American Museum Novitates

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK 24, N.Y.

NUMBER 1770 MAY 31, 1956

# The Systematics of the New Guinea Manucode, *Manucodia ater*

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## INTRODUCTION

*Manucodia ater,* one of the most primitive of the birds of paradise, occurs in tropical New Guinea and its principal satellite islands. Three races are currently recognized (Mayr, 1941, pp. 167–168): (1) *ater* of the western islands near the Vogelkop and the mainland of New Guinea east to the Huon Peninsula in the north, and to the Noord River in the south; (2) *subalter* of the Aru Islands and the southeastern New Guinea mainland west in the south to the region of the Noord River and in the north to the Kumusi River; (3) *alter* of Tagula Island (= Sudest Island) off the southeastern tip of New Guinea.

A preliminary examination of the extensive American Museum series from virtually all of the above localities, as well as recently collected material from the mainland of New Guinea, indicated that each population differed slightly from every other one, with the populations grading one into the other until at the extremes of the cline two distinct species seemed to be represented. The evidence suggested that perhaps (1) the populations should be lumped in whole or in part, or (2) the geographical ranges of some of the subspecies were in need of revision. The present study, which began with the afore-mentioned taxonomic problems in view, was then enlarged to include a number concerning speciation.

The author's attention was first called to this matter by Mayr, who pointed out that Rand (1942, p. 349) had identified specimens from the Fly River region as *ater,* the western race, and not as *subalter* as they should have been to fit with the ranges given in Mayr's "List of New

Guinea birds" (*op. cit.*). Junge (1939, p. 91) also considered Fly River birds the same as those from the Arfaks. Rothschild (1932), de Schauensee (1940), and Gyldenstolpe (1955) have also examined this peculiarly variable species.

I am most grateful to Drs. Mayr and Amadon for many valuable suggestions during the course of this study and for reading the manuscript. Also, I should like to thank Mr. R. W. Sims, who sent data pertaining to material in the British Museum, and Mr. W. Holmquist, who drew the graphs and maps.

## MATERIALS AND METHODS

Geographical variation of size and color, color differences due to age, sexual dimorphism, molt, and breeding cycles were some of the facets that entered into this study, which was based on 55 males (including the types of *subalter* and *alter*), five males?, 47 females, one female?, and observations made in the field by Dr. A. L. Rand (who was the first to observe the breeding habits of *Manucodia ater*) and by the author.

For a time it appeared that sibling species might be involved, and, as a result, data relating to molt, breeding seasons, weather, etc., were amplified beyond the requisites of the taxonomic problem.

## GEOGRAPHICAL VARIATION OF SIZE

Figures 1–4

From the measurements given in figures 1–4 it is apparent that the populations inhabiting the trunk of New Guinea are generally smaller than the geographically isolated populations of the satellite islands. Also, they average smaller (wing, tail, bill, tarsus) than populations inhabiting the more restricted peninsular regions of eastern and, to a lesser degree, western New Guinea.

The consistently larger size of the insular populations is of particular interest, and, in view of the discontinuous nature of their distribution, it strongly suggests that they have been subject to parallel variation under parallel conditions. One such condition might very well have been the relatively cooler environment of oceanic islands. This might have given rise to largeness in accordance with Bergmann's rule.

Another possible condition is that the island groups represent older populations which, because of the lesser pressures of their insular habitats, have varied less, and at more constant rates, whereas the mainland populations, having been subjected to greater selective pressures, have

varied more from the original form. The peninsular populations would be representative of intermediate stages.

## GEOGRAPHICAL VARIATION IN COLOR OF PLUMAGE

The dark plumage coloration was found to vary from glossy violet to dull glossy greenish. The greatest difference occurred in the flanks and

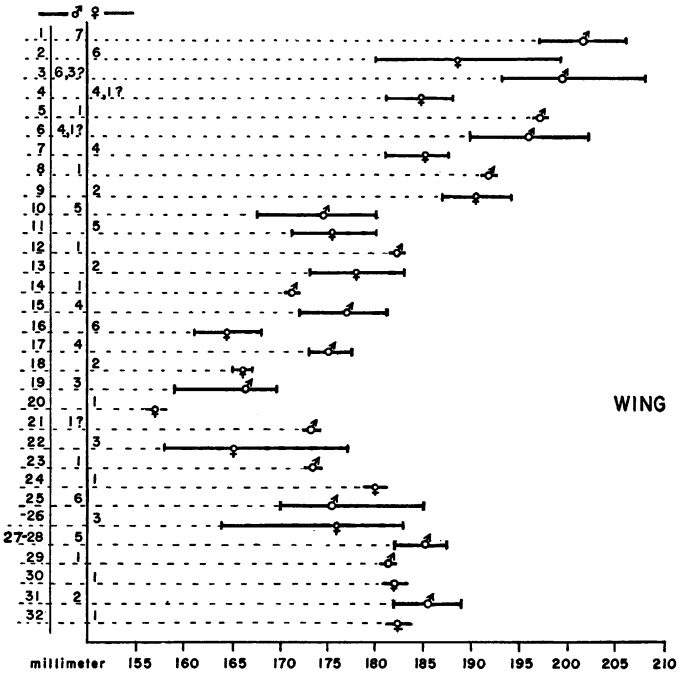


FIG. 1. Geographical variation in size of the wing in *Manucodia ater*. *Key to localities*: 1, 2, Tagula Island; 3, 4, Aru Island; 5, Sariba Island; 6, 7, Port Moresby to Yule Island; 8, Mailu Island; 9, Samarai Island; 10, 11, Fly River region; 12, 13, Snow Mountains; 14, Sattleberg; 15, 16, Madang, Sepik River, Wewak; 17, 18, Hollandia; 19, 20, Takar; 21, 22, Idenburg River; 23, 24, Wasior, Wandammen Mountains; 25, 26, Vogelkop; 27, 28, Waigeu Island; 29, Gebe Island; 30, 31, Misol Island; 32, Batanta Island.

abdomen, with the Tagula Island specimens being slightly but distinctly more glossy iridescent purple than any other, and with the feathers of the chest somewhat longer and with slightly more highly developed lanceolate feathering.

On the average, island populations were found to differ from those of the mainland by having the plumage much more purple and more glossy, less dull glossy greenish. Birds with bluish plumage occurred every-

where, but greenish plumage in adult birds was found to be virtually restricted to birds inhabiting the trunk of the mainland and the Vogelkop peninsula.

Plumage coloration was analyzed by grading in direct sunlight with the observer facing towards the sun and viewing the specimen from head towards tail. One hundred and eight skins were used. The most generally violet-colored birds formed one extreme of the gradient and the most generally greenish the other.

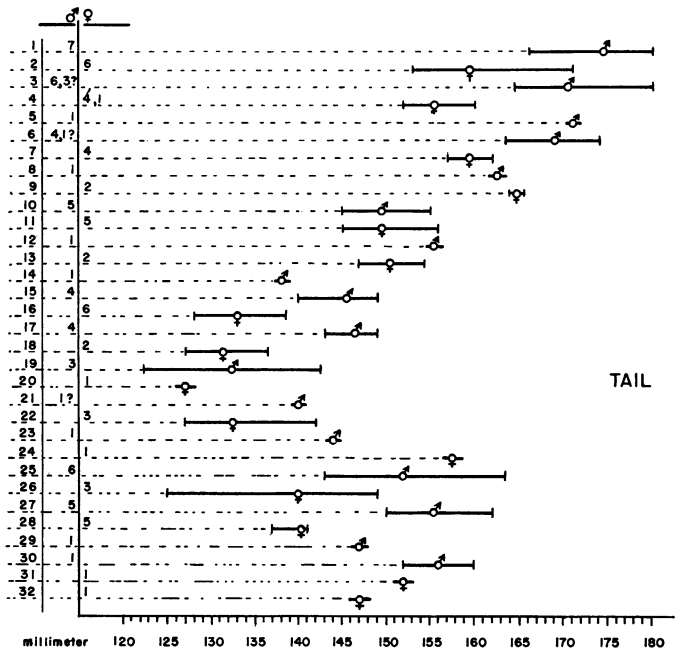


FIG. 2. Geographical variation in size of the tail in *Manucodia ater*. *Key to localities*: 1, 2, Tagula Island; 3, 4, Aru Island; 5, Sariba Island; 6, 7, Port Moresby to Yule Island; 8, Mailu Island; 9, Samarai Island; 10, 11, Fly River region; 12, 13, Snow Mountains; 14, Sattleberg; 15, 16, Madang, Sepik River, Wewak; 17, 18, Hollandia; 19, 20, Takar; 21, 22, Idenburg River; 23, 24, Wasior, Wandammen Mountains; 25, 26, Vogelkop; 27, 28, Waigeu Island; 29, Gebe Island; 30, 31, Misol Island; 32, Batanta Island.

DORSAL COLORATION: Forty-six birds fell in the violet group. Of these, all but 12 were from the satellite islands: Tagula (12 specimens), Samarai (one), Mailu (one), Yule (two), Aru (nine), Misol (one), Batanta (one), and Waigeu (seven). Only four of the 12 from New Guinea proper were from the trunk of the island. The other eight were

divided between the Vogelkop and the southeastern peninsula (Port Moresby region).

Blue-backed birds, of which there were 41, occurred everywhere without apparent correlation to geography. Specimens were found from the extremes of the range of the species: Tagula Island, Aru Islands, Hollandia, and Gebe Island.

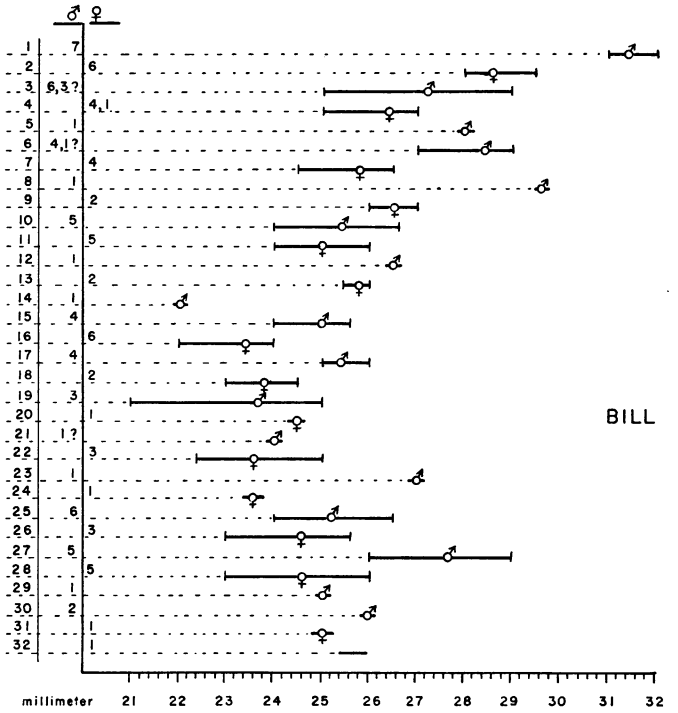


FIG. 3. Geographical variation in size of the bill in *Manucodia ater*. *Key to localities*: 1, 2, Tagula Island; 3, 4, Aru Island; 5, Sariba Island; 6, 7, Port Moresby to Yule Island; 8, Mailu Island; 9, Samarai Island; 10, 11, Fly River region; 12, 13, Snow Mountains; 14, Sattleberg; 15, 16, Madang, Sepik River, Wewak; 17, 18, Hollandia; 19, 20, Takar; 21, 22, Idenburg River; 23, 24, Wasior, Wandammen Mountains; 25, 26, Vogelkop; 27, 28, Waigeu Island; 29, Gebe Island; 30, 31, Misol Island; 32, Batanta Island.

Of the total of 21 green-backed birds, 18 came from the trunk of the mainland (13 from the north coast between Sattleburg and Takar; five from the Fly River Delta), and the remaining three came from the Vogelkop (Manokwari region = Dorey). None was found in the extensive satellite island series!

To express the color variation numerically the sample was divided into three classes, with a value of 1 given to green, 2 to blue, and 3 to violet. The quantitative results are shown in figure 5. Taken as a whole, the mainland populations (including the off-shore islands of southeastern New Guinea), with a value of 1.92 as against 2.77 for the island populations, show moderately stepped variations.

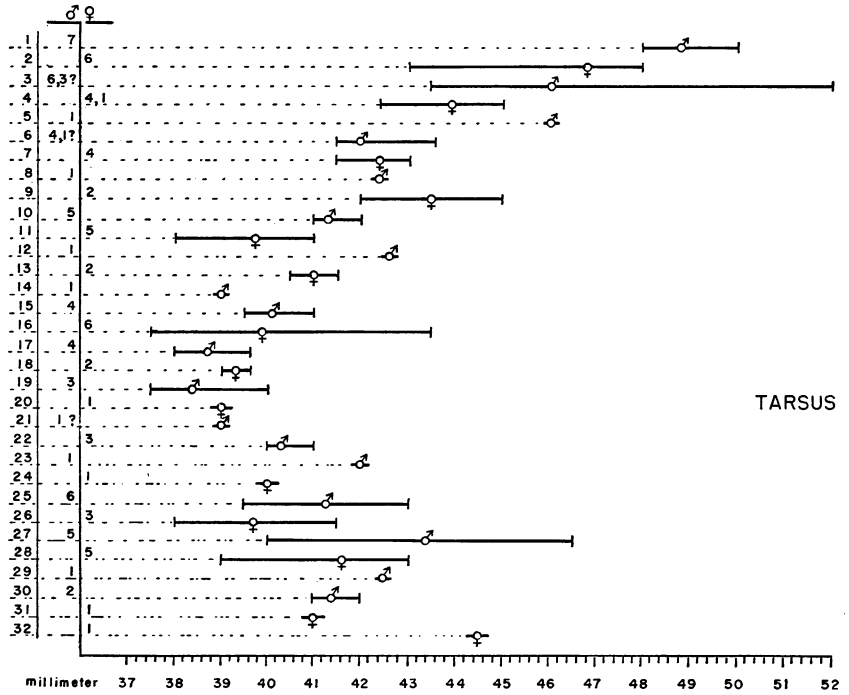


FIG. 4. Geographical variation in size of the tarsus in *Manucodia ater*. *Key to localities*: 1, 2, Tagula Island; 3, 4, Aru Island; 5, Sariba Island; 6, 7, Port Moresby to Yule Island; 8, Mailu Island; 9, Samarai Island; 10, 11, Fly River region: 12, 13, Snow Mountains; 14, Sattleberg; 15, 16, Madang, Sepik River, Wewak; 17, 18, Hollandia; 19, 20, Takar; 21, 22, Idenburg River; 23, 24, Wasior, Wandammen Mountains; 25, 26, Vogelkop; 27, 28, Waigeu Island; 29, Gebe Island; 30, 31, Misol Island; 32, Batanta Island.

The coloration of the ventral plumage was similarly graded with even more conclusive results: 26 specimens had the under parts strongly violet (all but two of these were from the satellite islands); 47 had the under parts bluish (these were not restricted geographically); and 27 had the under parts largely greenish (all but four of these were from the trunk of

New Guinea, with only two of the four having come from satellite islands).

To help emphasize the extraordinary differences between the extremes of these clines and to indicate how misleading it would be to include all populations in a single subspecies, measurements of the five specimens comprising the opposing ends of the dorsal gradient are given below.

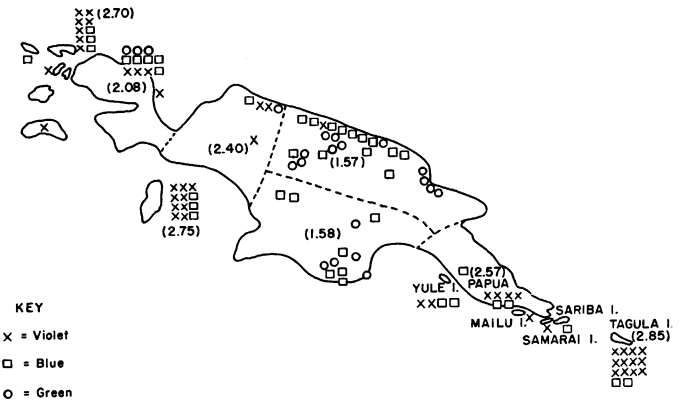


FIG. 5. Geographical variation in color of the dorsal plumage in 108 examples of *Manucodia ater*.

| | VIOLET-BACKED BIRDS (4 ♂, 1 ?) | GREEN-BACKED BIRDS (2 ♂, 3 ♀) |
|---|---|---|
| Wing | 206, 206, 200, 198, 186 | 171, 168, 166, 161, 158 |
| Tail | 180, 175, 174, 170, 150 | 145, 145, 138, 133, 127 |
| Tarsus | 49, 46, 46, 44, 42 | 42, 40, 40, 39, 38 |

The tendency for island populations of *Manucodia ater* to be more purplish violet, less greenish, than birds from the trunk of New Guinea is particularly significant, because the scattered nature of these populations presumably insures almost complete geographical isolation. An examination of the superspecies comprising *M. chalybatus* and *M. comrii* (Mayr, 1941, p. 168), which ranges widely over New Guinea (*chalybatus*), the D'Entrecasteaux Archipelago, and Trobriand Islands (*comrii*), reveals that there is also a parallel tendency towards purple (the wings and tail are much brighter) in the insular populations of this superspecies. Indeed, it appears likely that the history of speciation which affected this vividly colored group might have been much the same as that under which *M. ater* seems to be developing. The forces favoring purple and violet on oceanic islands remain unknown.

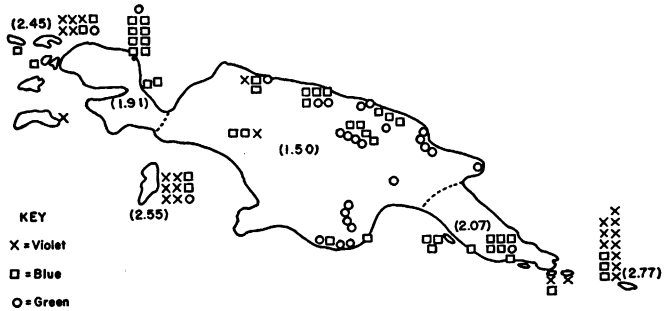


FIG. 6. Geographical variation in color of the ventral plumage in 100 examples of *Manucodia ater*.

## DIFFERENCES IN PLUMAGE DUE TO AGE

The juvenal plumage is sooty black. The immature plumage, which is acquired by an incomplete molt, is slightly more greenish, less bluish or purplish, than that of the adult. This has added somewhat to the problems of this study, because the afore-mentioned greenish plumage of the subadult can be confused with the greenish coloration noted for some mainland populations that is due to geographical variation and not to age.

In order to reduce the probability of error as far as possible, all the green birds in the Museum collection were included in the color gradient except those in which the distinctive dark brown iris color of the subadult was recorded on the field label.

## SEXUAL DIMORPHISM

The only difference is in size, with the male averaging slightly larger throughout. Rand (1938, p. 6) has shown that the nest duties (brooding and nest sanitation and probably feeding of young) are shared. Therefore it is probable that the male is at least seasonally monogamous. Similarity in size of the sexes frequently is correlated with this type of behavior which, among birds of paradise, is known only in *Manucodia ater* and to a lesser extent in *Macgregoria pulchra* (feeding of young). In plumed species, all of which lack pair formation, the males are distinctly larger than the females.

## MOLT, BREEDING CYCLES, AND WEATHER

These cycles were studied to see if they would reveal any evidence bearing on reproductive isolation between populations and thus divulge the presence of sibling species.

To simplify the investigation, studies of molt were centered on analyses

of wing and tail molt. In non-equatorial climes an integral part of the post-nuptial molt in passerine birds is the replacement of the wing and tail. It was thought that, if a similar postnuptial molt could be found, it would provide a valuable adjunct to the determining of breeding seasons from the plumage of Museum skins.

The series (108 specimens) was collected south of the Equator between the latitudes 1° S. and 11.5° S. during every month of the year. Data relating to gonadal development as given on field labels are given in figure 7. Because of the possibility of differing sexual cycles, testes and ovarian development are listed separately.

The September ovulation dates (see fig. 7) are from Rand (1938, pp. 2–3), who was the first to discover the species breeding. The December ovulation date alludes to a nest with two fresh eggs discovered by the author at Kanganaman, 196 miles up the Sepik River (north bank) on December 26, 1953.

Data relating to weather was obtained from an Australian meteorological report (Watt, 1940).

From figure 7 it appears that, although molt of the wing and tail may occur at any season of the year, the greatest number of birds molt during the first half of the year.

Correlations between molting and breeding seasons in *Manucodia ater* are only suggested by the meager data available. It is probable that no precise postnuptial molt will be found in this species, and that the breeding and molting cycles will be found to overlap.

## BREEDING SEASON

The fragmentary data further suggest that on the mainland the breeding season of *Manucodia ater* begins near the end of the dry or "winter" season, at a time when most of the population is apt to be in fresh plumage, and continues through the wet season into early March.

This is the time of high water, when the vast flood plain forests of the Fly and the Sepik are flooded and insectivorous food is abundant.

## DISCUSSION

Geographical speciation has given rise to pronounced variation in these populations, with the isolated sections of the species appearing so different from the groups inhabiting the central mainland that they might well be taken for distinct species. If the similarity of the various species of manucodes be considered, it is not impossible that the small green bird that predominates on the mainland, and the large violet bird that predominates in the insular populations, are sibling species subject to almost

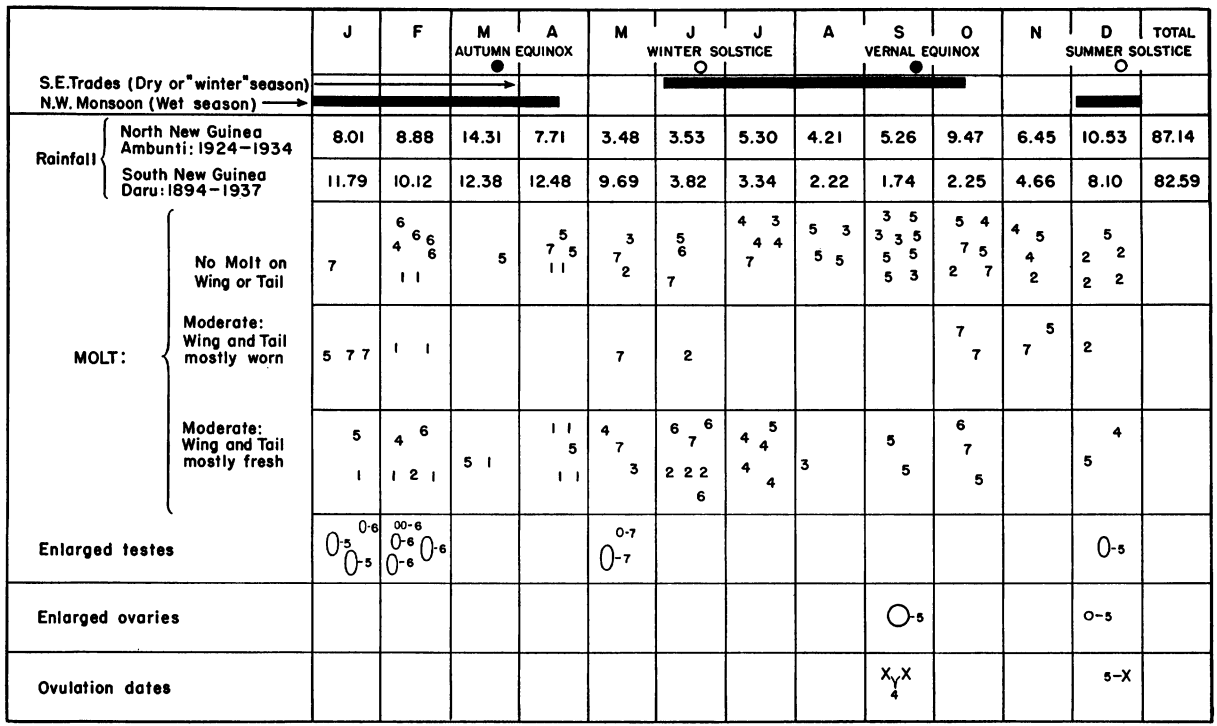


FIG. 7. Correlations between weather, molt, and breeding seasons in *Manucodia ater*. *Key to localities*: 1, Tagula Island; 2, Aru Islands; 3, southeastern New Guinea and off-shore islands (Sariba, Samarai, Mailu, etc.); 4, south central New Guinea; 5, north central New Guinea; 6, Vogelkop; 7, western Papuan islands.

complete fusion, but, if so, this study has failed to unmask them. The abundance of intermediate populations militates, however, against this possibility.

It would be of much interest to compare the life histories of *M. ater* from the Fly and Sepik rivers with the life history of an insular sample and to know which species each population competes with, as well as the comparative strength of the predator pressures of the insular and mainland habitats.

The only definitive steps that I have been able to find in these population gradients are: (A) bill length, with the Tagula Island birds being longer than any; (B) general size, with the insular and southeastern peninsular populations having the wings, tail, bill, and tarsus larger than in mainland and Vogelkop birds; (C) color, with insular and southeastern peninsular birds tending to purple and the mainland and Vogelkop birds tending to green, also with the Tagula Island population distinctly more violet on the flanks and abdomen than any other. Size intermediates nearly bridging B as well as color intermediates bridging C occur chiefly on the southeastern peninsula. These areas of intermediacy, which are of a clinal nature, may be the result of secondary intergradation between previously isolated populations.

If there is to be a division of populations, and this seems necessary (the very distinctness of the clinal extremes prohibits lumping), the primary division should be between the large violet insular type and the small, usually green bird of the mainland. A secondary division may be made between the large-billed Tagula population and other insular groups as advocated by Rothschild and Hartert (1929, p. 110).

Lesson's name *ater* is available for mainland populations, although the type description is based on a specimen from Dorey in the Vogelkop which is an area of intermediacy. From the following it is clear that Lesson based his description (1830, p. 639) on the greenish "mainland" type and not on the blue or violet types. He wrote, "The entire plumage is a metallic bluish green without any iridescent shimmering violet tints." Therefore this name can be applied to the greenish birds of mainland New Guinea.

The revision advocated is as follows:

*Manucodia ater ater* (Lesson)

*Phonygama ater* LESSON, 1830, Voyage autour du monde . . . sur . . . la Coquille pendant . . . 1822–25, vol. 1, p. 638; Dorey, northwestern New Guinea.

RANGE: New Guinea from the Vogelkop eastward in the north to about the Huon Gulf, and in the south to about the Purari River.

*Manucodia ater subalter* Rothschild and Hartert

*Manucodia ater subalter* ROTHSCHILD AND HARTERT, 1929, Bull. Brit. Ornith. Club, vol. 49, p. 110; Dobbo, Aru Islands.

RANGE: Western Papuan islands (Misol, Salawati, Batanta, Gemien, Gebe, Waigeu); Aru Islands; and southeastern New Guinea westward on the south coast to about the Purari River and on the north coast to about the Kumusi River, and islands off the coast (Yule, Mailu, Samarai, and Sariba).

*Manucodia ater alter* Rothschild and Hartert

*Manucodia ater altera* ROTHSCHILD AND HARTERT, 1903, Novitates Zool., vol. 10, p. 84; Sudest [=Tagula] Island.

RANGE: Tagula Island.

## REFERENCES

GYLDENSTOLPE, NILS
1955. Birds collected by Dr. Sten Bergman during his expedition to Dutch New Guinea, 1948–1949. Arkiv für Zool., ser. 2, vol. 8, no. 2, p. 373.

JUNGE, G. C. A.
1939. The birds of south New Guinea. Part II, Passeres. Nova Guinea, new ser., vol. 3, pp. 1–94.

LESSON, R. P.
1830. Voyage autour du monde . . . sur . . . la Coquille pendant . . . 1822–25 . . . par L. J. Duperry. Paris, Zoologie, vol. 1, pp. 1–743.

MAYR, ERNST
1941. List of New Guinea birds. New York, the American Museum of Natural History, 260 pp.
1942. Systematics and the origin of species. New York, Columbia University Press, 334 pp.

RAND, AUSTIN L.
1938. Results of the Archbold Expeditions. No. 22. On the breeding habits of some birds of paradise in the wild. Amer. Mus. Novitates, no. 993, pp. 1–7.
1942. Results of the Archbold Expeditions. No. 42. Birds of the 1936–1937 New Guinea Expedition. Bull. Amer. Mus. Nat. Hist., vol. 79, pp. 289–366.

ROTHSCHILD, W., AND E. HARTERT
1929. Notes to editor. Bull. Brit. Ornith. Club, vol. 49, pp. 109–110.

ROTHSCHILD, W., E. STRESEMANN, AND K. PALUDAN
1932. Ornithological results of the Stein Expedition, 1931–1932. 1. Birds of Waigeu. Novitates Zool., vol. 38, p. 140.

SCHAUENSEE, RUDOLPHE M. DE
1940. On a collection of birds from Waigeu. Notulae Nat., Acad. Nat. Sci. Philadelphia, no. 45, p. 14.

WATT, W. S.
1940. Results of rainfall observations made in Papua, Mandated Territory of New Guinea, Solomon Islands, New Hebrides, etc. Melbourne, Bureau of Meteorology, Commonwealth of Australia, 76 pp.