

AMERICAN MUSEUM NOVITATES

Published by
Number 1321 THE AMERICAN MUSEUM OF NATURAL HISTORY
New York City

June 6, 1946

EVOLUTION IN THE *RHIPIDURA RUFIFRONS* GROUP¹

BY ERNST MAYR AND MARTIN MOYNIHAN

As has been demonstrated in many recent papers, the knowledge of the systematics of birds has reached such a degree of completion that it can be used safely as a basis for studies on evolution. Island birds are particularly favorable material for such studies, because each water gap acts as a barrier reducing population movements and gene flow. Subspecies found on a series of neighboring islands often show character progressions which one might expect in fossil series, but hardly in contemporary geographical representatives. It appears in some of these cases as if each colonization of a new island was correlated with a certain amount of evolutionary change.

Lack's work on the Galapagos Finches (Lack, 1945, 1946) has shown how much interesting information can be obtained from an intensive study of the taxonomy of birds on a single archipelago. The fauna of the Malay Archipelago (*sensu lato*, as used by Wallace) is even better suited for such studies than the compact archipelagos of the Galapagos or Hawaiian Islands. In this far-flung island belt between Asia, Australia, and Oceania there are not only thousands of islands of all sizes but also different climatic belts.

There is perhaps no other area in the world in which a similar number of cases of active evolution can be found.

Among birds the genera *Ducula*, *Macropygia*, *Accipiter*, *Eos*, *Trichoglossus*, *Cacatua*, *Ninox*, *Halcyon*, *Edolisoma*, *Rhipidura*, *Monarcha*, *Dicaeum*, *Myzomela*, and *Zosterops* contain some of the most interesting cases of incipient and recently completed speciation. Of these the *Rhipidura rufifrons* group is selected in the present paper for a detailed analysis.

The aim of this investigation is to determine which forms of the rich and diversified genus *Rhipidura* belong to the species or superspecies *rufifrons* and what other species are most closely related to it.

Next, an attempt is made to establish the relationship of these forms, and to ascertain how and in what sequence they evolved from each other together with the range changes that accompanied this evolution.

Finally the geographical variation of definite characteristics, such as the color of the forehead or the shape of the tail, is traced through the entire range of the species group.

THE GENUS *RHIPIDURA*

The genus *Rhipidura* is very isolated, and no closely related genera are known. The "genus" *Chelidorhynch* does not deserve generic rank since it differs from the other *Rhipidura* only by being of smaller size and in having underparts of a yellow color.

The primitive monarch flycatchers, such as *Chasiempsis*, *Mayrornis*, and the African *Trochocercus*, are perhaps nearest to *Rhipi-*

dura among all other flycatchers. Fantails (*Rhipidura*) are characterized by the short, rounded wings, which are often drooping. The tail is usually very long, although shorter than the wing in a few species. The bill is rather flat, but usually with a pronounced keel and apical hook. The rictal bristles are numerous and long. The two sexes are alike in most species, but different in others, strikingly so in *Rhipidura atra*. Gray, brown, rufous, and

¹ BIRDS COLLECTED DURING THE WHITNEY SOUTH SEA EXPEDITION, No. 56.

white are the dominant colors, but there are three or four species with blue in the plumage and one with yellow (*hypoxantha*).

Fantails are very active and restless birds, flitting from branch to branch and occasionally sallying out after a flying insect. Most species have a tinkling call note and a short, melodious, often repeated song. The nest is a well-built cup, 2 to 5 feet off the ground, more or less cone shaped on the outside and often with fibers trailing off the bottom like a tail. The favorite habitat of fantails is the substage of the forest. Some of the common, widespread species, particularly in Australia and on the Asiatic continent, live in much more open country—second growth, gardens, tree groves, along the sea shore, and similar habitats.

The genus is composed of about 35 species, five of which reach the Asiatic

mainland, one of them as far as the north-western Himalayas. In the east the genus reaches Samoa (*R. nebulosa*) and the New Zealand group (*R. fuliginosa*). New Guinea, with no fewer than 12 species, is undoubtedly its center of distribution. Within the genus several well-defined groups of species can be distinguished, as well as a number of more or less isolated species. How these various groups of species are related to one another has not yet been worked out. However, there is little doubt about the close relationship of the species that we consider to belong to the *rufifrons* species group (see below). Three additional mountain species must be considered as being probably related to the ancestor of the *R. rufifrons* group. They are *R. brachyrhyncha* (New Guinea), *R. malaitae* (Malaita, Solomon Islands), and *R. nigrocinnamomea* (Mindanao, Philippines).

THE CLASSIFICATION OF THE *RHIPIDURA RUFIFRONS* GROUP

It seems probable that the ancestral form of this group lived somewhere in the Papuan region. From here several waves of immigrants colonized the surrounding islands, as will presently be described in more detail. However, to facilitate the understanding of the evolutionary changes within this group, the following short check list of the group is given. The bibliographic details of the original descriptions are given in so many standard works that they will not be repeated here. The forms of the Solomon Islands and Santa Cruz group have been described in detail by Mayr (1931, Amer. Mus. Novitates, no. 502, pp. 16-21).

I. Species of the *Rhipidura rufifrons* group.

A. 1. *superflua* Hartert, 1899. Buru, Moluccas.

2. *teijsmanni* Büttikofer, 1893. Celebes group.

Three races: *teijsmanni* Büttikofer (Lombo Batang, south Celebes); *toradja* Stresemann, 1931 (mountains of Celebes, except Lombo

Batang); *sulaensis* Neumann, 1939 (Taliabu, Sula Island).

3. *lepada* Hartlaub and Finsch, 1868. Palau Islands.

4. *dedemi* van Oort, 1911. Seran, Moluccas.

B. *opistherythra* Sclater, 1883. Tenimber Islands.

C. *rufidorsa* Meyer, 1874. New Guinea region.

Three races: *rufidorsa* Meyer (Misol, Japan, and western New Guinea, eastward in the south to the Fly River, in the north to Geelvink Bay or Astrolabe Bay); *kumusi* Mathews, 1928 (north coast of southeastern New Guinea between Kumusi River and Collingwood Bay); *kubuna* Rand, 1938 (south coast of southeastern New Guinea).

D. 1. *dahli* Reichenow, 1897. Bismarck Archipelago.

Two races: *dahli* Reichenow (New Britain); *antonii* Hartert, 1926 (New Ireland).

2. *matthiae* Heinroth, 1902. St. Matthias.

- E. *rufifrons* Latham, 1801. (See below.)
- II. Subspecies groups of *Rhipidura rufifrons* (29 subspecies).
- A. 1. *louisianensis-granti*, *commoda*, *rufifrons-brunnea*, *russata-kuperi-ugiensis*.
louisianensis Hartert, 1899 (Rosel and Misima, Bonvouloir group, Fergusson Island); *granti* Hartert, 1918 (central Solomon Islands); *commoda* Hartert, 1918 (northern Solomon Islands from Buka to Ysabel); *rufifrons* Ramsay, 1879 (Guadalcanal); *brunnea* Mayr, 1931 (Malaita); *russata* Tristram, 1879 (San Cristobal); *kuperi* Mayr, 1931 (Santa Anna); *ugiensis* Mayr, 1931 (Ugi).
2. *rufifrons, torrida*.
rufifrons Latham, 1801 (southeastern Australia; on migration and in winter to northern Queensland and south New Guinea); *torrida* Wallace, 1865 (Ternate, Batjan).
3. *uraniae-saipanensis-versicolor*.
uraniae Oustalet, 1881 (Guam); *saipanensis* Hartert, 1898 (Saipan, Tinian, Rota); *versicolor* Hartlaub and Finsch, 1872 (Yap).
- B. 1. *agilis* Mayr, 1931 (Santa Cruz Island).
2. *utupuae-melanolaema*.
utupuae Mayr, 1931 (Utupua, Santa Cruz Islands); *melanolaema* Sharpe, 1879 (Vanikoro, Santa Cruz Islands).
3. *kubaryi* Finsch, 1875 (Ponape).
- C. *semirubra* Selater, 1877 (Admiralty Islands).
- D. *henrici-squamata*.
henrici Hartert, 1918 (Southeast Islands [Koer, Manggoer group, Taam, Seran Laut], Kei Islands, and Pulu Babi [Aru Islands]); *squamata* Müller, 1843 (western Papuan Islands and Banda Islands).
- E. 1. *semicollaris - sumbensis - mimosae-celebensis*.
2. *elegantula-reichenowi-hamadryas*.
3. *dryas-streptophora*.
semicollaris Müller, 1843 (Wetar, Timor, Savu, Alor, Flores); *sumbensis* Hartert, 1896 (Sumba); *mimosae* Meise, 1929 (Kalao tua); *celebensis* Büttikofer, 1893 (Djampéa, Kalao); *elegantula* Sharpe, 1879 (Roma, Letti, Moa, Damar); *reichenowi* Finsch, 1901 (Babar); *hamadryas* Selater, 1883 (Tenimber); *dryas* Gould, 1843 (Northern Territory, Australia); *streptophora* Ogilvie-Grant, 1911 (Mimika River, south New Guinea).

THE EVOLUTIONARY HISTORY OF THE RHIPIDURA RUFIFRONS GROUP

The present distribution of this group suggests that the ancestral stock developed somewhere in the Papuan region, probably in New Guinea. An attempt can even be made to reconstruct the probable characters of this ancestral form if one allows the assumption that the characters of the ancestral form were what now appear to be the primitive characters of the *Rhipidura rufifrons* group: "Chin and throat white, breast of a light buffy gray; an indication of rufous on the forehead. Head and upper back grayish brown, merging gradually into a rufous lower back and rump. Tail dark brown with ill-defined rufous areas on base and tip." These characters are primitive because they are ancestral

to the characters of the more advanced forms and because they are common to the majority of species which for various reasons we consider the earliest offshoots of the ancestral stock.

It is a well-known phenomenon to the student of phylogeny and of zoogeography that evolutionary advances as well as zoogeographical expansions do not always proceed steadily, but on the contrary tend to occur in abrupt spurts. Periods of aggressive range expansions seem to alternate with periods of stagnation. Good indirect evidence for this phenomenon can be found in the *Rhipidura rufifrons* group. The remnants of the first colonizing phase are the species listed as I (A, B, C, D) of the

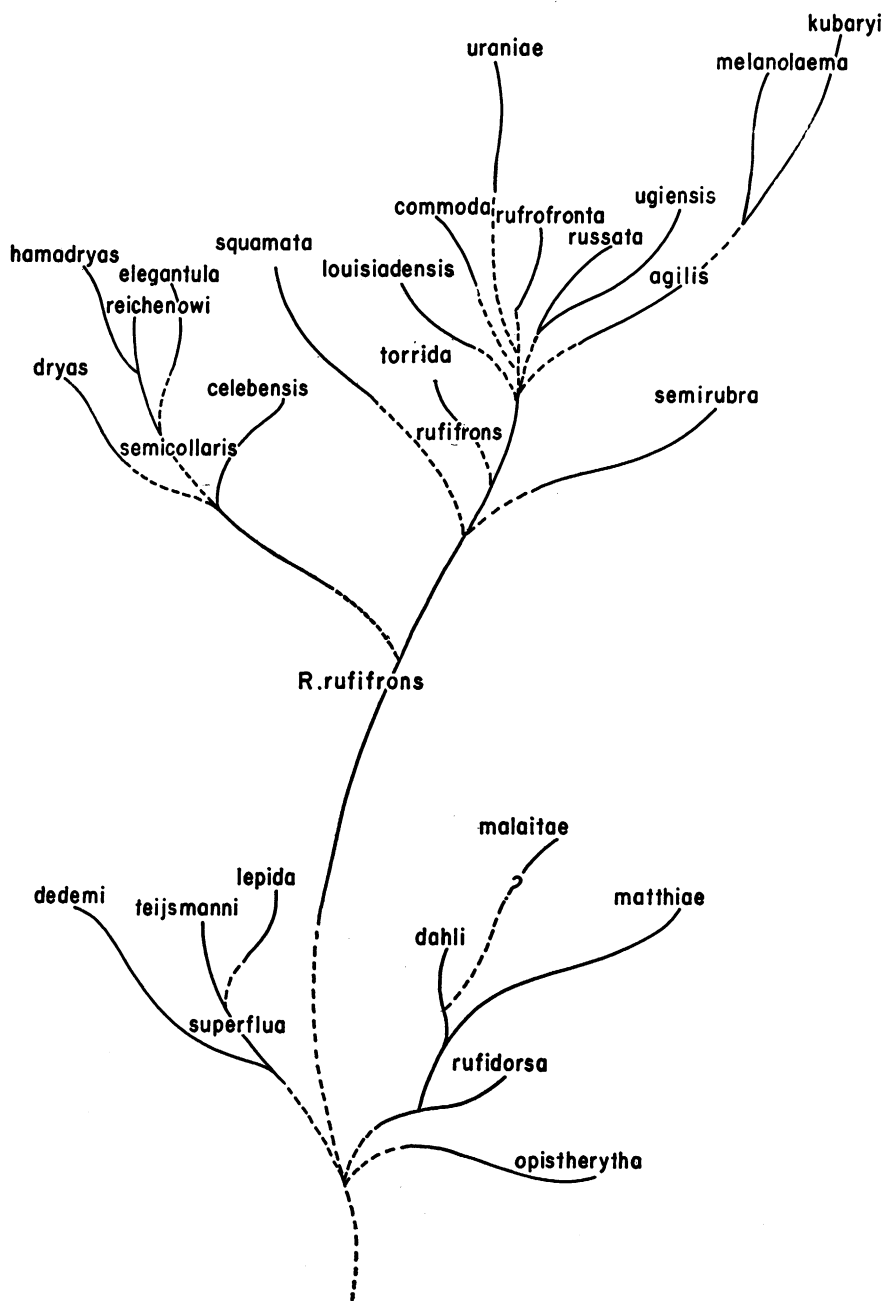


Fig. 1. Phylogeny of the *Rhipidura rufifrons* group. The lower cluster of branches represents the primitive species. The upper cluster consists of the subspecies of *Rhipidura rufifrons*. Some of the less distinct subspecies are not shown on this diagram.

above list. All of them are now confined to single islands or island groups, most of them are monotypic or have at best two or three subspecies, and many of them have a limited range in the mountains. For the sake of brevity these species are referred to as "primitive species" in the subsequent discussion. Among them four distinct branches can be distinguished.

The first branch spread westward and gave rise to *superflua* on Buru and to *teijsmanni* on Celebes. Both these species have acquired a dark gray pectoral patch, and *teijsmanni* has also developed faint scaling on the lower breast; otherwise they have remained very similar to the ancestral form. The Palau species, *lepida*, is a somewhat more specialized offshoot of this branch, characterized chiefly by a pure rufous head and back, and a blacker and more distinct breast band. The most specialized offshoot of this branch is *dedemi*, which inhabits the mountains of Seran. This species has a streaked breast, no rufous on the forehead, and a white superciliary stripe. It also has a white post-ocular stripe, a character otherwise unknown in the *rufifrons* species group. The white post-ocular stripe is, however, probably not of fundamental importance in the genus *Rhipidura* since it occurs in the melanistic phase of *Rhipidura fuliginosa*, while it is absent in the normal pied phase of this species (see Stresemann, 1923, Jour. f. Ornith., vol. 71, p. 515).

A second branch reached the Tenimber Islands in the Banda Sea, where it developed into *opistherythra*, an extremely aberrant species which is not closely related to any other form of the *rufifrons* species group. The whole plumage of *opistherythra* has acquired a grayish tinge. The rufous of the back is paler and is virtually restricted to the rump. The rufous base and tip of the tail feathers have been completely eliminated, and the whole tail is a plain gray-brown. Furthermore, the tail is longer and more pointed than that of the other primitive forms.

Another branch of the ancestral stock gave rise to *rufidorsa*, probably somewhere in northern New Guinea. This species differs from the hypothetical ancestral

form only in that the tail feathers are tipped with white, and there is a faint rufous superciliary stripe instead of a tinge of rufous over the whole forehead. It is quite close to true *rufifrons*.

Rather distantly related to *rufidorsa* is the *dahli-antonii-matthiae* group in the Bismarck Archipelago. The distinguishing features of the New Britain form, *dahli*, are as follows: a rufous-tipped tail, a dusky chin and throat, a white malar stripe, and a white superciliary stripe. The form from New Ireland, *antonii*, has a somewhat darker chin and throat, while the tail is almost pure rufous. This series reaches its culmination in the St. Matthias Island species, *matthiae*, which has perhaps the most specialized color pattern in the whole *rufifrons* species group. The most important characters of *matthiae* are a pure rufous tail, a broad white malar stripe, a white forehead and crown, and a black chin, throat, breast, and nape.

Rhipidura dahli is the only eastern fantail which at all resembles the very isolated all-rufous *Rhipidura malaitae* (Malaita, Solomon Islands). It is possible that *malaitae* is a modified offshoot of *dahli*.

All species discussed up to this point form the basic stock of the *rufifrons* species group. That they are old species is suggested by the pronounced differences between any two of these species. The original dispersal probably did not all take place at the same time, but it happened sufficiently long ago to permit the old stock to break up into nine well-defined species. Five of these (*dedemi*, *lepida*, *superflua*, *opistherythra*, and *matthiae*) are restricted to single small islands. Three other species (*teijsmanni*, *rufidorsa*, and *dahli*) live on large islands or groups of adjacent islands but have developed only two or three slight subspecies. All the species of this group are geographical representatives, and it must be assumed that the ancestral stock of the species *Rhipidura rufifrons* was an additional member of this superspecies. However, unlike all the other species of this group, *rufifrons* entered a second phase of successful evolution during which it produced no

fewer than 29 subspecies and colonized an area many times larger than the combined area of distribution of the eight other species of the *rufifrons* group. A close

analysis of the morphological characters of the subspecies of *rufifrons* permits the following reconstruction of the probable evolutionary history of the species.

EVOLUTION IN THE SPECIES *RHIPIDURA RUFIFRONS*

Those subspecies of *rufifrons* that are now found in the Louisiades and western Solomon Islands appear to be the least specialized of this species. Since within species the reverse of Matthew's rule seems to be generally valid, it may be assumed that the ancestral stock of *rufifrons* acquired its specific characters somewhere in that area. Forms of *rufifrons* spread from here in all directions, east and west, north and south, until now they virtually encircle the primitive species. Nevertheless, the ranges of the primitive species and of *Rhipidura rufifrons* do not overlap with three apparent exceptions. In all three localities there is a suggestion of an ecological separation between the two species, but appropriate data on the habitat preferences of these fantails are scanty. It is hoped that future naturalist-explorers will fill this important gap in our knowledge. One area of overlap is in southern New Guinea where both *rufidorsa* and *rufifrons streptophora* are found near the mouth of the Mimika River; *streptophora* is, however, apparently found only in the mangrove belt, while *rufidorsa* seems to prefer the inland forest. On Misol, a second area of overlap, *rufidorsa* again seems to be restricted to the forest of the mainland, while *rufifrons squamata* is recorded only from the shore and from off-coastal small islands. Nothing whatsoever is recorded of the habitat preferences of *opistherythra* (? inland) and *rufifrons hamadryas* (? coastal), two species which are both found in the Tenimber Islands.

The chief characteristics of the typical forms of the species *rufifrons* are as follows: a rufous forehead, a grayish brown head and upper back, a well-defined rufous rump; a white chin and throat, a black breast band with scaling at its lower edge, and a dark brown tail with a distinct rufous base and a white tip. The majority of these characters are common to the forms

that have spread east and south through the Louisiade Archipelago, the Solomon Islands, the Marianas, and eastern Australia.

As *rufifrons* spread farther to the east and reached the Santa Cruz Islands and Ponape, the rufous of the lower back was at first restricted to the upper tail-coverts (in *agilis*), and then finally eliminated completely (*melanolaema*, etc.). Correlated with the reduction and disappearance of the rufous, the brownish gray of the back darkened and became blackish. At the same time, the rufous base of the tail feathers was also eliminated, and the feathers of the forehead turned white. In addition, the Ponape form (*kubaryi*) developed much heavier black scaling on the breast.

Reference may be made at this point to *Rhipidura personata*, a species endemic on Kandavu, Fiji. This species is remarkably similar to the Santa Cruz group of *rufifrons*. However, it has a plain black breast band without any scaling, and the head pattern with its white post-ocular stripe is virtually identical with that of some of the forms of the *Rhipidura spilodera* group. In spite of the isolated position of Kandavu, it seems unlikely that such an aberrant form could have developed from the otherwise rather homogeneous eastern *rufifrons* group. On the other hand the possibility cannot be ruled out altogether that *personata* is a stabilized hybrid population between some colonists of *rufifrons* and of *spilodera* stock.

A form of *rufifrons* reached Manus Island in the Admiralty Islands (*semirubra*) where it developed several peculiar characters. The whole head and back of this form have become rufous, and the tail is proportionately much shorter than that of any other subspecies of *rufifrons*.

It seems probable that *rufifrons* has twice spread westward through Torres

Strait, as two rather distinct groups occur on the islands west of New Guinea. The more specialized, and probably the earlier, of these two groups to spread to the west reached the islands south of Celebes (*celebensis* and *mimosae*), the Lesser Sunda Islands (*semicollaris* and relatives), Tenimber (*hamadryas*), and western Australia (*dryas*). These forms differ from the more typical forms in the following characters:

rufous head and back. The western Australian form (*dryas*) appears to have invaded southern New Guinea comparatively recently near the mouth of the Mimika River, and there has evolved into the not very different form, *streptophora*. All these forms are closely related to one another and form a compact subdivision of *rufifrons*.

The second western group comprises *henrici* and *squamata*, which are found on

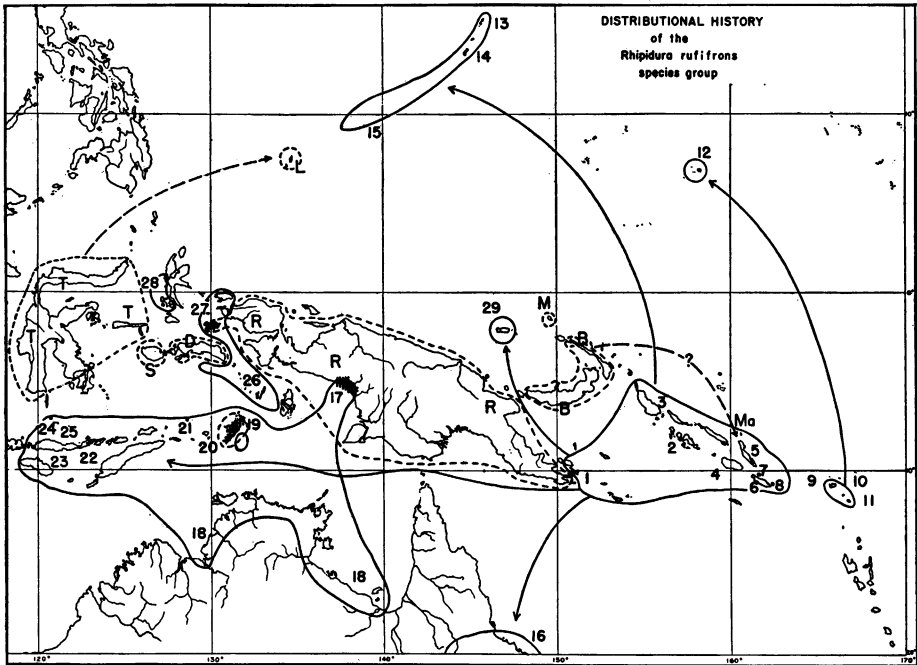


Fig. 2. Distributional history of the *Rhipidura rufifrons* group. Ranges of the primitive species indicated by broken lines and capital letters: L, *lepida*; T, *teijsmanni*; S, *superflua*; D, *dedemi*; O, *opistherythra*; R, *rufidorsa*; B, *dahli*; M, *matthiae*; Ma, *malaitae*. Heavy lines and numbers indicate the range and races of *Rhipidura rufifrons*: 1, *louisianensis*; 2, *granti*; 3, *commoda*; 4, *rufifrons*; 5, *brunnea*; 6, *rufofronta*; 7, *ugiensis*; 8, *kuperi*; 9, *agilis*; 10, *utupuae*; 11, *melanolaema*; 12, *kubaryi*; 13, *saipanensis*; 14, *uraniae*; 15, *versicolor*; 16, *rufifrons*; 17, *streptophora*; 18, *dryas*; 19, *hamadryas*; 20, *reichenowi*; 21, *elegantula*; 22, *semicollaris*; 23, *sumbensis*; 24, *celebensis*; 25, *mimosae*; 26, *henrici*; 27, *squamata*; 28, *torrida*; 29, *semirubra*. The subspecies 17, 19, and 27 overlap with the primitive species as indicated by cross hatching.

larger white tips on the tail feathers, a longer and more graduated tail, a shorter and less distinct rufous base on the tail feathers, and more rufous on the back. The Timor form (*semicollaris*) later spread to the South-West Islands and Tenimber and there gave rise to the rather aberrant forms, *elegantula*, *reichenowi*, and *hamadryas*. These forms have a paler, sometimes cream-colored forehead, and a plain

Misol, Batanta, Waigeu, and the Kei Islands. These forms are not so specialized as the forms of the other western group, and differ from the typical forms of the true *rufifrons* group chiefly in having a white forehead (but very different from that of *elegantula*), and a reduced rufous base on the tail feathers.

The subspecies from the high mountains of the Batjan and Ternate Islands, *torrida*,

is very puzzling, as it is very much like the eastern Australian subspecies, *rufifrons*, in both proportion and coloration. It is, however, separated from the latter form by a distance of several thousand miles. The subspecies that occur on the intervening islands, moreover, are *henrici* and *squamata*, which are quite different in color pattern from *torrida* and *rufifrons*. Nevertheless, it is possible that they are more closely related than it now appears, and that they have evolved in different directions, correlated with their different ecology. The subtropical Australian form,

rufifrons, and the form of the subtropical mountain forest in the northern Moluccas, *torrida*, may have evolved in one direction; and the forms inhabiting the coastal regions of low tropical islands, *henrici* and *squamata*, may have evolved more rapidly and in a different direction. Another possibility is that *torrida* is a remnant population of winter visitors of Australian *rufifrons*. At any rate, the extreme similarity of the eastern Australian and northern Moluccan subspecies is a very puzzling zoogeographical problem.

SUMMARY OF THE EVOLUTION OF THE *RUFIFRONS* SPECIES GROUP

The *rufifrons* species group undoubtedly originated somewhere in the Papuan region. From this ancestral home the group spread both eastward and westward. There were probably two distinct periods of dispersal, separated by a period of relative quiescence.

During the earlier period of dispersal the ancestral stock split into the following main groups:

1. A group that spread to the west and north, comprising *superflua* on Buru, *teijsmanni* on Celebes, and *lepida* on Palau. The form inhabiting the mountains of Seran (*dedemi*) is a specialized offshoot of this group.
2. A group that reached the Tenimber Islands in the Banda Sea, and there evolved into the aberrant species *opistherythra*.
3. The *rufidorsa* group, which probably evolved somewhere in northern New Guinea.
4. The *dahli-antonii-matthiae* series in the Bismarck Archipelago.
5. A group that spread to the south-east, and somewhere in southeastern New Guinea or the adjacent islands developed into the true *rufifrons* group.

During the second period of dispersal the forms of the true *rufifrons* group spread in all directions until they now virtually encircle the more primitive forms. The range of the true *rufifrons* group, however,

overlaps the range of the more primitive forms only in three small areas; in the Tenimber Islands, in southern New Guinea at the mouth of the Mimika River, and on the islands just west of New Guinea (Misol). During this dispersal the true *rufifrons* group split into five well-defined geographical sub-groups:

1. The typical group ranging over eastern Australia, the Louisiade Archipelago, the Solomon Islands, and the Marianas. The Batjan Island form, *torrida*, should probably be included in this group, but its resemblance to the eastern Australian form may be due to convergence.
2. The eastern group in the Santa Cruz Islands and Ponape.
3. The Manus Island form, *semirubra*, to the northwest of the typical group, should also be put in a group by itself because of its aberrant coloration and tail shape.
4. An earlier western group, which reached the islands off the south coast of Celebes, the Lesser Sunda Islands, Tenimber, western Australia, and southern New Guinea near the mouth of the Mimika River.
5. A somewhat later western group, consisting of the two forms *henrici* and *squamata* on Misol, Batanta, Waigeu, and the Kei Islands which are probably most closely related to the eastern Australian form *rufifrons* and to *torrida*.

CHARACTER GEOGRAPHY IN THE RHIPIDURA RUFIFRONS SPECIES GROUP

The student of evolution is not satisfied merely in tracing evolutionary history of populations, subspecies, and species. He wants to carry his analysis further and study the evolution of the individual attributes of which the species characters are composed. Ideally this would consist of a study of the genes controlling these characters or at least of the various gene arrangements. A promising beginning has been made in this field, both with regard to plants (e.g., *Gossypium*) and animals (e.g., *Lymantria*, *Drosophila*, *Canis*). Such "gene geography," however, is possible only in genetically well-known organisms. In all other species, and this is true for all birds, a simplified and admittedly less reliable method must be applied. It consists of studying phenotypes rather than genes, and is based on the tacit assumption that similar phenotypes of closely related forms have a similar genetic basis. In practice this method consists in the study of the geographical variation of definite characters, let us say the color of the forehead or of the tail tips, and it is therefore referred to as "character geography." The usefulness of this method, in spite of its obvious shortcomings, has been demonstrated by several recent authors (see Mayr, 1942, chap. 3 and 4 for a summary). *Rhipidura rufifrons*, a species rich in well-defined morphological characters and with a comparatively clear-cut evolutionary history, offers particularly satisfactory material for such a study.

COLOR CHARACTERS

CHIN AND THROAT: The ancestral form of the *rufifrons* species group undoubtedly had a light-colored, or white, chin and throat. Several aberrant and specialized forms, however, have independently acquired a black throat, and sometimes a black chin.

All the more primitive forms, except the *dahli-antonii-matthiae* series from the Bismarck Archipelago, have preserved the ancestral light-colored chin and throat. The throat of *dahli* is distinctly dusky, but a white malar stripe remains on either side. This tendency is carried further in *antonii*

which has a somewhat darker throat. The climax of this series is reached in *matthiae* which has a completely black chin, throat, and breast, and a broader white malar stripe.

In the species *rufifrons* all the forms from the Lesser Sunda Islands, the Moluccas, Australia, the Solomon Islands, and the Marianas have a white throat and chin, with only two exceptions. These two exceptions are the aberrant *ugiensis* on Ugi Island in the Solomons, and *uraniae* on Guam. The whole chin and throat has turned black in *ugiensis*, while in *uraniae* a very thin white malar stripe remains, and sometimes a little white on the chin.

All the forms from the Santa Cruz Islands and Ponape have acquired some black on the chin and throat. The Santa Cruz Island form, *agilis*, which is in some respects intermediate between the typical Solomon Islands forms and the southern Santa Cruz forms, has a distinct white chin, but the throat has turned black. The forms from the southern Santa Cruz Islands, *utupuae* and *melanolaema*, have a black chin and throat, and a white malar stripe, somewhat broader than that of *uraniae*. The Ponape form, *kubaryi*, has a smaller and shorter white malar stripe, but a few white feathers remain at the base of the bill.

It seems probable, therefore, that the black throat and chin has been independently acquired four times: (1) in the *dahli-antonii-matthiae* series; (2) in *ugiensis*; (3) in *uraniae*; and (4) in the *agilis-utupuae-melanolaema-kubaryi* group. The forms in groups 2, 3, and 4, are, however, all closely related to one another, even though they are members of normally white-throated groups. The method by which the black throat of *matthiae* has been acquired is rather different from that of the other three groups. The black chin and throat of *matthiae* is a development of the dusky throat of *dahli* and *antonii*, while the black throat of the other forms is merely an extension of the black breast band.

BREAST PATTERN: The more primitive forms, in general, have a uniformly colored breast without pattern. The New Guinea

form, *rufidorsa*, has a plain buffy gray breast, as has the Tenimber Islands species, *opistherythra*. The breasts of *dahli* and *antonii* are slightly more rufous in color, but otherwise very similar. In the aberrant species, *matthiae*, the black of the chin and throat extends over the breast.

marked off from the white throat, but is rather indistinctly marked off from the lower breast. The feathers of the lower breast are gray, faintly tipped with white or buffy, giving the breast a scaled appearance. The Palau species, *lepida*, has a plain, sharply defined, black pectoral

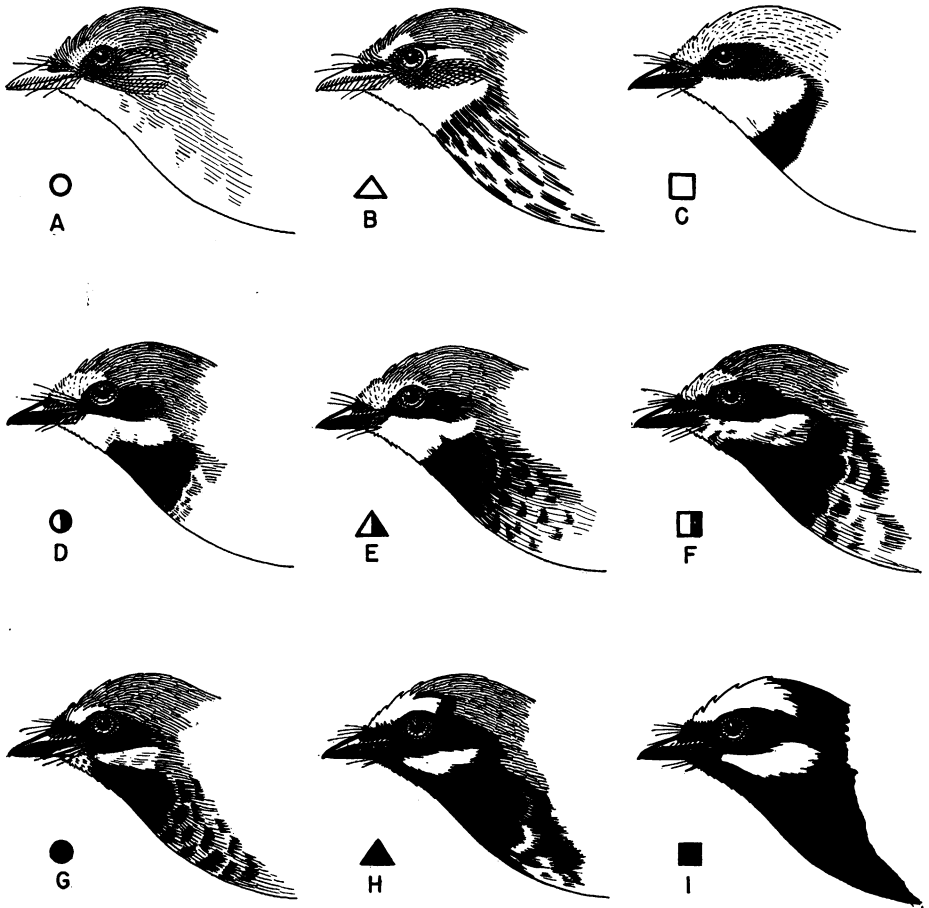


Fig. 3. Color pattern of forehead, throat, and breast in the *Rhipidura rufifrons* group. A, *rufidorsa*; B, *dedemi*; C, *lepida*; D, *celebensis*; E, *rufifrons*; F, *agilis*; G, *lubayi*; H, *utupuae*; I, *matthiae*.

A few feathers of the lower breast have, however, faint white tips.

The Buru Island species, *superflua*, has a dark gray, rather ill-defined, pectoral patch, while the rest of the breast is of a plain buff color. The Celebes species, *teijsmanni*, has a larger and darker pectoral patch. This pectoral patch is sharply

patch, while the rest of the breast is white.

The form from the mountains of Seran, *dedemi*, has a black breast band, sharply marked off from the white throat, but ill defined at its lower edge. The feathers of the lower breast have broad black shaft streaks and white edges. This gives the breast a streaked appearance, very dif-

ferent from the breast of any other form of the *rufifrons* species group.

In all the typical forms of *rufifrons* there is a distinct black breast band, sharply marked off from the throat. At the lower edge of the breast band, however, the feathers are black with white tips. The scaling is faintest in some of the western forms, such as *celebensis* and *mimosae*, which have virtually no scaling; and much the heaviest in the Ponape form, *kubaryi*,

known in the *rufifrons* species group, but present in other species of *Rhipidura*. The forehead feathers of these species are brown with a grayish brown base and do not differ from the feathers of the rest of the head. The St. Matthias Island form, *matthiae*, has, however, the whole top of the head white, except for a few feathers at the base of the upper mandible which are either plain black or black with a small white tip. The feathers forming this

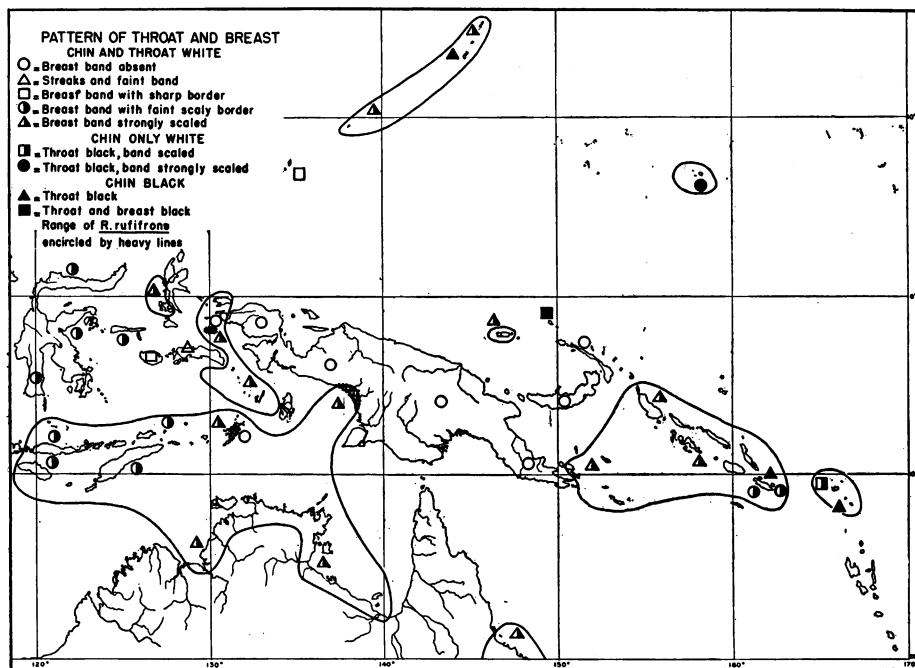


Fig. 4. Geographical variation of the color pattern of throat and breast in *Rhipidura rufifrons* and the primitive species. Areas of overlap indicated by cross hatching.

in which the scaling extends over the whole breast and part of the belly. In general, it can be said that the scaling is lightest in *rufifrons* in the western part of its range and gets progressively heavier towards the east, but there are numerous exceptions.

FOREHEAD PATTERN: Among the more primitive forms, the Bismarck Archipelago species, *dahli*, and the Tenimber Islands species, *opistherythra*, have only a small white superciliary stripe. The Seran form, *dedemi*, has in addition a white post-ocular stripe, a character otherwise un-

white head patch have small black bases, but toward the rear of the head the black base becomes more extensive, and the feathers of the nape are plain black.

The forehead feathers of the New Guinea species, *rufidorsa*, are very similar to those of *dahli* and *opistherythra*, but *rufidorsa* has a rufous instead of a white superciliary stripe. This forehead pattern of *rufidorsa* is probably very close to the ancestral forehead pattern of the true *rufifrons* group and of the *superflua-teijsmanni* group. The forehead of *superflua* has a

slightly rufous tinge, but it is otherwise very similar to that of *rufidorsa*. In the Celebes species, *teijsmanni*, the rufous forehead patch is distinctly marked off from the rest of the head and extends farther back over the eyes. The forehead feathers of this species have a distinct, but small, gray black base. The rufous of the back of the Palau species, *lepida*, has spread all over the top of the head, and no pattern is visible. The juveniles of *lepida*, however, have a plain grayish brown nape and crown, and a rufous forehead similar to that of *teijsmanni*.

All the subspecies of *rufifrons* have rufous foreheads similar to the forehead of *teijsmanni*, with the exception of three, not too closely related, groups: (1) *utupuae*, *melanolaema*, and *kubaryi*, from the eastern Santa Cruz Islands and Ponape; (2) *henrici* and *squamata* from the islands just west of New Guinea; and (3) *reichenowi* and *elegantula* from the South-West Islands. (See fig. 6.)

In the first two groups, the black base of the forehead feathers has independently been greatly extended, and the tip has turned white. Occasionally some of the feathers at the back of the forehead lack the white tips and form a black band separating the white forehead from the rest of the head. This is especially noticeable in *melanolaema*, *squamata*, and *henrici*. The size of the white forehead patch varies widely among the different forms; *kubaryi*, *henrici*, and *squamata*, have only a few white-tipped feathers at the base of the upper mandible and a white superciliary stripe. On the other hand, *utupuae* and *melanolaema* have distinct white foreheads broadly connected with the white superciliary stripe.

The forehead feathers of the Babar Island form, *reichenowi*, are virtually identical with those of the typical *rufifrons* forms, except that the tips of the feathers have become noticeably paler. This tendency is carried further in *elegantula* from Roma, Moa, and Damar Islands. This form has the apical half of the forehead feathers a pale creamy white; then there is a distinct patch of rufous, and the base of the feathers is black. Individuals of both

forms, however, are sometimes found with foreheads of an almost normal rufous color.

It is obvious, therefore, that in the *rufifrons* species group as a whole the white forehead has been acquired in three distinct ways by: (1) *matthiae*; (2) the *henrici-squamata* group, the *utupuae-melanolaema-kubaryi* group; and (3) *elegantula*. Groups 1 and 2, although only very distantly related, show marked similarities in the character of the white forehead feathers. On the other hand, *elegantula*, which is much more closely related to the forms in group 2 than any one of them is to *matthiae*, has acquired its white forehead in a very distinct manner.

BACK PATTERN: The ancestral form of the *rufifrons* species group probably had a grayish brown top of the head, nape, and upper back; and a rather ill-defined rufous lower back and rump. All the more primitive forms have retained this pattern, with the exception of *opistherythra*, *matthiae*, and *lepida*. The back of the Tenimber Islands form, *opistherythra*, is of a somewhat more grayish tone, and the rufous is virtually restricted to the rump. The St. Matthias Island species, *matthiae*, has the nape and upper back black, blending with the rufous of the lower back and rump. The Palau species, *lepida*, has a plain rufous back and head.

The typical back pattern of the true *rufifrons* group is that of the forms from the western Solomon Islands, Australia, Batjan Island, and the Marianas Islands. This pattern differs from the ancestral one in that the brown of the upper back has expanded, leaving only the rump rufous.

To the west of the typical group, in both the *celebensis-mimosae-sumbensis-semicollaris* group and the *henrici-squamata* group, the rufous is more extensive. These forms have a back pattern similar to that of most of the primitive forms, that is, a grayish brown crown, nape, and upper back, and a rufous lower back and rump. They differ from the primitive group, however, in that the rufous and the gray brown are much more clearly demarcated.

The forms from San Cristobal and the neighboring islands, *russata*, *kuperi*, and *ugiensis*, have acquired a completely

rufous back, but still retain the gray brown top of the head and nape.

In two rather distantly related groups, the *semirubra* group from Manus Island and the *reichenowi-elegantula* group from the South-West Islands, the rufous has spread over the whole top of the head, nape, and back.

The opposite tendency, namely, a reduction of rufous, appears in *rufifrons* in the eastern part of its range, in the Santa Cruz Islands, and Ponape. The rufous of the back is first restricted to the tail-coverts in the Santa Cruz Island form, *agilis*, and then is eliminated completely, although a trace of brown still remains on the tail-coverts of the forms (*utupucae* and *melanolaema*) from the southern Santa Cruz Islands. Correlated with this reduction and final disappearance of the rufous, the grayish brown color of the back darkens and becomes blackish.

In the *rufifrons* species group as a whole, the variation in the back pattern is due to the fluctuating proportions of the brownish gray and the rufous on the back. This fluctuation is largely independent of the geographical distribution of the various forms. For instance, the whole back has become rufous in four distantly related, and geographically widely separated groups: (1) in the *reichenowi-elegantula* group; (2) in *semirubra*; (3) in *lepida*; and (4) in the *russata-kuperi-ugiensis* group. Although the gray brown has several times spread over the larger part of the back, the rump always remains rufous, except in the *agilis-utupucae-melanolaema-kubaryi* series.

The black of the nape and upper back of *matthiae* is merely an extension backwards of the black on the breast and throat of this species. The amount of rufous on the back is not reduced, and the whole process has nothing in common with the darkening of the back of the *agilis-utupucae* series.

TAIL PATTERN: The most primitive tail pattern seems to be that of *superflua* on Buru Island. The tail of *superflua* is a plain dark brown with a variable rufous tip (7.1 per cent to 16.8 per cent of the total length of the outermost tail feathers)

and an indistinct rufous base. The Palau species, *lepida*, has a similar tail, but the rufous tip measures 32 per cent of the total length of the outermost tail feathers. The tail of the species from the mountains of Seran, *dedemi*, has a rather small and indistinct rufous tip, somewhat like that of *superflua*. The rufous at the base of the tail feathers, however, extends farther up the tail, forming about 35 per cent of the total length of the tail feathers. The Tenimber Islands form, *opistherythra*, is unique in the whole species group in the fact that all pattern on the tail has been lost, and the tail is a plain gray brown.

The New Britain form, *dahli*, has a medium-sized rufous tip, 24 per cent of the total length of the outermost tail feathers, and a rufous base that extends over 52 per cent of the total length of the tail. The rufous tip fuses with the rufous base in the New Ireland form, *antonii*, and only an indistinct darkish area remains on the central tail feathers. The culmination of this series is reached in the St. Matthias Island species, *matthiae*, which has a plain rufous tail without any brown, and in the possibly related species *malaitae* (Malaita, Solomon Islands).

The species from New Guinea, *rufidorsa*, has a rather specialized tail pattern, insofar as the tips of the tail feathers are white (20 per cent to 24 per cent of the length of the outermost tail feathers), and are very distinctly marked off from the rest of the tail. The base of the tail of *rufidorsa* has merely an indication of rufous along the edge of the feathers.

The typical tail pattern of the species *rufifrons* is that of the forms from the western Solomons, the Louisiade Archipelago, Manus Island, and the Marianas Islands. This pattern is, on the whole, very similar to that of *rufidorsa*, with a distinctly marked off white tip and a rufous base. The white tip is, however, somewhat smaller, varying from 15 per cent to 20 per cent of the total length of the outermost tail feathers; and the rufous base is both more extensive and more distinct, measuring from 32 per cent to 45 per cent of the total length of the tail. The Batjan Islands form, *torrida*, and the western

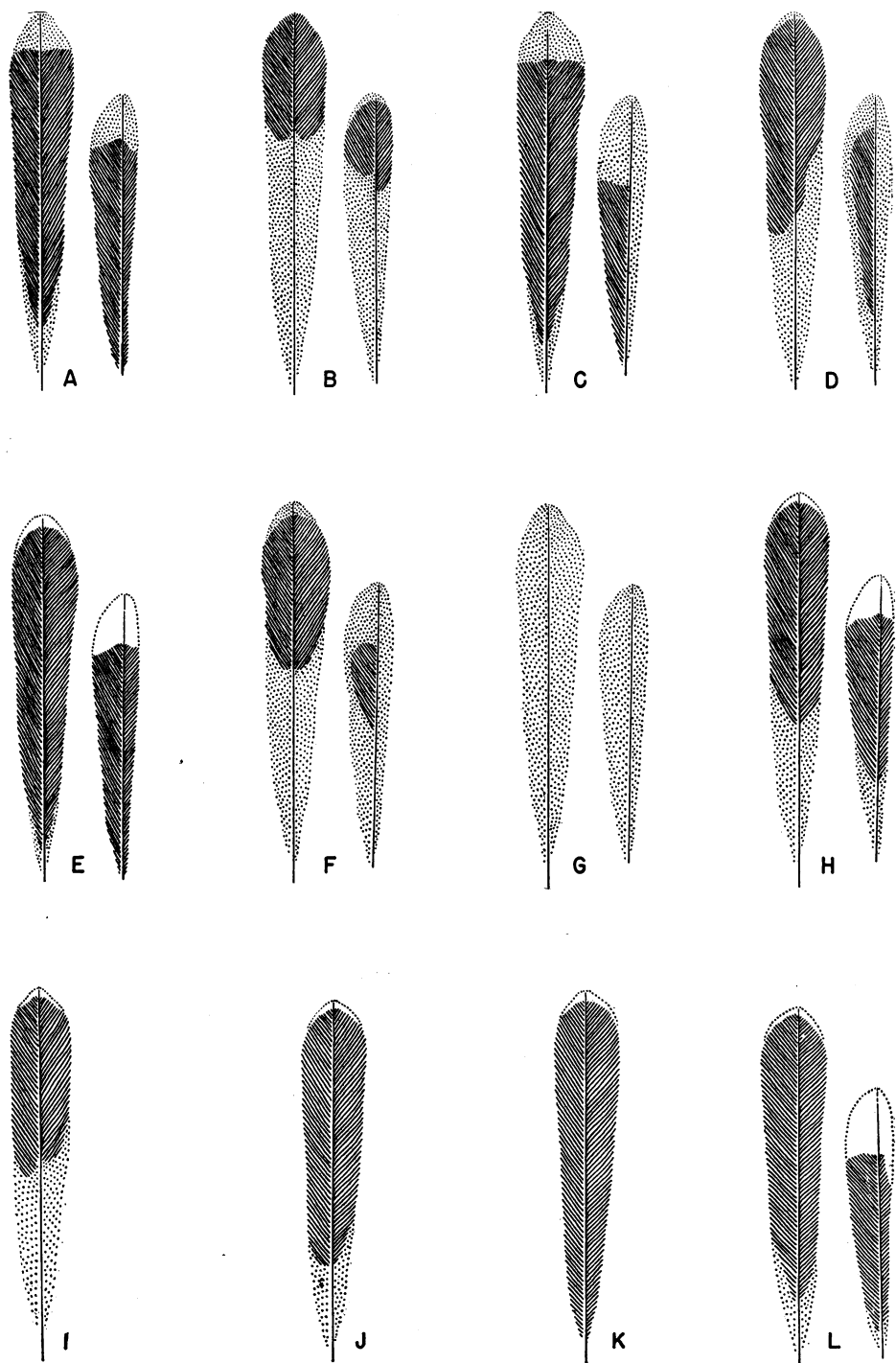


Fig. 5. Tail pattern in the *Rhipidura rufifrons* group. The striped parts of the feathers are brown; the dotted parts are rufous red. A, *superflua*; B, *teijsmanni*; C, *lepada*; D, *dedemi*; E, *rufidorsa*; F, *dahli*; G, *matthiae*. Subspecies of *Rhipidura rufifrons*: H, *commoda* (typical for eastern forms); I, *rufifrons*; J, *rufifrons*; K, *utupuae* (Santa Cruz group); L, *sumbenis* (typical for western forms).

Australian form, *rufifrons*, have an identical white tip, but the rufous base extends farther up the tail, forming approximately 52 per cent of the total length.

In the Malaita and Guadalcanal forms, *brunnea* and *rufofronta*, however, the extent of the rufous base is reduced to approximately 27 per cent of the total length of the tail, and is rather indistinctly demarcated. The forms from San Cristobal, Ugi, and Santa Anna Islands (*russata*, *ugiensis*, and *kuperi*) have a rufous base intermediate in length between that of the typical forms and that of *brunnea* and *rufofronta*. Both these groups have the white tip very similar to that of the typical western Solomon Islands forms.

The tail feathers of the form from Santa Cruz Island, *agilis*, also have a reduced rufous base. This tendency is carried further in the forms from the southern Santa Cruz Islands, *utupuae* and *melanolaema*, which have only a very faint indication of brown at the base of the tail. Even this is lacking in the Ponape form, *kubaryi*, which has a blackish base. The white tips of the tail feathers of these forms are similar to those of the preceding groups.

The two forms from the islands just west of New Guinea, *henrici* and *squamata*, have the white tips very much like those of the typical forms, and the rufous base, measuring from 25 per cent to 30 per cent of the total tail length, is indistinctly delimited. This pattern is very much like the tail pattern of *rufofronta* and *brunnea*, but was, of course, independently acquired.

The tail pattern of the other western group, the *celebensis-sumbensis-elegantula* series, is quite specialized. The white tip is definitely larger than that of any of the preceding groups, varying from 25 per cent to 29 per cent of the total length of the outermost tail feathers. The rufous base of the tail is small and rather indistinct, usually measuring barely a fifth of the total length of the tail. The white tip of the tail feathers reaches its highest development in *dryas* from western Australia, in which it measures 36 per cent of the total length of the outermost tail feathers. In all other respects the tail pattern of *dryas* is identical with that of *semicollaris*. In

this group, as a whole, the brown of the tail feathers has a grayish tinge.

It is obvious from the above that the variation in the tail pattern of the *rufifrons* species group is due chiefly to the variation in the length and distinctness of the rufous base and the variation in size, distinctness, and color of the tips of the feathers.

The length of the rufous base varies widely among the different forms of this group. For instance, the St. Matthias Island form, *mathiae*, has a plain rufous tail, as the rufous base has been extended until it has met and fused with the rufous tip. The Ponape form, *kubaryi*, represents the other extreme. The rufous has been completely eliminated from the tail, which has a plain dark brown base. Virtually every intermediate stage between these two extremes can be found in one or the other of the various *rufifrons* forms. This variation is, in many cases, independent of both relationship and geographical distribution, as closely related forms on neighboring islands may have the rufous base of very different extent. Sometimes the rufous base is not distinctly marked off from the rest of the tail, and gradually blends into the dark brown of the central portion of the tail. This occurs more often in the primitive forms than in the more advanced ones.

The majority of the more primitive forms have rufous-tipped tails. The length of this rufous tip varies from approximately 2 per cent to 32 per cent of the total length of the outermost tail feathers. In *lepada*, *dedemi*, and *dahli*, it is fairly distinctly marked off from the rest of the tail, but in the other forms there is no distinct line of demarcation.

All the races of *rufifrons* and *rufidorsa* have white-tipped tails. The white tip is always distinctly marked off from the rest of the tail, and it does not vary greatly in length. With one exception, the white tip never measures less than 15 per cent or more than 29 per cent of the total length of the outermost tail feathers. The only exception is the form from western Australia, *dryas*, which has a white tip measuring 36 per cent of the total length of the outermost tail feathers. Even so the variation in the length of the tip is far less

in the white-tipped forms than in the rufous-tipped forms.

SIZE, RELATIVE TAIL LENGTH, TAIL SHAPE

Size and proportions vary geographically as decidedly as the characters of color pattern. Unfortunately the weights are known of only so few forms of the *Rhipidura rufifrons* group that this most reliable indicator of size (Amadon, 1943) is not available to us. Instead we must use as size indicator the length of the wing which is known to be moderately well correlated with general body size within a restricted taxonomic group of sedentary birds.

WING LENGTH (TABLE 1): Small-sized and large-sized populations, that is, birds with a long and with a short wing, are found in nearly every section of the *rufifrons* group. Among the primitive species, *superflua*, *rufidorsa*, and *dahli* are small (mean of wing length of adult males 66, 64–65, 66–67),¹ *teijsmanni*, *opistherythra*, *matthiae*, and *dedemi* are medium (72–76), and *lepida* is large (79). In the species *rufifrons* also, small-sized and large-sized populations occur in various parts of the range. *R. r. russata* and *kuperi* (eastern Solomons), *uraniae* and *saipanensis* (Marianas), and *celebensis* and *mimosae* (Flores Sea) are small. Most subspecies are medium (70–75), but *louisianensis-granti* (Louisianes, central Solomons), *kubaryi* (Ponape), *utupuae* (Santa Cruz group), *rufifrons* (eastern Australia), and *elegantula* (Wetar group) are large with a mean wing length of over 75.

RELATIVE TAIL LENGTH (TABLE 1): In the conventional definition of the genus *Rhipidura* it is stated that the tail is longer than the wing. This is indeed true for the majority of the species and subspecies of the genus, but there are a number of notable exceptions. In the *Rhipidura rufifrons* group, for example, the tail index² is 99 in *dedemi* (and only 94.5 in males of *malaitae*). There are four well-defined population groups in the *rufifrons* group that are characterized by a short tail: one is on Seran (*dedemi*, 99), one in the Bis-

marck Archipelago (*dahli*, 106; *antonii*, 104; *matthiae*, 103), one on Santa Cruz Island (*agilis*, 106), and one in the Admiralty Islands (*semirubra*, 103.5). Most of the species and subspecies have a medium long tail (index 108–120). Exceptionally long tails have developed only twice, in the primitive species *opistherythra* (Tenimber, 129.5) and in the western subspecies of *celebensis-semicollaris-elegantula-dryas* (125–135). Most of the geographical variation of these proportions is quite irregular, as is to be expected in island birds. However, there are a few indications of progressive, clinal changes, as, for example, in the *agilis* (106)-*utupuae* (113.5)-*melanolaema* (116.6)-*kubaryi* (119.1) line and in the *dahli* (106)-*antonii* (104)-*matthiae* (103) line. (Fig. 6.)

TAIL SHAPE (TABLE 1): The shape of the tail varies from rounded to strongly graduated. This tail shape can be expressed numerically, by giving the length of the outermost tail feather as percentage of the length of the central feather. A study of these figures (table 1) shows that a fairly close correlation exists between tail shape and tail length. If these figures are plotted on a system of coordinates, the points of the various species and subspecies are found to be scattered along a single diagonal line. This correlation can be expressed as follows: the longer the tail, the more graduated it is. *Rhipidura dedemi* with the shortest tail (99) has also the least graduated tail (outermost tail feather 86.5 per cent of central tail feather). *R. opistherythra* (129.5) has the most graduated (62.7). Very strongly graduated tails are also found in the *celebensis-dryas*, *henrici-squamata*, in the *utupuae-melanolaema-kubaryi*, and in the *louisianensis-granti* groups (some of them with a medium long tail). Rather rounded tails are found in *teijsmanni*, *dahli-antonii*, *commoda-brunnea-rufofronta*, *rufifrons-torrada*, *agilis*, and *semirubra*. This group includes all the short-tailed and a few medium-tailed, but none of the long-tailed forms.

GEOGRAPHICAL VARIATION IN THE ECOLOGY

As mentioned previously, there is some evidence of ecological segregation at the three places where different species of the

¹ All measurements were taken by M. Moynihan.

² Length of tail as expressed in percentage of wing length.

rufifrons group overlap. Such differences in habitat preference of closely related sympatric species are the rule, as pointed out recently by Lack (1944). The selective advantage of this reduction of mutual competition is at once apparent, but to base on this ecological difference a theory of sympatric speciation, as was done by several older as well as recent authors, is by no means justified. In the case of the three overlaps in the *rufifrons* group, it is

of the *rufifrons* group seem to be very common, although the available data are scanty.

Among the primitive species, *superflua* (above 800 meters), *teijsmanni* (1000-2300 meters) and *dedemi* (also *malaitae*) are inhabitants of the mountain forest. *R. lepida*, *opistherythra*, and *matthiae*, three species that are found on low islands, seem to be restricted to the lowland forest. Two species, *rufidorsa* and *dahli*, seem somewhat

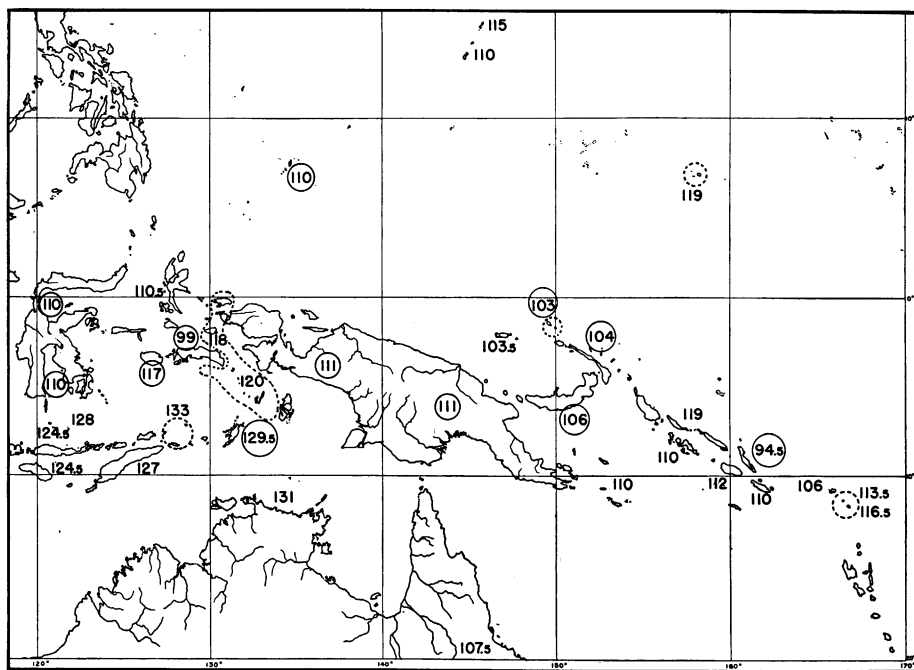


Fig. 6. Geographical variation of the relative tail length in the *Rhipidura rufifrons* group. Figures inside the circles refer to primitive species. The ranges of the subspecies with a white forehead are encircled by broken lines.

quite evident that the contacts are of recent date and the overlapping populations are of highly different phylogenetic age and origin. In all three cases the overlap occurs between a "primitive" species of the *rufifrons* group and a "recent" subspecies of the species *rufifrons*.

Furthermore, it can be shown conclusively that the ecological difference existed even before the two populations came in contact. In fact, ecological differences between the various populations

less narrow in their ecological requirements. They range from the lowlands well into the mountains (1000 meters), and although the primeval forest is their main habitat they are also found along the edge of the forest. It is obviously no coincidence that these forms from the largest islands (New Guinea, New Britain) have the widest ecological tolerance.

Little is known about the exact habitat requirements of the 29 subspecies of *Rhipidura rufifrons*, but what is known

indicates striking ecological differences. Two races seem to be entirely restricted to the mountains, *torrida* (above 600 meters) in the northern Moluccas and *brunnea* (above 700 meters) on Malaita. It is noteworthy that *rufifrons*, which extends into the temperate parts of Australia, is the nearest relative of *torrida*. On the other hand, *brunnea* is exceedingly closely related to *rufifrons* and *commoda*, two forms of the lowlands and the coastal zone. Little is recorded of the habitat preference of the forms of the Santa Cruz group and of Micronesia. At least some of the forms, for example *kubaryi*, live in the true primeval forest and ascend fairly high into the mountains. Other forms are found on small or very small islands (*lousiadensis*, *kuperi*) and seem to be most common near

the coast. *R. r. semirubra* (Manus) lives inland in true forest and second growth.

West of New Guinea all subspecies of *rufifrons* (except *torrida*) are lowland birds, and most of them are restricted to small islets (*henrici*, *squamata*, *celebensis*, *mimosae*) or to the coastal formations and mangrove belts of larger islands. However, *sumbensis* and *semicollaris* (up to 2000 meters) have been found from the coast up to the mountains. All these forms, however, seem to live in much more open formations than the subspecies from the islands east of New Guinea.

The striking geographical variability in the habitat preference of the 29 races of *R. rufifrons* furnishes a favorable basis for further spreading.

CONCLUSIONS

TAXONOMY

The *Rhipidura rufifrons* group consists of two sections. One is composed of eight (or, if *malaitae* is included, nine) allopatric species, all of which are separated by pronounced inter-species gaps. Most of these species are monotypic or composed of very slight subspecies. The whole picture of this section is that of an old group, now stagnant as far as evolution is concerned, remnants of an early aggressive phase of the ancestral *rufifrons* stock. The second section consists of the eminently successful species *rufifrons* with its 29 subspecies. Its enormous range is several times as large as that of the combined ranges of all the species of section 1. It presents the prototype of a species at the peak of evolution. Except for some sections of the mainlands of Australia and New Guinea, all the races live on smaller or larger islands. Many of these island races are separated from one another by clear-cut diagnostic key characters. Ornithologists of the "old school" who insist on intergradation as an indispensable subspecies criterion would be forced to keep *rufifrons*, *russata*, *ugiensis*, *uraniae*, *versicolor*, *agilis*, *utupuae*, *melanolaema*, *kubaryi*, *semirubra*, *squamata*, *semicollaris*, *celebensis*, *elegantula*, *hamadryas*, and *dryas*,

as separate species. Each of these 16 forms can be identified by the description without reference to comparative material and does not intergrade with any of the other 15 forms. The superiority of the modern polytypic species concept over the "pulverization method" is at once apparent. It alone brings out the close relationship of these forms and delimits them as a group against the much more distinct other species of the rich genus *Rhipidura*.

CHARACTER ANALYSIS

Character progressions of a gradual or clinal type are typical for continental species, as Huxley and others have pointed out. Irregularity of variation, on the other hand, is typical for island populations. Basic potentialities of a species are often realized independently on islands situated far apart from one another (Mayr, 1942). This principle is well illustrated by the geographical variation of the various characters in the *R. rufifrons* species group, as described in detail above in the discussion of character geography. A black throat, for example, has been acquired independently four times (fig. 4). A white forehead also was acquired independently by four unrelated subspecies groups (fig. 6). Similar observations can be made for

the rufous color of the back, tail pattern, relative length of tail, and tail shape. The protean aspect of *Rhipidura rufifrons* may be one of the clues to the success of this widespread species, indicating an unusual ability to select from its store of genic variability the particular combination that is best suited for a particular locality. This assumption is somewhat contradicted by the uniformity that is characteristic for most other successful widespread species. Perhaps there are two ways to achieve such success, either having a genotype that is suited for all sorts of situations, or having a genotype with a great store of "inter-changeable genetic spare parts" which permit quick adaptation to specific situations.

ZOOGEOGRAPHY

Anyone who has seen a Rufous-fronted Fantail in the field, with its short rounded wings and weak flight, feels certain that the bird could not possibly fly for more than a few miles before becoming completely exhausted. However, appearances are utterly deceiving, as so often in the evaluation of dispersal faculties, since *R. rufifrons* is one of the most successful transoceanic colonizers. The aggressiveness of its colonizing activities is indicated by the fact that the species group undertook no fewer than three independent colonizations of Micronesia (fig. 2): (1) *lepida* (Palau), (2) *uraniae*, etc. (Marianas, Yap), and (3) *kubaryi* (Ponape). The Moluccas likewise were colonized at least three times: (1) *superflua-dedemi* (Buru, Seran), (2) *squamata-henrici* (Banda-Kei), (3) *torrida* (Batjan-Ternate). Some of the colonization flights must have been of considerable length, as for example those which established the following races and species: *lepida* (Palau, from Celebes or southern Moluccas), *uraniae* (Guam, from Solomon Islands), *kubaryi* (Ponape, from Santa Cruz), *torrida* (Ternate and Batjan, ? from eastern Australia). Interesting also is the fact that at least two colonizations passed through Torres Strait, an earlier one of the *celebensis-semicollaris* group, and a later of the *squamata-henrici* group. The two colonizations took place

probably before and after one of the Pleistocene connections between Australia and New Guinea.

On the reverse side, it may be mentioned that the *R. rufifrons* group is unaccountably absent from several islands in the midst of the general range, for example, from Biak, Halmahera, Obi, and from most of the D'Entrecasteaux and Aru Islands. Finally, it must be emphasized that the present distributional picture of the group is consistent with the assumption that no major changes of the distribution of water and land have occurred in the area. The entire distribution can be explained without the construction of a single land bridge.

ECOLOGY

The most striking aspect of the ecology of the *R. rufifrons* species group is the extraordinary geographical variation of habitat requirements. As described above in more detail, there are species and subspecies restricted to the mountains, others to the lowlands, others extending from the sea coast to the mountains. Some are restricted to the deep forest, others occur both in forest and second growth, while still others seem to prefer mangroves, coastal scrub, and other marginal habitats. Except for open grasslands and other open arid habitat, there is hardly any major type of landscape in the Australo-Papuan region that is not occupied by one or another member of the *Rhipidura rufifrons* group. This fact must be considered together with the other fact, that at least 16 of the 29 subspecies of *R. rufifrons* have nearly reached the species level, as far as the external morphology is concerned. They can certainly be classified as incipient species. The two factors together have set the stage for a potential outburst of "explosive speciation." If through some geological event the now insular ranges of these various forms should become joined together, we would have at least a dozen units, all closely related, but all sufficiently distinct to permit the assumption that they have acquired some degree of sexual isolating, and all of them with a considerable degree of, if not complete, ecological

divergence. The simultaneous transformation of the polytypic species *R. rufifrons* into 12 new species would be a distinct possibility under such circumstances. Such a sequence of events should be carefully considered by those who postulate mysterious cosmic events of "explosive speciation" to explain the existence of sympatric species swarms.

Of the nine species of the *Rhipidura rufifrons* group, only one (*rufifrons*) has entered a second phase of aggressive expansion. Although *rufifrons* has colonized an enormous area during this period of expansion, it has curiously stayed out of nearly all the islands occupied by the other eight species of the species group. This is true for Palau (the home of *lepida*), Celebes (*teijsmanni*), Buru (*superflua*), Seran (*dedemi*), New Britain and New Ireland (*dahli*), and St. Matthias (*matthiae*). The wide range of *rufidorsa* (New Guinea and adjacent islands) is barely touched by *rufifrons* at two spots (Mimika River, Misol) (fig. 2). Tenimber Island is the only place where a wide overlap seems to exist between two species of the *rufifrons*

group (*opistherythra* and *rufifrons hamadryas*). Even in these cases of geographical overlap, the evidence points to the existence of ecological segregation, as described above.

Finally an interesting parallel must be pointed out between phylogenetic age and ecological behavior. The "primitive" species of the *rufifrons* group are invariably inhabitants of the mountain forest or of the primeval lowland forest and its edge. Of the races of *R. rufifrons*, however, many are restricted to coastal plant formations, second growth, and other non-climax plant communities. Some of these races (particularly the *louisiadensis*, *squamata*, and *celebensis* groups) are the only ones that have been able to colonize the very small coral islets off the coasts of the larger islands. Much of the recent spreading of races of *R. rufifrons* seems to have occurred via such habitats. This ecological behavior is to some extent paralleled in the plant kingdom, where widely and recently spread forms with a young and active evolutionary history also seem to favor disturbance communities, while the older species are often restricted to the climax.

TABLE 1

	WING	TAIL SHAPE	RELATIVE TAIL LENGTH ^a	
<i>superflua</i>	66.25 mm.	73.7	117	m
<i>teijsmanni</i>	70.4-74.0	77.7	110	m
<i>lepida</i>	79	73.3	110	m
<i>dedemi</i>	75.5	86.5	99	s
<i>opistherythra</i>	72.66	62.7	129.5	l
<i>rufidorsa</i>	64-65	71.7-72.7	111	m
<i>d. dahli</i>	66	74.5	106	s
<i>d. antonii</i>	67	78.7	104	s
<i>matthiae</i>	73	74.1	103	s
<i>rufifrons</i>				
<i>louisiadensis, granti</i>	76, 77	69.8, 71.1	110	m
<i>commoda</i>	71.7	76.1	119	m
<i>brunnea, rufifrons</i>	74, 75	76.6, 74.2	112	m
<i>russata, kuperi</i>	68-69	73.9, 73.2	110	m
<i>ugiensis</i>	71	71.8	109	m
<i>rufifrons, torrida</i>	78, 72	78.2, 77.4	107.6, 110.5	s m
<i>uraniae, saipanensis</i>	69	73.4, 72.2	110, 115	m
<i>agilis</i>	71	78.7	106	s
<i>utupuae</i>	78	65.7	113.5	m
<i>melanolaema</i>	72	68.6	116.6	m
<i>kubaryi</i>	76	64.6	119.1	m
<i>semirubra</i>	71.2	76.1	103.5	s
<i>henrici, squamata</i>	74, 75	63.2, 62.8	120, 118	m
<i>celebensis, mimosae</i>	66.5, 71	71.9, 68.5	124.5, 128	l
<i>sumbensis, semicollaris</i>	72.5, 70	66.1, 64	124.7, 127	l
<i>elegantula</i>	75.5	64.4	133	l
<i>dryas</i>	71.3	67.9	131	l

s, Short (up to 109); m, medium (110-119.9); l, long (120 or more).

BIBLIOGRAPHY

AMADON, DEAN

1943. Bird weights as an aid in taxonomy. *Wilson Bull.*, vol. 55, no. 3, September, pp. 164-177.

LACK, DAVID

1944. Ecological aspects of species-formation in passerine birds. *Ibis*, vol. 86, July, pp. 260-286.
1945. The Galapagos finches (Geospizinae). A study in variation. *Occas. Papers California Acad. Sci.*, no. 21, May 30, 159 pp.

1946. Darwin's finches. Cambridge, Cambridge University Press. [In press.]

MAYR, ERNST

1931. Birds collected during the Whitney South Sea expedition. XVI. Notes on fantails of the genus *Rhipidura*. *Amer. Mus. Novitates*, no. 502, November 9, pp. 1-21.
1942. Systematics and the origin of species. New York, Columbia University Press, 334 pp.

