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The Ecology of Hybridization in New Guinea Honeyeaters (Aves)

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INTRODUCTION

Taxonomists are generally agreed that new species develop in isolation and that when gene exchange diminishes or ceases the isolated segments may differentiate independently. They are further agreed that if, upon coming together again, the segments display differences by continuing to live as separate entities, they may be regarded as having reached the level of good species. In other words, reproductive isolation, regardless of the nature of the isolating mechanisms on which it rests, has long been accepted as the standard by which to establish species. Conversely, when the isolated segments come together, if they interbreed freely and produce fertile, viable offspring, they may not be regarded as having reached the level of good species. In other words, they are considered to be conspecific without regard for other considerations such as pronounced morphological differences, provided, however, that there is free interbreeding of natural populations.

This *modus operandi* works most of the time, but occasionally situations develop that seem to throw doubt on the validity of reproductive isolation as the primary criterion for measuring completeness of speciation. These situations generally concern groups that interbreed in zones of secondary contact in spite of being morphologically very different from one another.

The two groups of New Guinea honeyeaters herein discussed offer an excellent example of this phenomenon. They appear to represent

two very different species, and, indeed, they apparently behave like good species in parts of their range that are ecologically little disturbed, whereas in many areas that have been disturbed they appear to have broken through ethological and ecological barriers to produce hybrid swarms, but the genetic complex of each such swarm appears to be different.

In areas where intermingling is impeded, some of the swarms tend to be less variable (more stable), and two such swarms have become uniquely different from both of the parent groups. These stabilized populations seem to represent a rare and little-understood phenomenon, namely, the establishment of successful new gene complexes through the effects of hybridization between valid species.

Specifically some of the questions to which this study is addressed are:

1. The biological status of these two groups of honeyeaters: are they species or subspecies?
2. The connection between habitat disturbance and species barriers
3. The question of taxonomic discrimination of populations of hybrid ancestry that have become sufficiently stabilized to be distinguished from each of the parent groups

Touched upon also is the apparent need of modifying some of the criteria for judging species so as to include the postulated phenomena of the origin of species through (1) the occasional free hybridization of natural units under conditions of ecological disturbance, followed by (2) the secondary isolation of such hybrid swarms, and occasionally (3) their stabilization and the origin from hybrids of taxonomically discrete groups.

Finally, after reviewing earlier evidence (Meise, 1936; Miller, 1941; Yamashina, 1948; Chapin, 1948) for the stabilization of hybrids as a rare natural mechanism of speciation, the writer considers the effects, if any, that might accrue from third or fourth isolations of such swarms. Specifically he postulates that the peculiar species swarms that have arisen on certain volcanic archipelagoes having a long history of eustatic movement (i.e., moas, elephant-birds, *Geospiza* finches) may in part owe their phenomenal radiations to the repeated disturbance, shuffling, and re-isolations of hybrid swarms.

An earlier study (Mayr and Gilliard, 1952b) of the altitudinal hybridization of these two groups of honeyeaters (called the "black bills" and the "wattle birds") indicated that, excluding the Vogelkop populations, the two groups could best be dealt with by lumping them in the single species category *Melidectes belfordi*. To identify the

populations forming the various hybrid swarms, regardless of their degree of stabilization, it was suggested that locality and altitude should be added in parentheses to this binomial.

Concerning the material used in the earlier studies, in 1950 and again in 1952, the present author collected these honeyeaters in the Hagen, Bismarck, Kubor, and Waghi-Divide Mountains, obtaining examples between the altitudes of about 5000 and 11,000 feet. This

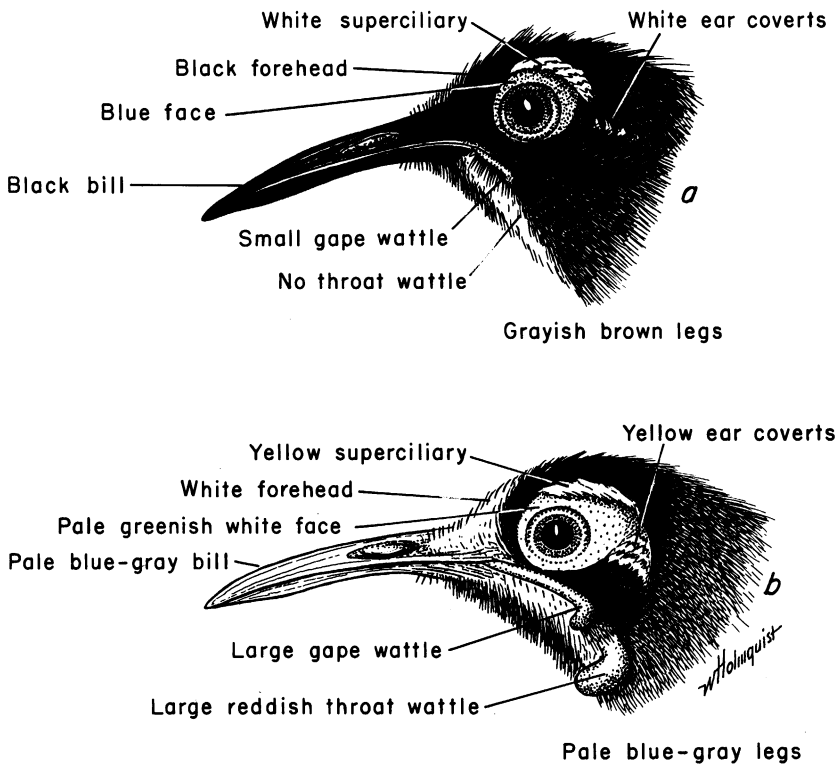

FIG. 1. Morphological differences between black bills (A) and wattle birds (B) of mainland New Guinea.

series of skins proved to be extremely variable and later, in New York, Mayr concluded that this variation was due to hybridization between two conspecific but morphologically very different groups. The following simple diagnosis illustrates the morphological differences (see fig. 1):

Wattle birds (fig. 1B): naked face ivory white washed with pale green, not deep sky blue as in black bills (fig. 1A); bill blue-gray, not black; forehead

LOCALITY	Number	Sex	Weight in gr.	ALTITUDE IN FEET	Color of face & base of bill	15 Bill / wing	15 Throat wattle	10 Gape wattle	5 Ocular area	15 Super-ciliary	5 Ear coverts	20 Fore-head	10 Bill color	5 Bill feathering	HYBRID INDEX	Gape wattles	Throat wattles	Color of feet	Color of bill in life
Ilkivip, Hindenburg Mts.	1	♂	74	7300	"Whitish yellowish green"	15	14	10	5	15	1	15	10	3	88	"Pale whitish yellow"	LARGE Red-orange	"Whitish pale blue shading"	Palest blue-gray
"	2	♂	84	7300	"Pale whitish yellow"	15	13	10	5	15	5	18	10	0	91	Palest greenish white	LARGE Deep orange	"Whitish gray"	Pale gray-blue
"	3	?	70	7300	"Pale yellowish green"	10	13	10	5	0	0	16	10	0	64	Creamy white	LARGE Red-orange	Pale blue-gray	Pale blue-gray to pale aqua at base
MEDIAN					*Pale yellowish green*	*15*	*13*	*10*	*5*	*15*	*1*	*16*	*10*	*0*	*85*	*Pale yellowish white*	*Reddish orange*	*Pale gray*	*Pale blue-gray*
UNCHEMCHI	COLOR PHOTO.			5850	Pale whitish	?	15	?	5	15	?	15	10	?	(?) 75	?	Deep orange-red	Pale gray	Pale gray
Mt. Ifal, Victor Emanuel Mts.	4	♂	74	7500	"Shading from pale aqua to light cerulean blue"	8	0	4	1	0	0	0	0	0	13	White	NONE	"Brownish gray"	Black with gray on underside
"	5	♂	80	7200	Light cerulean blue	5	0	4	1	0	0	0	0	0	10	White with traces of yellow	NONE	Light blue-gray	Dark gray blackish gray
"	6	♂	70	7300	Light cerulean blue	7	0	4	2	0	0	0	0	0	13	White	NONE	Mottled gray-brown	Mainly black with blue-gray on outer half of mandible
"	7	♀	63	7200	Light cerulean blue	8	0	3	2	0	0	0	0	0	13	White	NONE	Mottled grayish brown	Black
"	8	♀	57	7200	Light cerulean blue	5	0	3	2	0	0	0	0	0	10	White	NONE	Grayish brown	Black
"	9	♀	55	7400	Shading from pale cerulean blue at eyes to pale aqua yellow on head; skin at bill base pale cerulean blue	6	0	2	2	0	0	0	0	0	10	White	NONE	Grayish brown	Black
"	10	♀	67	7200	Pale cerulean blue	7	0	3	1	0	0	0	0	0	11	White	NONE	Mottled grayish brown	Black
MEDIAN					*Pale cerulean blue*	*6.5*	*0*	*3*	*1.5*	*0*	*0*	*0*	*0*	*0*	*11*	*White*	*NONE*	*Grayish brown*	*Blackish*
Deikimdikin, Mittag Mts.	11	♀	44	7000±	Pale cerulean blue	10	0	4	1	0	0	10	0	0	25	White	NONE	"Dark brown with gray lines between scutes"	Black

FIG. 2. Character (hybrid) analysis of newly collected specimens of black bills and wattle birds from the Telefolmin region of New Guinea.

white, not black; gape wattle large, not small; throat wattle large and brick-red, not lacking; superciliary stripe bright yellow, not clear white; ear coverts yellow, not white; legs and feet pale blue-gray, not grayish brown.

Next a detailed study was made, in which the author served as collaborator. This study revealed six areas where the wattle birds and the black bills freely interbreed, forming hybrid swarms that are in the nature of altitudinal belts. It was found that the wattle birds tended to favor the lower, more open forest and forest edge, whereas the black bills favored the higher, more dense forests. The fact that the forests of the lower mountain areas had been largely fragmented or removed by primitive man was not taken into consideration.

NEW EVIDENCE

The present studies, which are based on observations and specimens collected in 1954, grew out of a desire of the author to add supplementary ecological notes and hybrid indices to reënforce the conclusions of the earlier work. However, the new material, plus a searching study of the literature of hybridization and a reëxamination of the old material, led to the altered conclusions expressed in this paper.

In 1954 the author and his wife carried out ornithological surveys in the Hindenburg and Victor Emanuel Mountains which border the little Telefolmin Valley at the headwaters of the Sepik River. Special efforts were made to collect *Melidectes* honeyeaters but, because of tribal unrest and restrictions, only 11 specimens could be obtained. (All are listed in fig. 2.) These proved to be exceedingly interesting. All were taken by the expedition collectors and not by local natives. Each specimen was labeled as to locality, altitude, color, and weight. The perishable colors were described by Margaret Gilliard, who also weighed each specimen.

Specimens from the high camp on Mt. Hindenburg were shot on the northern watershed within 1000 feet of the height of land that divides the headwaters of the Sepik River from those of the Fly River. The trail leading up to this camp followed a sharp ridge through tall open forest. In places the forest gave way to limestone areas with only a thin covering of grass. These natural forest clearings were narrow and long and seemed to be caused by lack of humus on the limestone ridge and lack of ground water rather than by human deforestation. Most of the wattle birds were taken at 7300 feet on Mt. Hindenburg, but one record is at 5850 feet. This latter specimen was taken in a bushy, limestone-floored, grassy clearing, after having become trapped in a Japanese "mist" net which had been stretched beside a limestone

"chimney." This specimen was photographed in color (see fig. 4), but it escaped during the operation. The photograph must, therefore, serve in lieu of a specimen. It is recorded in figure 2.

Although a fair amount of hunting was done in the valley bottom in the vicinity of the expedition base camp near the Telefolmin airfield, neither wattle birds nor black bills were found. The altitude there is about 4800 feet. Base camp was located in one of four or five small fields which had been cleared in the tall original forests by primitive man. It seemed likely that the wattle birds, if not the black bills, would be present along the edges of the clearings, as they were found only a few miles north and in the same watershed and only some 700 feet higher. The mystery of the apparent absence of these birds (both groups) may be due to the fact that the clearings are ringed with forest and not contiguous with the true forest edge bordering the main valley river (the Takin) which, presumably, is the optimum habitat of the wattle birds. At the same time the clearings are perhaps too low for the black bills, which appear to find their optimum habitat in high dense forest.

Northwest of the Telefolmin station (also in the same watershed) no wattle birds were encountered. Instead, only pure black bills were found living in the original forests of Mt. Ifal. At and above 7000 feet these birds were relatively common, as can be seen from the fact that six specimens were taken in a few days in an area where, because of the steepness of the terrain, collecting proved extremely difficult.

All the new material (see below) was analyzed according to indices and procedures established by Mayr and Gilliard (1952b, pp. 327–328) in which a typical wattle bird scored a theoretical 100 points and a typical black bill scored a theoretical zero.

Black Bills from the Victor Emanuel Mountains

Character Index[1]: Males, 10, 13, 13; females, 10, 10, 11, 13.

This slight deviation from zero is almost entirely due to the presence of a very small gape wattle and to the bill/wing ratio. This is the condition also affecting *kinneari*, the race found much farther west in the Nassau and Oranje Mountains of Netherlands New Guinea. In both groups there is very little indication of wattle-bird genes, and both may be considered to be nearly "pure" black bills.

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[1] Ernst Mayr has suggested the adoption of this term in place of "hybrid index" as used in the earlier study.

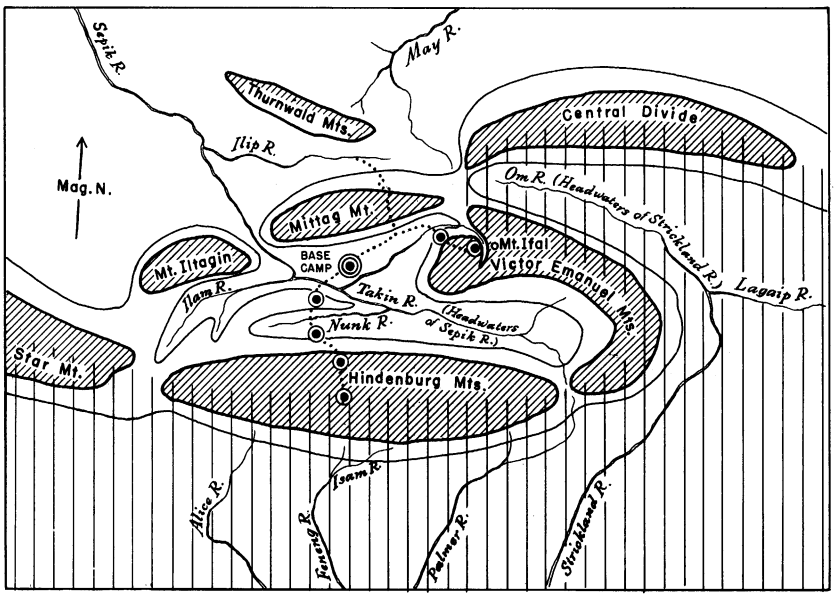

FIG. 3. Telefolmin region. Dotted lines indicate areas in which birds were observed and collected. Circles represent camps.

HYBRID POPULATION FROM THE MITTAG MOUNTAINS

CHARACTER INDEX: Female, 25.

This single specimen is closest to the black bills, but there are several strong indications of wattle-bird genes. The most noticeable is the forehead, which is narrowly white, not black as in the pure black bills. This is the only specimen that was collected in an area that could not be inspected personally by the author. It was brought to his camp by professional native gunboys who shot it on their way back from the Ilaptamin Valley, a distant lowland valley of the northern watershed that is more heavily farmed than the Telefolmin Valley. The hunters stated that they killed it on a trail leading over the Mittag Mountains.

WATTLE BIRDS FROM THE HINDENBURG MOUNTAINS

CHARACTER INDEX: Males, 88, 91; unsexed specimen, 64; photographed specimen, 85.

The indices of the two males and the unsexed photographed specimen are so high that these birds may be considered to be pure wattle birds. They are virtually inseparable from a series of males from the Schraderberg Mountains. The unsexed skin scored only 64 points. This specimen shows indications of black-bill genes in having white superciliaries and ear coverts (see below).

With regard to the coloration of the superciliaries and the problem of deciding what part of the variation, if any, in the coloration is due to introgression or to age, seasonal, or sex differences, the following comparative analysis of nestlings from different parts of New Guinea is enlightening. One (A.M.N.H. No. 342777) is from Lake Habbema in the Snow Mountains of Netherlands New Guinea (6600 feet); one (A.M.N.H. No. 705838) is from Mt. Wilhelm in the Bismarck Mountains (10,000 feet); and one (A.M.N.H. No. 421044) is from Mt. Albert Edward in the mountains of southeastern New Guinea (11,000 feet). The first is from an area occupied by presumably "pure" black bills called *kinneari*. The second is from the heart of a hybrid area. The third is from an area occupied by a "pure" black-bill group called *belfordi*.

The nestling *kinneari* is one of 44 specimens (the remainder are adult) in the American Museum collections from the Nassau and Snow Mountains. Unlike all but two of the 43 adults, this young bird has the superciliaries and ear coverts yellow, not white. However, the yellow of this nestling is bright and rich, whereas the yellow of the two adults (A.M.N.H. Nos. 342731 and 342748) is pale.

The presence of rich yellow in a nestling of *kinneari* is difficult to interpret. However, as yellow does occur in a few Snow Mountain adults, it seems more probably to be due to the introgression of wattle-bird genes than to a developmental phase in the growing young, although there seems to be a lightening or fading of the yellow as the bird matures.

The second nestling is from the Bismarck Range. This range is bordered both to the north and to the south by broad belts of hybridization. This specimen was collected in forest just below the alpine grasslands of Mt. Wilhelm at an altitude of more than 10,000 feet. It, too, has the superciliaries and ear coverts bright yellow, as do three of five adults that the author collected near the top of Mt. Wilhelm (all skins marked with altitudes lower than 10,000 feet have been eliminated from this comparison). However, once again the yellow of the adults is pale and washed-out, while that of the nestling is relatively much richer, which suggests again that richness of color is correlated with ontogeny, but that yellow is due to the introgression of wattle-bird genes.

Still another nestling of approximately the same age and development was collected by Rand in eastern New Guinea on the top of Mt. Albert Edward. Unlike the other nestlings from western and central New Guinea, this bird has the superciliary and ear coverts pure white!

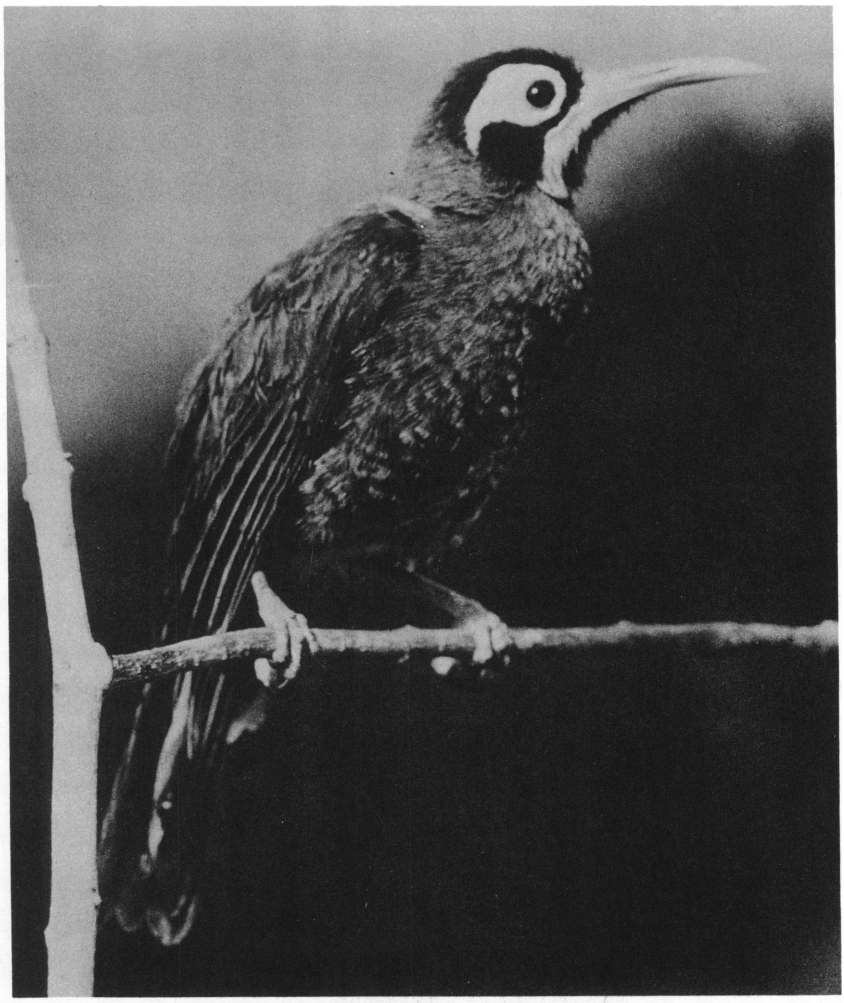

FIG. 4. Wattle bird trapped at Unchemchi, Hindenburg Mountains, at 5850 feet.

A close examination of adult black bills from southeastern New Guinea (two races) reveals that none in the American Museum collections shows any indication of yellow or any other indication of wattlebird genes.

In addition to these specimens, in May of 1952 natives in the Kubor Mountains, in another area of pronounced hybridization, brought the author a nest containing a well-grown nestling black bill which they

had collected at about 7500 feet. Films made of this specimen show that it had the superciliary bright yellow.

Although the material observed is too limited for final conclusions to be reached, it is probably significant that the only nestling observed that lacked yellow on the head was from an area that is geographically remote from regions in which wattle birds are known to occur. Therefore it seems reasonable to assume that yellow in the superciliaries is an indication of wattle-bird genes, which would mean that the effects of introgression are evident to a slight degree in the Snow Mountains of Netherlands New Guinea and are discernible even at high altitudes.

The following is a collation of evidence that sheds light on this problem but which was not available at the time of the original study.

A hybrid population of honeyeaters was discovered in the southern watershed at Mt. Giluwer by Fred Shaw-Mayer (Sims, 1956, p. 434) in 1951. Using the character index system devised by Mayr, Sims scored a black bill from Mt. Giluwer with an index of 22 and a wattle bird with an index of 89. Both specimens were taken at elevations prone to hybridization (7500 to 7800 feet). Sims (*loc. cit.*) also reported the character indices of three specimens taken in the Tomba region of Mt. Hagen by Shaw-Mayer. These came from a locality in the south watershed, where in 1950 the present author also found a hybrid swarm. One of Shaw-Mayer's specimens was phenotypically a perfect black bill (character index, 3); another was nearly so (character index, 11); and one was a well-marked hybrid (character index, 60).

Still other new evidence comes from the southern watershed of the Wahgi-Divide Mountains near Nondugl. There Gyldenstolpe (1955, p. 162) obtained an extensive collection in 1951. His material has not been scored, but among his 27 specimens Gyldenstolpe found 18 wattle birds with yellow superciliaries, seven wattle birds with white superciliaries, and only two "black bills." The paucity of black bills suggests that Gyldenstolpe's material consists of birds collected chiefly below 7000 feet in fragmented forests. These specimens plus a series collected in this region in 1950 by the present author indicate that this area of the southern watershed is occupied by a hybrid swarm with the most wattle-bird-like birds occurring in the forest edge and in the wooded draws that incise the grass-covered valley floor.

Taxonomic Studies of Black Bills

As shown above, the honeyeaters from the Victor Emanuel Mountains appear to be nearly pure black bills, of which there are four named populations. Comparisons with these indicate that the Victor

Emanuel birds are nearest to the high-altitude race *belfordi* of eastern New Guinea, the only difference being that the bill of the former averages somewhat longer. This difference seems insignificant, because there are much individual variation and overlapping in bill length. Therefore there seems to be no alternative to placing the birds of central New Guinea and those of the high mountains of southeastern New Guinea in a single category, despite the fact that a broad belt of hybridization separates the two.

Diagnosis of the Victor Emanuel Mountain series of *Melidectes belfordi:* Compared with *joiceyi,* much darker, more sooty above, not strongly washed with olive green. Compared with *kinneari,* wing averaging slightly longer; also differing slightly by averaging darker both

TABLE 1

MEASUREMENTS OF BLACK BILLS

	Wing	Tail
kinneari		
Snow Mountains	11 ♂ 133–151 (142)	♂♂ 123–130 (127.2)
Snow Mountains	13 ♀ 116–135 (126)	♀♀ 114–121 (116.3)
belfordi		
Victor Emanuel Mountains	♂♂ 145–152 (147.3)	♂♂ 124–134 (127.6)
Victor Emanuel Mountains	♀♀ 133–137 (134.2)	♀♀ 115–120 (117.2)
Mt. Albert Edward	5 ♂ 147–153[a]	4 ♂ 128–136[a] (133.5)
Mt. Albert Edward	1 ♀ 139	1 ♀ 123[a]
brassi		
Mt. Tafa and Murray Pass	8 ♂ 139–144[a] (141.2)	8 ♂ 119–125[a] (121.4)
Mt. Tafa and Murray Pass	9 ♀ 123–139[a] (130.2)	7 ♀ 108–123[a] (112.8)

[a] From Mayr and Rand (1937, pp. 223, 224).

above and below, the body plumage being slightly darker bluish gray, less smoky gray, and the under tail coverts being slightly darker, more chocolate brown, less amber; furthermore, differing by the fact that the extent of the naked eye patch, particularly in the postocular region, seems to average considerably larger, but this may be due to variations in the techniques of skin making. Compared with *belfordi* (from Mt. Albert Edward), virtually indistinguishable, but bill averaging slightly longer. Compared with *brassi,* wing and tail considerably longer.

FIELD NOTES ON BEHAVIOR

Interesting evidence illustrating the interfertility of black bills and

wattle birds has come to light since publication of the paper by Mayr and Gilliard (1952b). It consists of observations and a photograph by Mr. Loke Wan Tho of a hybrid wattle bird feeding its hybrid young in the vicinity of Tomba on Mt. Hagen, an area that both Gilliard and Shaw-Mayer found to be occupied by a hybrid swarm.

The photograph shown here as figure 5 was first published in Gyldenstolpe's report (1955, pl. 14). No data on this bird are given in the body of that paper, but under the photograph is the following legend: "Adult bird with a fledgling. Tomba, south slope of Mt. Hagen, Western Highlands, 8000 ft., October 6, 1952." However, Sims (1956, p. 434) quotes at length field notes by Loke Wan Tho that al-

FIG. 5. Hybrid wattle bird feeding young at Mt. Hagen (southern watershed). Photograph by Mr. Loke Wan Tho.

most certainly refer in large part to the bird in the Loke photograph that is feeding its young:

"The young bird had a black head with a fringe of sandy coloured down around the crown and a lighter coloured patch around each eye. The upper-parts were dark gray and the under-parts somewhat lighter in colour, with white streaks on each side of the chin; the under-tail coverts were cinnamon. The bill was mainly grey in colour with some white on it. Both of the parents fed the young bird, but one did so less frequently than the other and usually remained close by the nest. The food appeared to consist mainly of insects; but it is probable that nectar was given also because sometimes one of the adults would return to the nest and stand over the juvenile and rapidly flick its long

reddish tongue in and out of the young bird's mouth. When neither of the adults could be seen they could still be heard near by making clucking noises; generally they were very noisy. One loud call that they made frequently was one of the common calls of the forest. Their alarm call could not be established with certainty, but it appeared to be either, 'Quick-quick-quick-quick, kiow- kiow- kiow-kiow,' or 'tolle-tolle-tolle, kiow-kiow-kiow-kiow'; in response to this call the young bird would freeze in the middle of the nest and close its eyes. They were very shy birds and easily disturbed."

Certain other observations, either new records or records that are widely scattered, are the following:

During the course of recent studies of bowerbirds near Tomba on Mt. Hagen, the author made some observations of what appeared to be black bills. In these forests this honeyeater was found to be fairly common. Its chief calls were harsh "kraas" and "kriis," also fairly rich whistles, "phew, phew." These cries were heard from early in the morning (the earliest was heard at 5:58 A.M.) and were usually the first calls of diurnal birds to be heard. Often several birds would be heard calling more or less together. Black-billed honeyeaters were observed feeding in the forest. They kept to the middle and upper limbs, moving out to the limblets and the leaves apparently to feed among buds and small fruit growing from the sides of leaf stems. They moved methodically, sometimes stopping to stand still for many seconds. They kept back from the limb tips, which are the foraging territory of *Ptiloprora perstriata* and other smaller birds.

Rand's observations (Mayr and Rand, 1937, p. 225) of a black bill, made on the summit of Mt. Albert Edward some 11,000 feet above sea level, are of the rare *M. b. belfordi*, which is restricted to a few square miles of mountain top on the aforementioned peak and on Mt. Knutsford. He wrote: "This bird was as common and noisy as its lower altitude representative; like it, frequenting flower trees and driving other birds from them . . . On June 30 on Mt. Albert I found a young bird barely able to fly." Rand also studied the race from Mt. Tafa (Mayr and Rand, 1937, p. 224) and described its habits in some detail.

In summary it may be said that no differences aside from habitat preference have been found between black bills and wattle birds.

DISCUSSION

The Hypothetical Common Ancestor

In order better to evaluate the taxonomic position of these two very

different subgroups of honeyeaters, it is important to try to reconstruct the common ancestor. At the present time the black-bill group occupies all of the high central ranges exclusive of the Vogelkop. All the populations closely resemble one another, and the four named races tend to grade one into the other, although in ecologically disturbed intermediate areas there is an intrusion of wattle-bird genes. Conversely the wattle-bird group consists of three elements that replace one another geographically in three widely separated, peripheral mountain areas. These are (a) the mountains of the Vogelkop in western New Guinea; (b) the Sepik Mountains of north-central New Guinea; and (c) the mountains of the Huon Peninsula of northeastern New Guinea. Geographic isolation between these three groups of wattle birds is virtually complete, so much so that the Vogelkop group has long since reached the level of a good species, and the other two groups (especially the Huon Mountain group) may easily be distinct species. In other words, judging from geographical as well as from morphological evidence, the three groups of wattle birds have long been isolated, and each has undergone independent evolutionary differentiation to such a degree that at present the three seem to represent component parts of a superspecies rather than of a species. It is noteworthy that the groups that are geographically the most remote from the black bills display the greatest morphological differences. Also significant is the fact that, despite their differences, the three groups of widely differing wattle birds have a number of characters in common, none of which appears in the pure black bills. Some of these are as follows: gray bills, white foreheads, large gape wattles, and large throat wattles. These similarities between such widely isolated and otherwise very different-appearing groups seem not to be due to convergence, and therefore the three wattle birds probably represent radiations of an old stock from which the black bills split off quite early. Mayr (Mayr and Gilliard, 1952b, p. 333), observing dissimilarities rather than similarities, reached somewhat similar conclusions as follows: "The conspicuous differences between the three wattle bird populations and the essential similarity of the black bills suggest that the wattle birds have long been isolated, while the black bills either have had an essentially continuous distribution or have spread fairly recently."

The Origin of Hybrid Swarms

Mayr (Mayr and Gilliard, 1952b, pp. 333–334), making deductions from the present distribution of many north New Guinea birds, has postulated that in earlier times much greater geographical isolation

existed between the main ranges of New Guinea and those of the northern portions of the island, which, he suspects, may have once been a real island separated by water, or an ecological island, or a combination of both. It is known that the distribution and evolution of a large number of New Guinea birds have been affected by a geographical barrier (a gulch) that runs lengthwise through the northern lowlands of New

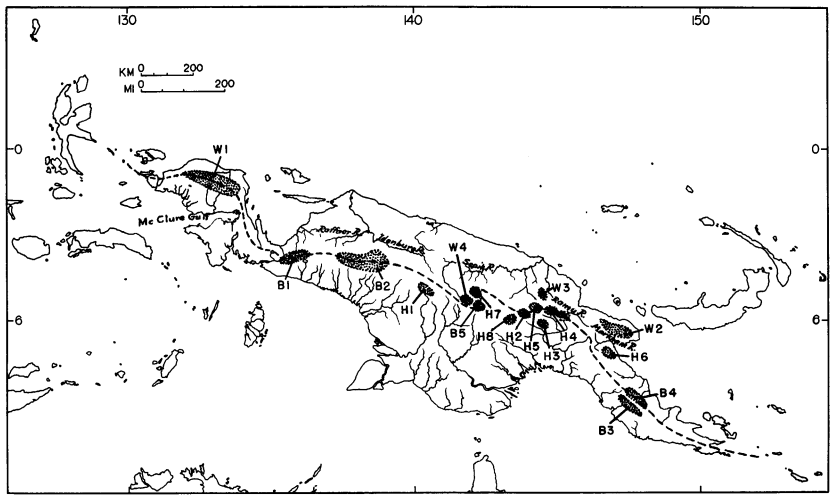

FIG. 6. Distribution of the known populations of honeyeaters of the *Melidectes leucostephes-rufocrissalis-belfordi* group. *Symbols:* W, wattle birds; W1, *M. leucostephes,* Arfak Mountains; W2, *M. rufocrissalis foersteri,* Saruwaged Mountains; W3, *M. r. rufocrissalis,* Schraderburg, Sepik Mountains; W4, *M. r. rufocrissalis,* Hindenburg Mountains. B, black bills; B1, *M. belfordi joiceyi,* Weyland Mountains; B2, *M. b. kinneari,* Nassau, Oranje Mountains; B3, *M. b. brassi,* southeast New Guinea, low altitude; B4, *M. b. belfordi,* southeast New Guinea, high altitude; B5, *M. b. belfordi,* Victor Emanuel Mountains. H, hybrid populations; H1, *M. b. griseirostris,* Mt. Goliath; H2, *M. rufocrissalis* × *belfordi,* Mt. Hagen; H3, *M. rufocrissalis* × *belfordi,* Mt. Kubor; H4, *M. rufocrissalis* × *belfordi,* Mt. Wilhelm; H5, *M. rufocrissalis* × *belfordi,* Wahgi-Divide Mountains; H6, *M. belfordi stresemanni,* Herzog Mountains; H7, *M. rufocrissalis* × *belfordi,* Mittag Mountains; H8, *M. rufocrissalis* × *belfordi,* Mt. Giluwer.

Guinea. This barrier is still very effective. Some of its present features are McClure Gulf and the virtually contiguous valley systems of the Rauffaer, Idenburg, Sepik, Ramu, and Markham rivers. (See fig. 6.)

It is to be noted that in places the long depression formed by this system of valleys is only a few miles wide, and that throughout most of its length, of nearly 1000 miles, the depression is very low and usually

less than 300 feet above sea level. Although very narrow, it divides mountains that have avifaunas of a level of difference suggestive of moderately isolated oceanic islands. One has only to compare the birds of the Huon Mountains with those of the Bismarcks (notably those of the southern Finisterre Mountains with those of the northern Bismarcks) to comprehend the magnitude of these differences. Examples are *Astrapia rothschildi* versus *A. stephaniae, Paradisaea guilielmi* versus *P. rudolphi, Parotia wahnesi* versus *P. lawesi, Sericulus bakeri* versus *S. aureus;* and, of course, the wattle bird of the Huon Peninsula and the black bill of the mountains to the south of the grass belt. Yet these two mountainous areas face one another only 6 miles apart across a tropical grassland valley. Near the headwaters of the Ramu and Markham rivers this valley becomes a thin flat belt of grassland approximately 4 miles wide, with only a small stream running through it.

It seems phenomenal that the birds of the opposing woodlands should be so different, but the fact remains that many of the non-tropical groups are represented on each side by such distinct species that formerly they were placed in different genera.

Often birds with discontinuous ranges on widely isolated mountains situated north of the depression are more closely related than are populations inhabiting mountain ranges sometimes less than a dozen miles apart, but located on opposite sides of the depression. This is the situation in the wattle birds and the black bills, in the astrapias and in the parotias, to mention a few examples. From such evidence it seems likely that the barrier was much stronger in earlier times and that, when the barrier became weaker and invasions and re-invasions were frequent, there was a corresponding enrichment of the avifauna both to the north and to the south of the barrier.

There is a body of evidence that strongly suggests that the barriers that divide the wattle bird and the black bills at the present time are largely ecological rather than geographical. Also there are strong indications that the mechanisms that act to maintain this ecological isolation are and have been easily shattered by habitat disturbances, particularly by forest fragmentation (patch-cutting) and by forest removal. There is also evidence that when mechanisms of ecological isolation fail and hybrid swarms occur between the two groups (hereafter called parent A for the wattle birds and parent B for the black bills) some of the hybrid swarms have become secondarily geographically isolated from both parents and have then become uniquely stabilized in some of their characters.

"Hybrid Gap"

One of the most interesting aspects of this secondary isolation and speciation of hybrid swarms is that they seem to have happened as a result of ecological disturbances created by man. To understand how this may have happened one must remember that wattle birds are essentially birds of the northern watershed, where they are found at lower altitudes than those inhabited elsewhere by black bills. Also it must be remembered that wattle birds are essentially birds of the lowland forest edge, whereas black bills are essentially birds of the deep forests, and that the forested mountain range is a barrier to one (the wattle bird) and not to the other (the black bill). These things being true, it is logical to expect that if, through habitat disturbance (the cutting of the lowland forests), the black bills and the wattle birds were brought into hybrid contact, hybrid zones would take the form of broad altitudinal "belts" at the main points of contact and that these belts would taper to nothing at their ends, or would form "rings" if the belts happened to encircle isolated mountains. In these honeyeaters it appears that at one extremity of the northern belt (east), and at one extremity of the southern belt (west), there are hybrid "rings" that have become disconnected from the belts themselves, in other words, swarms of hybrids that have become isolated both from the parents and from the swarm. It is perhaps significant that only one of these is sharply stabilized, and that it is quite remote from the chief domain of the wattle birds.

It was not until the writer had been over the ground several times in the vicinity of a place called Hybrid Gap that he began to understand how a wild swarm of hybrids might become "trapped" and thus partially or wholly isolated from the genetic reënforcement of its parent groups.

Hybrid Gap is a low pass in the wall-like cordillera that divides the north and south watersheds of New Guinea for nearly a thousand miles (see fig. 7). This mountain wall has very few low spots, and the lowest so far discovered seems to be Hybrid Gap. Because a number of hybrid birds have been found there (for example: *Astrapia mayeri* × *A. stephaniae; Paradisaea rudolphi* × *P. apoda; P. apoda* × *P. minor*), Mayr and Gilliard (1954, p. 321) named this unusual terrain feature Hybrid Gap.

Formerly Hybrid Gap was thickly forested. At present it is virtually devoid of forest and overgrown with grass. (For a photograph, see Mayr and Gilliard, 1954, pl. 16.) The grass belt extending through the gap is 5 to 10 miles wide. Its western side is the fragmented forest edge

on Mt. Hagen. Its eastern border is the forest edge at the western tip of the Wahgi Mountains. Throughout the low part, or floor, of the gap (the low point is at about 5500 feet) the forest has been entirely removed by natives (except for one small patch that crowns a hill near the middle of the belt of grassland). So effectively does this broad grass belt link the grasslands of the northern and southern watersheds that fires started in either drainage often burn across to the other. Thus the

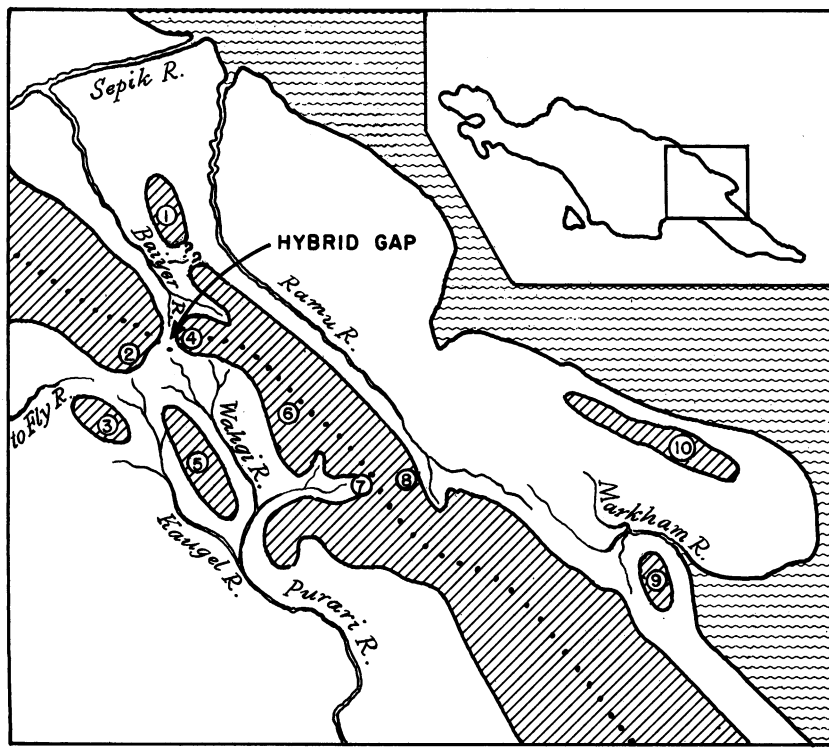

FIG. 7. Hybrid Gap, showing the location of the only known grassland link between the northern and southern watersheds of New Guinea.

flames pass through an area that formerly, in its natural state, was impervious to fire, having been entirely covered with wet mountain forest.

At the present time on the northern watershed near Hybrid Gap the grass extends upward to 6000 feet (with wide lobes of forest descending to 4000 feet) on the mountains of the Wahgi Divide. However, on the Mt. Hagen side the grass extends upward to about 6000 feet on steep

grades and to about 8000 feet on more gradual inclines. There can be no doubt that virtually all the areas of grassland found in this large region are the product of primitive man's practice of cutting gardens in the forest edge. He habitually cuts large plots in the virgin forest, burns the logs, and then plants chiefly sweet potatoes. These grow very large in newly cut and burned areas, but later the potatoes become small. After a series of periods during which the land is per-

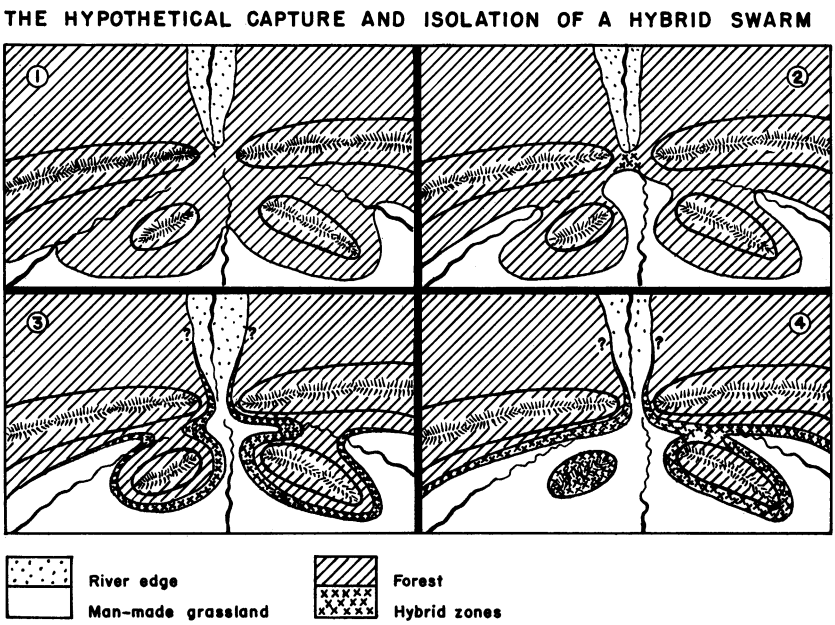

FIG. 8. The optimum habitat of wattle birds is along undisturbed forest edges such as are shown by dotted areas. The optimum habitat of black bills is in high undisturbed forest.

mitted to lie fallow and then is reburned and replanted, the ground is abandoned in favor of a new forest patch. The abandoned land thereafter is burned annually or more frequently. The fires plus wood-gathering activities soon eliminate the marginal forest strips, and it is then that the former forest area ceases to be fragmented forest and becomes solid grassland. This man-made ecological succession slowly drives the forest higher on the sides of the mountains or deeper into the interior. Garden plantings are occasionally killed by frost at and above 8000 feet, and it is probably for this reason that forest cutting ceases at about that altitude. Man-made grasslands are the domain of

pigs. The areas are burned for the purpose of flushing the semi-feral animals from their cover, which prohibits the establishment of any sort of vegetational succession that might tend to reëstablish the forest.

Thus it is that primitive man establishes, and perpetuates, zonal barriers and zones of disturbed habitat—hybridized habitat. His activities doubtless have "forced" certain species, and notably these honeyeaters, to live together, whereas under "natural" conditions they do not coëxist in the same habitat.

Figure 8 illustrates how the cutting of the contiguous mountain forests, and their replacement by grasslands along the beds of valleys, enabled (1) the two parent groups to come into contact at Hybrid Gap and (2) made possible the isolation of certain hybrid swarms that formed on the sides of isolated mountains. One may doubt that the replacement of forest by grassland can serve as an effective trap for such mobile creatures as birds, especially when the grass barriers are narrow. However, Skutch (1954, p. 281) makes it very clear that many species of forest- and bush-loving birds such as wrens, antbirds, and Chisel-billed Caciques apparently prefer to face fire rather than risk a flight over open grassland. From a reading of his report (see below) it seems that artificial grasslands may be as effective as water as barriers to many birds. Skutch, in observing the activities of trapped birds in a burning patch of forest surrounded by grassland, wrote: "As the flames spread with a loud crackling and a dense cloud of smoke, the more mobile and wide ranging of the birds flew well in advance of the conflagration. Flycatchers and tanagers flew away first, then the pigeons and doves of several kinds. The more shy and secretive birds, which rarely expose themselves beyond the shelter of the thicket, were the last to show themselves at the edge of the burning tangle of bushes and vines. Finally, when the flames had come very near, a skulking Chinchirigui Wren [*Thryothorus modestus*] could endure it no longer and rushed forth, flying slowly and laboriously over the open fields beside the smoking thicket. But a pair of White-barred Antshrikes [*Thamnophilus doliatus*] and three Chisel-billed Caciques [*Amblycercus holosericeus*] refused to desert the sheltered thicket, and braving heat and smoke, stuck steadfastly in a small corner, a few yards across, which escaped being burnt."

Other Examples of Hybrid Swarms

One of the first to observe a correlation between hybrid swarms and hybrid habitats was Anderson (1948, p. 7) who concluded that hybrid

swarms can survive only in "hybridized habitats" and that such habitats are generally the result of human intervention. However, many hybrid swarms, particularly in the Holarctic region, were apparently brought about by habitat disturbances resulting from post-Pleistocene glacial recessions (see Mayr, 1942, p. 263). Habitat disturbance by primitive man seems to account for the typical swarms found in these New Guinea honeyeaters, but additional factors are needed to explain why a few of the swarms are morphologically unique.

To recapitulate this phenomenon as the author understands it, when interfertile species,[1] having arisen initially through the agency of geographical isolation, come into hybrid contact as a result of the shattering effects of habitat disturbance, they may interbreed freely and produce fertile, viable offspring. If the hybrid combinations and recombinations are frequent, a swarm will develop in the general area of contact which will probably consist of birds that are somewhat less fertile than either of the parent species. If less viable (reproductively somewhat impaired), the swarm will tend to remain more or less confined, not because the hybrid swarm would perish if genetic reënforcement from the parent species ceased, but presumably because the slightly impaired hybrids are selected against (are at a disadvantage) when forced to compete with the parent species (Gause's rule). However, as postulated herein, a very different situation would obtain if the swarm were to be freed from competition with either of the parent species through the medium of geographical or ecological isolation. Should this occur, and it seems to have done so in these honeyeaters, the isolated swarm would tend to select and discard characters and thus to accumulate differences exactly as in the geographical speciation of a non-hybrid population. In time the isolated swarm would evolve into a derived entity which, at least in some characters or character combinations, is consistently different from either of the parent species. But at the same time certain characters, which have not been acted upon selectively, would continue to be apparent. In "young" populations, such as the "gray-billed black-bills" of Mt. Goliath, these "swarm" characters would be quite obvious and frequent. In "old" populations so derived, there is a good chance that the occasional variations, not yet stabilized, would be confused with polymorphism.

[1] Regarding the interfertility of good species, Mayr (1942, p. 163) writes: "It has been proven again and again for birds and many other animals that several species can live side by side in nature without normally hybridizing, even though they are highly or completely fertile with one another in artificial crosses."

An excellent example is the Snow Mountain population of black bills in which two of 43 adults have superciliaries yellow, whereas the remainder have the superciliaries white.

This hypothesis, in which habitat disturbance plays a major part, is reënforced by the recent discovery of black bills and wattle birds living at the same altitudes within a few miles of each other on the same (northern) watershed of New Guinea (at Telefolmin) and showing little evidence of hybridization, apparently because the forests in this new area are largely intact, which seems to be because the human inhabitants of the Telefolmin region are few in number and more primitive than the people inhabiting the valleys near Hybrid Gap. Therefore they devote more time to hunting and less to gardening and forest destruction.

An analogous situation, in which two sympatric subgroups of birds tend to act as valid species in some regions and not in others, is described by Chapin (1948, p. 124), in which two species of drongos appear to be, and behave as, good species in one region of Africa and yet successfully interbreed in another. It is significant that Chapin believes that this condition is due to ecological shifts resulting from habitat disturbances caused by man, followed by the breakdown of the ecological isolation and then by hybridization. Another analogous situation is given by Sibley (1950, pp. 176–177; 1954, pp. 252–290) who found that different degrees of reproductive isolation exist in each of the four zones of secondary contact that are known among the Red-eyed Towhees of Mexico (*Pipilo erythropthalmus* and *P. ocai*). He found that at one extreme the two species live sympatrically without interbreeding, and, at the other, highly variable hybrid populations are produced.

From these and other studies of birds living under "natural" conditions, it becomes evident that some good species successfully interbreed and produce hybrid swarms that may become stabilized and subspecifically distinct (judging by morphological criteria). Such "races" provide a strong reason for suspecting that there exists a rare mechanism for the origin of species which operates through interspecific hybridization. If such a mechanism exists, one would expect to find evidence of it in archipelagoes where peninsulas are likely to become mozaics of islands and then peninsulas over and over again. The peculiar species swarms (for example, the Dinornithidae of New Zealand with 20 species, and the Geospizidae of the Galapagos Islands with 13 species) that have arisen on certain archipelagoes that have long been subject to vulcanism and the habitat-disturbing effects of eustatic

movement may owe part of their extraordinary radiation to this phenomenon.

Other possible examples of the origin of species through interspecific hybridization are: (a) the one given by Meise (1936) who found that in certain isolated Algerian oases there existed stabilized hybrid populations (*"flückigeri"*) between two distinct species of sparrows (*Passer domesticus* and *P. hispaniolensis*), whereas in other less isolated areas he found hybrid swarms; (b) an apparently stabilized hybrid population (*"cismontanus"*) between *J. hyemalis* and *J. oreganus* which Miller (1941) recognizes; and (c) a stabilized population of Saipan Island ducks (*"oustaleti"*) which Yamashina (1948) believes to have been derived from the Mallard (*A. platyrhynchos*) and the Gray Duck (*A. superciliosa*), both of which must have reached the island as stragglers.

As a result of these studies, the author concludes that the wattle birds and the black bills represent two interfertile groups (species). In his opinion the stabilized hybrid populations, which probably developed as a result of the coëntrapment in a hybrid habitat of elements of each species, should be recognized taxonomically if they conform to the 75 per cent rule for subspecies.

Thus morphology and not manner of origin should constitute the criteria for judging the existence of a race. One reason for this conclusion is that the manner of origin is not so radical as it might seem in such subspecies. For example, in developing from a swarm, the hybrid race seems to develop only under conditions of secondary geographical isolation. In short, it evolves in much the way that "standard" populations do, in isolation through the in part fortuitous discarding and selection of characters that have value in the new surroundings.

REVISION OF THE WATTLE BIRDS AND THE BLACK BILLS

An enigmatic question concerning morphologically "new" races that have developed (been derived) from hybrid swarms between species is, To which of the two parental species shall the "new" race be assigned, if either?

The following solutions were considered: (a) to assign a race that has developed in this manner to the parent species it most nearly resembles; and (b) to regard the parent groups as conspecific and to discard racial designations, regardless of morphological distinctness, if they prove their lack of reproductive isolation by hybridizing wherever they come in contact. The latter is the taxonomic solution adopted in the earlier study (Mayr and Gilliard, 1952b) before adequate informa-

tion on habitat disturbance was available. However, with the new information for study, a new classification is suggested, as follows:

WATTLE BIRDS
Melidectes leucostephes
Vogelkop
Melidectes rufocrissalis foersteri
Saruwaged Mountains
Melidectes rufocrissalis rufocrissalis
Schraderberg Mountains
Hindenburg Mountains
HYBRID SWARMS
Melidectes rufocrissalis × *belfordi*
Wahgi-Divide Mountains
Mt. Hagen
Mt. Giluwer
Mt. Kubor
Mt. Wilhelm
?Mittag Mountains
HYBRID RACES
Melidectes belfordi griseirostris
Mt. Goliath
Melidectes belfordi stresemanni
Herzog Mountains
BLACK BILLS
Melidectes belfordi joiceyi
Weyland Mountains
Melidectes belfordi kinneari
Nassau and Snow Mountains
Melidectes belfordi belfordi
Victor Emanuel Mountains and mountains of southeastern New Guinea
Melidectes belfordi brassi
Mountains of the southern watershed of southeastern New Guinea

SUMMARY

Observations shedding new light on the hybridization of wattle birds and black-billed honeyeaters (Mayr and Gilliard, 1952b) are presented. Evidence is presented that the two groups are not conspecific, despite their interfertility under certain widespread conditions of habitat disturbance.

New collections from the Victor Emanuel, Hindenburg, and Mittag Mountains, as well as nestlings from three widely separated regions of eastern, central, and western New Guinea, are analyzed. It is demonstrated that wattle birds are essentially forest-edge birds of the northern watershed and that the black bills are essentially pure forest birds of the central range and southern watershed.

The hypothesis is advanced that, as a result of the removal of the mountain forests by man, these two morphologically very different groups were brought into hybrid contact and that zones of hybridization formed along the artificial forest edges in the midst of what had formerly been pure mountain forest. In such "belt"-shaped areas of disturbance, in which the mechanisms of ecological isolation between the two groups of honeyeaters had been destroyed, wattle-bird genes flowed into new regions with black-bill genes to form hybrid swarms that sometimes became secondarily isolated. Two such swarms are postulated to have become stabilized and to have become taxonomically distinct from the parent species. The question of taxonomic recognition for "races" of hybrid ancestry between valid species is studied, and the conclusion is reached that morphological criteria and not lines of descent should dictate whether such races are valid or not. The problem of the assignment of such a race to a species group is studied. It is decided to assign it to the parent it more nearly resembles.

These conclusions are expressed in a revision of these two groups of hybridizing honeyeaters in which the wattle birds and the black bills are recognized as constituting two distinct species. Two races of hybrid ancestry (but nearest in composition to black bills) are recognized.

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