatric speciation. Our own analysis has convinced us that Endler has failed to make his case, and our aim in this paper is to refute his claims for the occurrence of parapatric speciation and to reaffirm the validity of the evidence supporting allopatric speciation in tropical forest refuges during the Pleistocene. We show that not only the data of contact zones, but also of endemic and disjunct taxa, corroborate the refuge theory.

#### *Endler's Arguments Against the Refuge Theory*

Endler attempts to refute the Pleistocene refuge hypothesis by arguing that two predictions following from the hypothesis are not borne out by the evidence. These predictions are 1) that the majority of contact zones should be about half-way between postulated refuges, because "there is no reason to assume that the dispersal rates of two closely related species or subspecies should be very different" (Endler 1982a p. 642), and 2) that contact zones of rapidly reproducing taxa (such as butterflies) should be wider than contact zones of more slowly reproducing taxa (such as birds), because one can calculate the width of a contact zone by the equation  $w = kl\sqrt{T}$ , where  $w$  is contact zone width,  $l$  is the "gene flow distance,"  $T$  the number of generations since contact, and  $k$  is a constant. (See Endler [1977, 1982a] for detailed discussions of this equation.) We will now discuss these two predictions and Endler's tests of them and then will discuss some additional distributional patterns which support the refuge hypothesis, but which were not considered by Endler.

#### *Contact Zone Positions*

It is by no means necessary to assume that dispersal rates of closely related

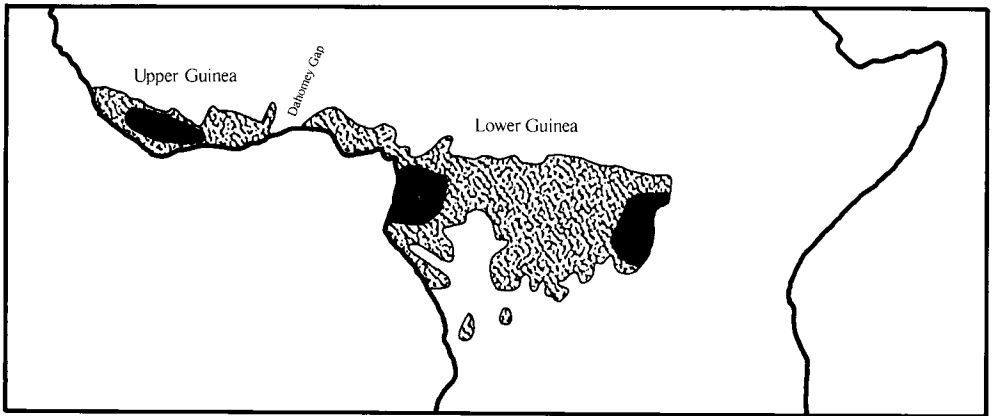


FIG. 1. Present distribution of tropical lowland forest (stipple) in Africa and postulated locations of Pleistocene forest refuges (black). Forest distribution after Hall and Moreau (1970); refuge locations after Endler (1982a).

species or subspecies should be similar, as Endler asserts (1982a p. 642). This will often be the case, we agree, but many well known bird species contain both migratory and nonmigratory populations. Dispersal tendency is to some extent under genetic control (Mayr and Diamond, unpubl.), but the possibility is high that a considerable chance component exists. Hence, the distance a given refuge inhabitant spreads, as compared to other species in the same refuge or to other populations of the same species in different refuges, is not precisely predictable. Consistently asymmetrical expansion from refuges in Australia has apparently occurred in the sitella genus *Daphoenositta*, in which western forms from drier forest pockets regularly spread more rapidly than their vicars in the more mesic eastern forests (Mayr, 1963 p. 373). Nevertheless, in spite of the above reservations, we agree that if the refuge hypothesis is true, most zones of contact should be found approximately midway between proposed refuges. "The relatively simple situation in tropical Africa provides a possible test of this . . . prediction" (Endler, 1982a p. 642).

Students of mammals, birds, reptiles and amphibians, and butterflies, recognize three lowland forest refuge areas in West Africa: the Upper Guinea Forest

(UG), the West Lower Guinea Forest (WLG), and the East Lower Guinea (or East Congo) Forest (ELG) (Fig. 1). The distributions of African lowland forest birds in relation to these refuges have been well mapped by Hall and Moreau (1970) and Snow (1978), and Endler bases his analysis of contact zone positions on the data presented in the first of these publications. He concludes that "only 9 percent of the contact zones [between forest taxa] occur between postulated refuges" (1982a p. 643, fig. 35.2). Our analysis of the same data comes to entirely different conclusions. We do not know which of the several hundred taxa mapped by Hall and Moreau are used in Endler's calculations, but he may have used an inappropriately heterogeneous sample. He states, for instance, that "52 percent of the contact zones occur between forest forms and forms found outside the forest" (1982a p. 643). Such cases are irrelevant to the problem, since the forest refuge hypothesis deals only with taxa inhabiting the lowland forest. In another of Endler's categories, where contact zones occur *within* postulated refuges (said to make up 39% of the total), a great many are apparently between lowland and montane forest taxa, either in the Cameroon or East Congo highlands. These are likewise irrelevant, because it has never

TABLE 1. Lowland forest bird taxa for which contact zones can be determined. Double slash indicates Upper Guinea/Lower Guinea contact, single slash indicates West Lower Guinea/East Lower Guinea contact; NP = non-passeriform (map numbers from Snow [1978]), P = passeriform (map numbers from Hall and Moreau [1970]).

Taxa	Map number
<i>Fringilla achantensis</i> // <i>F. squamatus</i>	NP122
<i>Tauraco persa</i> // <i>T. schutti</i>	NP237
<i>Tauraco m. macrorhynchus</i> // <i>T. m. verreauxi</i> *	NP238
<i>Centropus leucogaster</i> // <i>C. anselii</i> / <i>C. leucogaster</i>	NP253
<i>Bycanistes f. fistulator</i> // <i>B. f. sharpei</i> + <i>duboisii</i>	NP335
<i>Melignomon sp.</i> // <i>M. zenkeri</i>	NP374
<i>Campethera maculosa</i> // <i>C. cailliautii permista</i>	NP379
<i>Dendropicos pyrrhogaster</i> // <i>D. xantholophus</i>	NP388
<i>Criniger b. barbatus</i> // <i>C. b. chloronotus</i>	P78
<i>Criniger olivaceus</i> // <i>C. ndussumensis</i> *	P79
<i>Prionops caniceps</i> // <i>P. rufiventris</i>	P95
<i>Neocossyphus finschi</i> // <i>N. fraseri</i>	P155
<i>Sylvietta v. flaviventris</i> // <i>S. v. virens</i>	P234
<i>Macrosphenus kempfi</i> // <i>M. flavicans</i>	P240
<i>Muscicapa ussheri</i> // <i>M. infuscata</i> *	P242
<i>Platysteira b. blisetti</i> // <i>P. b. chalybea</i>	P265
<i>Anthreptes r. rectirostris</i> // <i>A. r. tephrolaema</i> *	P282
<i>Anthreptes fraseri</i> "green group"/ <i>A. fraseri</i> "gray group"	P285
<i>Ploceus n. castaneofuscus</i> // <i>P. n. nigerrimus</i>	P326
<i>Ploceus n. brachypterus</i> // <i>P. n. nigricollis</i>	P338
<i>Malimbus ibadanensis</i> // <i>M. erythrogaster</i>	P346
<i>Nigrita c. emiliae</i> // <i>N. c. canicapilla</i> group*	P375
<i>Lamprotornis cupreocauda</i> // <i>L. purpuriceps</i> *	P413

\* Actually allopatric across the Dahomey Gap, but presumably would be in contact there if the forest were continuous.

been suggested that the mountain forms evolved in lowland forest refuges. Since the history of each species is somewhat different from that of every other, the pooling of cases is not necessarily informative. We therefore present a reanalysis of the contact zone positions of African birds, in which we specify the taxa we have considered. We examine not only the passeriform taxa from Hall and Moreau (1970), but also the non-passeriforms from Snow (1978).

There are 222 lowland forest species or species groups according to our analysis of the maps in Hall and Moreau (1970) and Snow (1978). This includes 47 non-passeriforms and 62 passeriforms (see Appendix) that are uninformative because they occur throughout all the lowland forests and have not developed important geographical races. There are four species of non-passeriforms (Snow, 1978 #244, 262, 353, and 428) and nine species of passeriforms (Hall

and Moreau, 1970 #61, 112, 154, 163, 165, 221, 222, 345, 382, and 404) whose geographical distributions and contact zones are complex and are not readily explained by the refuge hypothesis, nor by any other factors known at present. (Individual studies of some of these complex cases have been made, however; see Chapin [1948] on *Terpsiphone*, Erard [1975] on *Batis*, Payne [1982] on *Vidua*, and the recent review by Prigogine [1984].) The remaining 100 taxa are consistent with and supportive of the refuge hypothesis. We have grouped these into three broad categories: A) subspecies groups or allospecies now in contact, with distinct contact zones; B) subspecies groups or allospecies which are endemic to one or two of the three forest regions (UG, WLG, ELG) but absent elsewhere; and C) subspecies groups or allospecies which have disjunct distributions (no contact zones exist). We will discuss category A here because it is the category

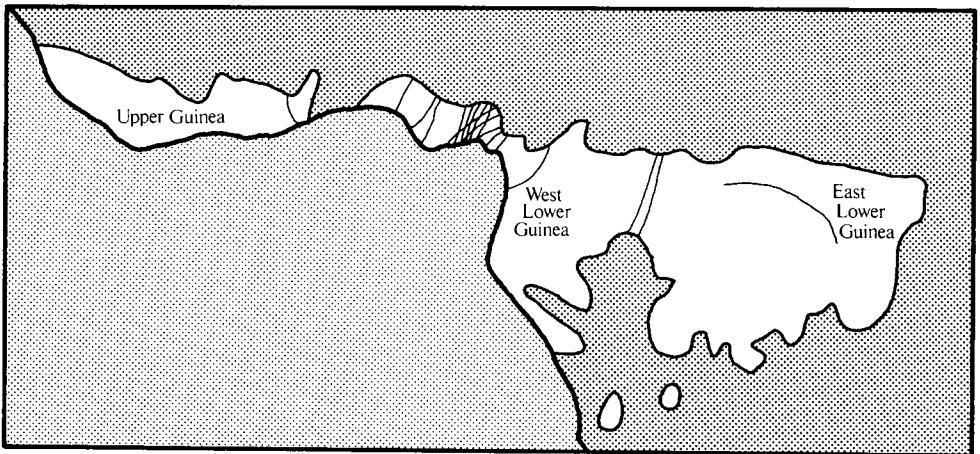


FIG. 2. Locations of contact zones between the lowland forest bird taxa listed in Table 1. The six taxa whose distributions are broken by the Dahomey Gap are not indicated.

specifically analyzed by Endler. Categories B and C we will discuss below in the section on endemic and disjunct taxa; these categories of taxa were not analyzed by Endler, but we believe they provide some of the strongest evidence in favor of the refuge hypothesis.

The forest taxa (eight non-passeriform and 15 passeriform) for which contact zones can be readily determined are enumerated in Table 1. Endler, as remarked above, maps the distribution of such contact zones (on the basis of an unstated assortment of taxa), and concludes that “only 9 percent of the contact zones occur between postulated refuges” (1982a p. 543, fig. 35.2). Our map of contact zone positions (Fig. 2) leads to a contrary conclusion. Of the 23 contact zones we identify, six fall in the Dahomey Gap (the savanna barrier between the Upper and Lower Guinea forests), 15 others are also between Upper and Lower Guinea but not at the Dahomey Gap, and three are between West Lower Guinea and East Lower Guinea. (Taxa separated by the Dahomey Gap are not strictly in contact, but probably would be if the forest were continuous.) All of these contact zones are where the refuge hypothesis predicts them to be. We therefore consider refuted Endler’s claim that the positions of con-

tact zones are not in accordance with the refuge hypothesis.

#### *Widths of Contact Zones*

Endler derives his second argument against the forest refuge hypothesis from his thesis that the widths of contact zones should be determined entirely by the time since contact was established, the number of generations since that time, and the “dispersal or gene flow distance.” On the basis of these assumptions, “butterflies, with a shorter generation time, would have a larger  $w$  [width of contact zone] than birds” (1982a p. 646), and the data available, Endler argues, are not in agreement with this prediction. They therefore do not support the refuge hypothesis, because the refuge hypothesis assumes that all contact zones were established at approximately the same time.

We see a number of fallacies in the above argument. First, the refuge hypothesis does not predict that all contact zones should have been established at the same time. We argue below that many taxa were isolated in refuges but have not yet come into secondary contact, while other taxa isolated in the same refuges have extensive contact zones.

Secondly, for those taxa in which contact zones do exist, the widths of these

zones cannot be evaluated realistically on the basis of Endler's fairly simple assumptions. Analyses of temperate region contact zones (there are no well studied tropical forest cases), such as the situation between *Corvus corone* and *C. cornix*, have revealed a zone of contact which is very narrow even though it was evidently established many thousands of years ago (Meise, 1928). Furthermore, the southern portion of the *Corvus* zone was established earlier than the northern portion (perhaps by more than 1,000 years), yet is no wider, and in fact is even narrower over considerable stretches. The same has been shown for many other temperate region hybrid zones in Europe (Selander et al., 1969) and North America (Dixon, 1955; Johnson and Johnson, 1985).

Why do we find Endler's assumptions about the control of contact zone width inadequate? As Dobzhansky (1941) pointed out, and as many subsequent authors have since confirmed, there is often strong counter selection against alien genes crossing a hybrid zone into the range of a sister species. This has perhaps been best studied for the hybrid belt between *Mus musculus* and *M. domesticus* in Denmark, where Selander et al. (1969) have shown the differential rate of penetration of different genes, and where Ferris et al. (1983) have shown that the mitochondria of one of the species have penetrated hundreds of kilometers into the Scandinavian range of the other species. Endler's arguments based on theoretical considerations are invalid without attention to the power of natural selection and the resistance of genotypes to the invasion of alien genes. There may be cases in which selection is relatively unimportant (see Barrowclough [1980] on *Dendroica*), but such cases must be empirically demonstrated. In addition, as we argue below, many fragmented taxa have not established secondary contact, and their existence forces the rejection of another of Endler's assumptions, that all contact zones were established at approximately the same time. The apparent

narrowness or width of contact zones, therefore, does not in itself conflict with the forest refuge hypothesis.

Even if selection were irrelevant to the problem, Endler's calculations would be too imprecise in the African case to be realistic. Endler makes his estimates of bird contact zone widths primarily from Hall and Moreau (1970). Hall and Moreau's map (1970 p. xi) shows that gaps of 50–200 miles between collecting localities are common, however, and these would be significant in Endler's equations. In addition, it is well known how dynamic some zones of contact can be, changing in extent and position within several years or decades (see, for example, the analysis of *Vermivora* by Gill [1980]). The distributional maps of Hall and Moreau are composites of well over 100 years of data and do not take such changing conditions into account.

Endler's estimates of gene flow distances are also open to dispute. Almost no actual data are available for the tropical taxa in question, and generalizations across genera or families are not necessarily legitimate. As noted above, there are well studied, individual species of birds that contain both migratory and non-migratory populations which undoubtedly have different average gene flow distances.

#### *Endemic and Geographically Disjunct Taxa*

Two categories of African forest bird taxa, not analyzed by Endler, provide considerable additional support for the refuge hypothesis. These are our categories B and C above: taxa endemic to one or two of the forest regions, but absent elsewhere, and taxa with disjunct distributions. We will discuss the taxa in each of these categories here.

*Category B.*—The taxa endemic to particular forest regions are enumerated in Table 2. Four are endemic to the Upper Guinea Forest, four to the West Lower Guinea Forest, four to the East Lower Guinea Forest, and 17 to the Lower Guinea Forest as a whole (East and West).

TABLE 2. Lowland forest bird taxa endemic to particular forest regions. NP = non-passeriform (map numbers from Snow [1978]), P = passeriform (map numbers from Hall and Moreau [1970]).

Taxa	Map number
<b>A. Endemics of the West Lower Guinea Forest</b>	
<i>Glaucidium sjostedti</i>	NP271
<i>Hirundo fuliginosa</i>	P38
<i>Bradypterus grandis</i>	P178
<i>Ploceus batesi</i>	P339
<b>B. Endemics of the East Lower Guinea Forest</b>	
<i>Francolinus nahani</i>	NP129
<i>Afropavo congensis</i>	NP134
<i>Ploceus flavipes</i>	P342
<i>Spermophaga poliogenys</i>	P383
<b>C. Endemics of the Lower Guinea Forest (East and West)</b>	
<i>Guttera plumifera</i>	NP137
<i>Caprimulgus batesi</i>	NP275
<i>Merops breweri</i>	NP318
<i>Dendropicos elliotii</i>	NP389
<i>Nicator vireo</i>	P92
<i>Dryoscopus senegalensis</i>	P99
<i>Prinia bairdii</i>	P207
<i>Muscicapa sethsmithi</i>	P245
<i>Muscicapa griseigularis</i>	P249
<i>Platysteira tonsa</i>	P266
<i>Trochocercus nigromitratus</i>	P269
<i>Antheptes aurantium</i>	P284
<i>Nectarinia batesi</i>	P299
<i>Nectarinia rubescens</i>	P302
<i>Nectarinia reichenbachii</i>	P308
<i>Quelea anomala</i>	P359
<i>Nigrita luteifrons</i>	P375
<b>D. Endemics of the Upper Guinea Forest</b>	
<i>Ceratogymna elata</i>	NP336
<i>Hirundo leucosoma</i>	P33
<i>Trichastoma rufescens</i>	P166
<i>Nectarinia adelberti</i>	P301

Representative distributions of several of these taxa are shown in Figure 3. There are no lowland forest taxa which are endemic to regions between postulated refuges; it is obvious that these areas of endemism are not random, and correspond to the proposed refuge locations. The recent analyses of Diamond and Hamilton (1980) and Crowe and Crowe (1982) have come to exactly the same conclusions. This pattern of distribution is consistent with the postulate that the vicars of these endemic taxa in the other refuges became extinct during the period

of greatest forest contraction, when only isolated islands of suitable habitat remained. Extinction of insular populations is a particularly well documented process.

*Category C.*—Forest taxa which have disjunct distributions provide some of the strongest evidence in favor of the refuge hypothesis. We have counted twenty non-passeriform and 28 passeriform taxa that appear to have gaps in their distributions; these are listed in Table 3, and the ranges of several are mapped in Figure 4. Some of these taxa have speciated, and some have subspeciated, while others have not diverged significantly at all. This is completely consistent with much data which suggest that rates of phenotypic divergence in different taxa are not equal (Simpson, 1953). Neither we nor any other workers so far as we know accept Endler's claim (1982a p. 647) that, under the refuge hypothesis, "allopatry necessarily leads to differentiation."

We recognize that the absence of a particular species in an area is difficult to prove conclusively, and we would not be surprised if some of these gaps could be narrowed or closed by additional collecting. The recent work of Louette (1984) in the collections of the Musée Royal de l'Afrique Centrale in Tervuren, for example, has shown that 14 taxa which appear from Hall and Moreau (1970) and from Snow (1978) to be allopatric across the Congo basin are actually present in small numbers throughout Lower Guinea. For many other taxa, however, Louette found no additional records, and thus their distributional disjunction is even more strongly supported. So many taxa fall into this category that they cannot all be accounted for by insufficient collecting. By far the simplest explanation of these disjunct distributions is that the respective populations were isolated in forest refuges and have just not yet come into secondary contact.

### Conclusions

We have attempted to show in this paper that the evidence adduced in support

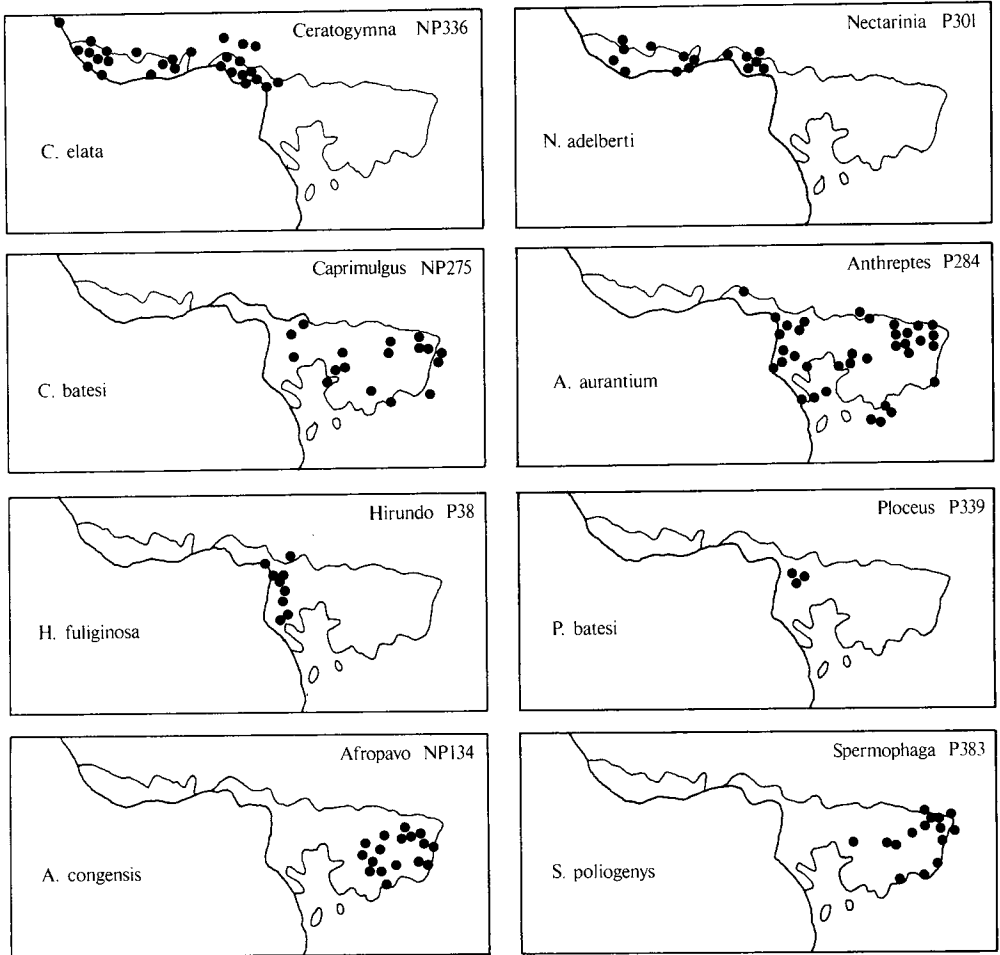


FIG. 3. Distributions of several of the bird taxa endemic to particular forest regions listed in Table 2. NP = non-passeriform (map numbers from Snow [1978]), P = passeriform (map numbers from Hall and Moreau [1970]).

of Endler's alternative to the Pleistocene forest refuge hypothesis is incorrect and incomplete. We have confined ourselves to the situation in Africa, because this was the region specifically analyzed by Endler. Endler is correct in saying that the refuge hypothesis has precipitated a lot of bandwagon-jumping, and we agree that there are undoubtedly many uncritical applications of the refuge theory in the literature. The situation in the New World tropics, for example, is far more complex than that in Africa, and requires very detailed studies of individual cases. Although questioning the refuge hypoth-

esis, the recent statistical analysis of the neotropical situation by Beven et al. (1984 p. 394–395) nevertheless found, even at a very coarse level of geography, "some refugia and centers-of-endemism . . . having improbably small numbers of species boundaries traversing them." The work of these authors suggests that biogeographers must be very specific, both taxonomically and geographically, when they are proposing explanations for present-day distributional patterns. We have attempted to provide an example of this type of specificity in the present paper.

It is distressing to us as evolutionary



TABLE 3. Lowland forest bird taxa with disjunct distributions. UG = Upper Guinea, LG = Lower Guinea, WLG = West Lower Guinea, ELG = East Lower Guinea; NP = non-passeriform (map numbers from Snow [1978]), P = passeriform (map numbers from Hall and Moreau [1970]).

Taxa	Map number
<i>Bostrychia rara</i> UG//LG	NP41
<i>Accipiter castanius</i> UG//LG	NP84
<i>Agelastes meleagrides</i> // <i>A. niger</i>	NP136
<i>Columba unicincta</i> UG//LG	NP213
<i>Poicephalus gularis</i> UG//WLG/ELG	NP229
<i>Agapornis swinderniana</i> UG//LG	NP232
<i>Chrysococcyx flavigularis</i> UG//LG	NP251
<i>Jubula lettii</i> UG//LG	NP264
<i>Scotopelia ussheri</i> // <i>S. bouvieri</i>	NP269
<i>Glauucidium tephronotum</i> UG//LG	NP272
<i>Raphidura sabinii</i> UG//LG	NP288
<i>Neafrapus cassini</i> UG//LG	NP291
<i>Apaloderma aequatoriale</i> WLG/ELG (Lower Guinea only)	NP301
<i>Ispidina lecontei</i> UG//LG	NP307
<i>Phoeniculus castaneiceps</i> UG+WLG/ELG	NP332
<i>Indicator conirostris</i> UG//LG	NP367
<i>Indicator m. maculatus</i> // <i>I. m. stictithorax</i>	NP368
<i>Melichneutes robustus</i> UG//LG	NP371
<i>Sasia africana</i> UG//LG	NP376
<i>Campethera caroli</i> UG//LG	NP382
<i>Smithornis sharpei</i> WLG/ELG (Lower Guinea only)	P2
<i>Campephaga lobata</i> // <i>C. oriolina</i> WLG/ELG	P60
<i>Campephaga petiti</i> WLG/ELG (Lower Guinea only)	P61
<i>Coracina azurea</i> UG//LG	P64
<i>Laniarius l. luhderi</i> WLG/ELG (Lower Guinea only)	P106
<i>Malaconotus bocagei</i> WLG/ELG (Lower Guinea only)	P109
<i>Malaconotus multicolor</i> UG//absent?/ELG	P111
<i>Lanius mackinnoni</i> WLG/ELG (Lower Guinea only)	P117
<i>Ceratotrachus leucosticta</i> UG//absent/ELG	P138
<i>Alethe d. diademata</i> // <i>A. d. castanea</i>	P142
<i>Cossypha cyanocamptus</i> UG+WLG/ELG	P149
<i>Sheppardia cyornithopsis</i> UG//LG	P153
<i>Neocossyphus poensis</i> UG//LG	P154
<i>Turdus princei</i> UG//WLG/ELG	P161
<i>Turdus camaronensis</i> WLG/ELG (Lower Guinea only)	P162
<i>Phyllanthus atripennis</i> UG//absent/ELG	P175
<i>Picathartes gymnocephalus</i> // <i>P. oreas</i> /Uganda population?	P176
<i>Apalis nigriceps</i> UG//WLG/ELG	P217
<i>Bathmocercus cerviniventris</i> // <i>B. rufus</i> WLG/ELG	P225
<i>Muscicapa epulata</i> UG//WLG/ELG	P245
<i>Hylia v. nehrkorni</i> // <i>H. v. violacea</i> WLG/ELG	P259
<i>Platysteira concreta</i> UG//WLG/ELG	P264
<i>Platysteira blissetti</i> / <i>P. jamesoni</i>	P265
<i>Parus funereus</i> UG//WLG/ELG	P276
<i>Ploceus preussi</i> UG//WLG/ELG	P340
<i>Ploceus dorsomaculatus</i> WLG/ELG (Lower Guinea only)	P340
<i>Ploceus albinucha</i> UG//WLG/ELG	P343
<i>Malimbus coronatus</i> WLG/ELG (Lower Guinea only)	P347

biologists that some ecologists have been trying to explain biogeography entirely in terms of now-existing environmental situations. These are not two opposed alternatives. All currently observed distributional patterns are the result of an

interplay of historical and ecological factors, and to invoke ecological explanations to the exclusion of historical ones is unwise. There are many aspects of biogeography, such as the details of archipelagic distributions, that cannot be ex-

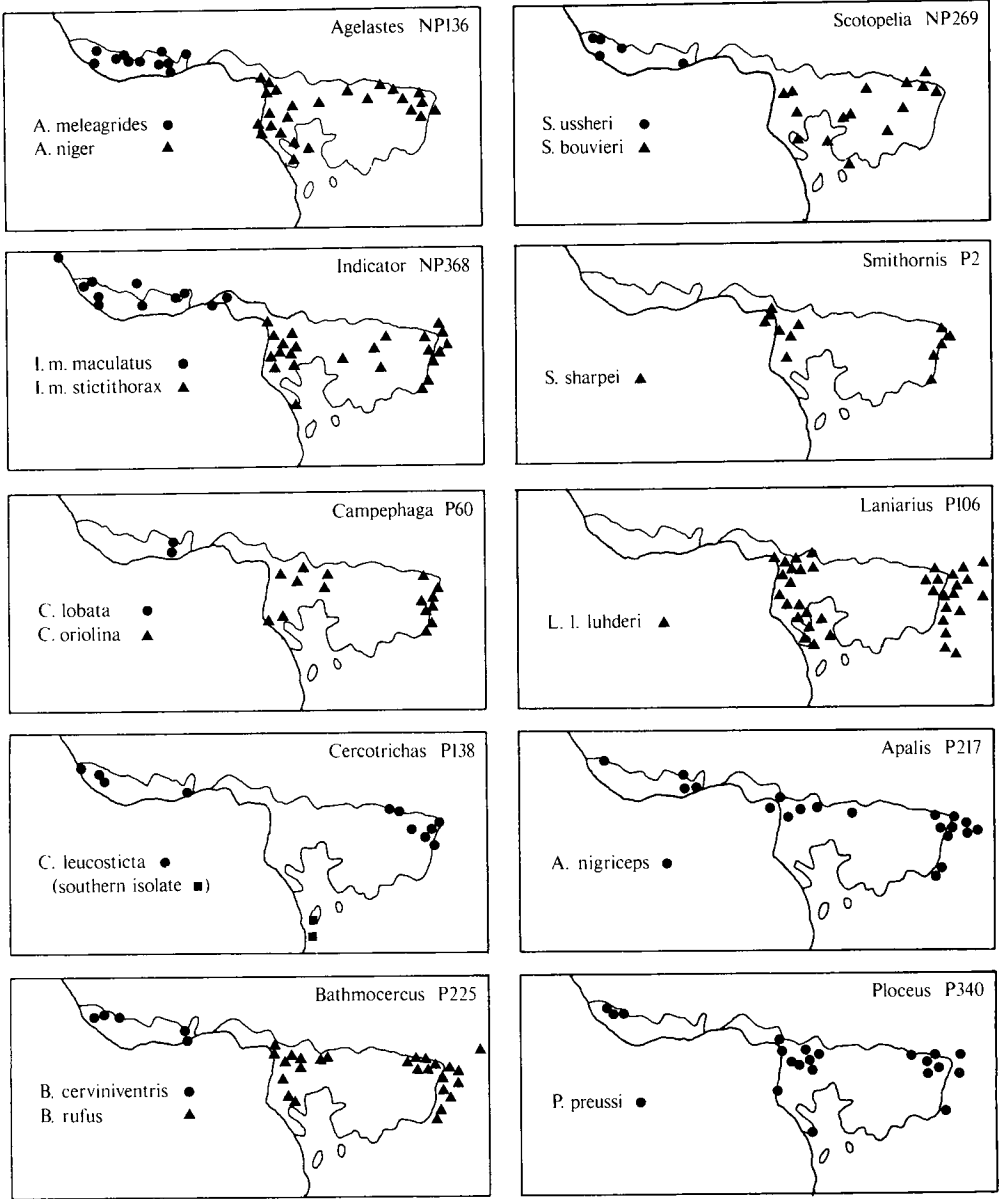


FIG. 4. Distributions of several of the geographically disjunct taxa listed in Table 3. NP = non-passeriform (map numbers from Snow [1978]), P = passeriform (map numbers from Hall and Moreau [1970]).

plained simply in terms of present physico-geographic factors.

Given the views expressed here, what type of additional research is needed to enhance further our understanding of tropical diversity? First and foremost,

much more extensive and careful collecting needs to be done. Detailed distributional data form the basis of all biogeographic studies, and many biologists fail to realize how scanty such data are, even in relatively well collected groups

such as birds. The need for additional collecting is urgent in view of the rapid destruction of tropical habitats; this must be one of our highest priorities (Short, 1984).

Second, careful systematic work to determine the exact branching sequences of taxa will enlighten historical biogeographic work. Systematics is the cornerstone of all evolutionary biology, and new systematic analyses often overturn evolutionary hypotheses based on inadequate earlier classifications. Systematists will be able to purge errors in historical biogeographic analyses by showing that the actual branching sequence of the taxa involved is not concordant with their proposed biogeographic history.

Last, we need studies of the dynamics of specific contact zones. These studies should include not only current techniques of genetic analysis (see the example provided by Barrowclough [1980]), but also detailed behavioral and ecological comparisons, both within contact zones and outside them. Investigations of this type on tropical taxa have barely begun.

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Corresponding Editor: D. Jablonski

## APPENDIX

Taxa without significant geographical variation found throughout the lowland forest. NP = non-passeriform (map numbers from Snow [1978]), P = passeriform (map numbers from Hall and Moreau [1970]).

<i>Pteronetta hartlaubi</i>	NP53	<i>Andropadus gracilirostris</i>	P68
<i>Dryotriorchis spectabilis</i>	NP80	<i>Andropadus curvirostris</i>	P68
<i>Accipiter toussenelii</i>	NP85	<i>Andropadus latirostris</i>	P71
<i>Accipiter minullus</i>	NP86	<i>Calyptocichla serina</i>	P73
<i>Urotriorchis macrourus</i>	NP90	<i>Thescelocichla leucopleura</i>	P74
<i>Spizaetus africanus</i>	NP98	<i>Chlorocichla simplex</i>	P75
<i>Francoelinus lathamii</i>	NP129	<i>Criniger calurus</i>	P79
<i>Himantornis haematopus</i>	NP139	<i>Bleda syndactyla</i>	P80
<i>Canirallus oculus</i>	NP140	<i>Bleda eximia</i>	P80
<i>Sarothrura pulchra</i>	NP141	<i>Baeopogon indicator</i>	P81
<i>Columba iriditorques</i>	NP214	<i>Ixonotus guttatus</i>	P82
<i>Turtur brehmeri</i>	NP226	<i>Phyllastrephus icterinus</i>	P88
<i>Psittacus erithacus</i>	NP231	<i>Phyllastrephus albicularis</i>	P90
<i>Corythaeola cristata</i>	NP234	<i>Dryoscopus sabinii</i>	P100
<i>Cercococcyx mechowi</i>	NP247	<i>Laniarius leucorhynchus</i>	P108
<i>Cercococcyx olivinus</i>	NP248	<i>Alethe poliocephala</i>	P141
<i>Ceuchmochares aereus</i>	NP258	<i>Stiphornis erythrothorax</i>	P145
<i>Otus icterorhynchus</i>	NP262	<i>Illadopsis rufipennis</i>	P164
<i>Bubo poensis</i>	NP267	<i>Apalis sharpii</i>	P220
<i>Bubo shelleyi</i>	NP267	<i>Camaroptera superciliaris</i>	P228
<i>Bubo leucostictus</i>	NP268	<i>Camaroptera chloronota</i>	P228
<i>Caprimulgus binotatus</i>	NP277	<i>Eremomela badiceps</i>	P233
<i>Telacanthura melanopygia</i>	NP290	<i>Sylvietta denti</i>	P234
<i>Alcedo quadribrachys</i>	NP305	<i>Macrosphenus concolor</i>	P239
<i>Alcedo leucogaster</i>	NP306	<i>Hylia prasina</i>	P241
<i>Halcyon malimbica</i>	NP312	<i>Muscicapa olivascens</i>	P243
<i>Halcyon badia</i>	NP313	<i>Muscicapa cassini</i>	P244
<i>Merops muelleri</i>	NP320	<i>Muscicapa comitata</i>	P246
<i>Merops gularis</i>	NP320	<i>Muscicapa tessmanni</i>	P246
<i>Eurystomus gularis</i>	NP329	<i>Fraseria cinerascens</i>	P253
<i>Bycanistes cylindricus</i>	NP334	<i>Fraseria ocreata</i>	P253
<i>Ceratogymna atrata</i>	NP336	<i>Bias musicus</i>	P256
<i>Tropicranus albocristatus</i>	NP338	<i>Megabyas flammulatus</i>	P257
<i>Tockus fasciatus</i>	NP341	<i>Platysteira castanea</i>	P266
<i>Tockus hartlaubi</i>	NP342	<i>Erythrocercus mccallii</i>	P267
<i>Tockus camurus</i>	NP343	<i>Trochocercus nitens</i>	P270
<i>Lybius hirsutus</i>	NP351	<i>Anthoscopus flavifrons</i>	P277
<i>Pogoniulus duchaillui</i>	NP355	<i>Pholidornis rushiae</i>	P279
<i>Pogoniulus scolopaceus</i>	NP357	<i>Nectarinia johanna</i>	P289
<i>Pogoniulus subsulphureus</i>	NP360	<i>Nectarinia superba</i>	P290
<i>Pogoniulus leucolaima</i>	NP361	<i>Nectarinia chloropygia</i>	P292
<i>Pogoniulus atroflavus</i>	NP362	<i>Nectarinia minulla</i>	P292
<i>Trachyphonus purpuratus</i>	NP363	<i>Nectarinia seimundi</i>	P299
<i>Prodotiscus insignis</i>	NP372	<i>Nectarinia olivacea</i>	P300
<i>Campethera nivosa</i>	NP381	<i>Nectarinia cyanolaema</i>	P304
<i>Dendropicos gabonensis</i>	NP386	<i>Ploceus aurantius</i>	P327
<i>Smithornis rufolateralis</i>	P2	<i>Malimbus rubricollis</i>	P347
<i>Hirundo nigrita</i>	P31	<i>Malimbus malimbicus</i>	P348
<i>Psalidoprocne nitens</i>	P42	<i>Malimbus nitens</i>	P348
<i>Andropadus virens</i>	P66	<i>Amblyospiza albifrons</i> 'rufous'	P350
<i>Andropadus gracilis</i>	P67	<i>Nigrita bicolor</i>	P376
		<i>Nigrita fusconota</i>	P376
		<i>Spermophaga haematina</i>	P383
		<i>Poeoptera lugubris</i>	P407
		<i>Lamprotornis splendidus</i>	P411
		<i>Onychognathus fulgidus</i>	P416
		<i>Oriolus brachyrhynchus</i>	P430
		<i>Oriolus nigripennis</i>	P431