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ALTITUDINAL HYBRIDIZATION IN NEW GUINEA HONEYEATERS

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The evolutionary significance of hybridization in nature is still in dispute. It is evident that there are pronounced differences between animals and plants with respect to the frequency of hybridization, and that even within the animal kingdom there is considerable variation in the nature and frequency of hybridization. A full understanding cannot be expected until more cases of hybridization have been analyzed. The discussion of an unusual case of hybridization in a group of New Guinea honeyeaters is the object of the present contribution.

The mountain honeyeaters, which in the recent ornithological literature are combined in the superspecies *Melidectes leucostephes*, were originally described as four separate species. These belong to two rather distinct types which we might refer to as "wattle-birds" and "black-bills" (fig. 1, table 1). These two types are so different from each other that in the past they were sometimes placed in different genera, *Melidectes* and *Melirrhophetes*. The black-bills are rather uniform throughout their essentially continuous range; the wattle-birds are more variable (table 2). Ignoring for the time being the characters of the more isolated populations of wattle-birds (*leucostephes, foersteri*), the essential differences between black-bills and wattle-birds are summarized in table 1.

Table 1

Essential Differences between Black-bills (*belfordi*) and Wattle-birds (*rufocrissalis*)

Character	Black-bills	Wattle-birds
Bill (color)	black	gray
Bill (size)	short	long
Forehead	black	white
Gape wattle	small	large
Throat wattle	absent	large
Superciliary	white	yellow
Vertical range	higher	lower

The black-bills are restricted to the high mountains of the central ranges of the main portion of New Guinea from the Weyland Mountains (subspecies *joiceyi*) in the west to the mountains of southeastern New Guinea (subspecies *brassi*) in the east (Mayr, 1941). Variation within this area is limited on the whole to size and to the tints of gray and olive.

The wattle-birds are found on more or less isolated mountain ranges north of the central chain: the Arfak Mountains on the Vogelkop (*leucostephes*), Schraderberg in the Sepik Mountains (*rufocrissalis*), and the Saruwaged Mountains in the Huon Peninsula (*foersteri*) (fig. 2). The three forms are so different from each other that they were originally described as three separate species, and indeed *leucostephes* is sufficiently aberrant in its coloration to be still treated as a species. The differences between these three major types of wattle-birds are listed in table 2 in comparison with the characters of *brassi*.

All the populations of wattle-birds and black-bills are allopatric, and after a gray-billed "black-bill" (*griseirostris*) had been discovered on Mount Goliath (Oranje Mountains) it was proposed by Stresemann (1923) to consider all these forms, except *leucostephes*, as conspecific. This arrangement has been followed by most recent authors.

Since 1923 other populations have been found in east-central New Guinea which

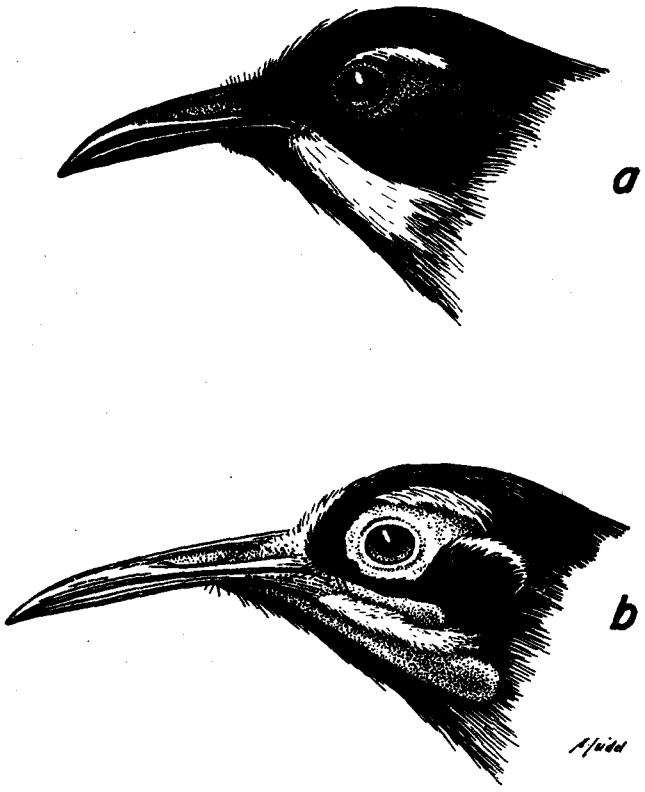

Fig. 1. Differences between a typical "black-bill" (*a*) and a typical "wattle-bird" (*b*). *a* = *Melidectes belfordi belfordi*; *b* = *M. b. rufocrissalis*.

provide additional confirmation for the assumption that black-bills and wattle-birds are not reproductively isolated. In 1929 Mayr found a new subspecies (*stresemanni*) in the Herzog Mountains which by its variability has all the earmarks of a hybrid population between wattle-birds of the *rufocrissalis* type and black-bills. E. T. Gilliard found

Table 2

Differences between the Three Major Types of Wattle-birds and a Black-bill (*brassi*)

	White on forehead	Wing	Bill	Nape and chest	Edges of feathers on back	Superciliaries and ear spots	Under tail coverts
leucostephes	extensive	short	medium	black	white	white	buff
foersteri	small area	very long	short	dark gray	white on upper back	white	ochre
rufocrissalis	rather extensive	medium	long	ash gray	pale gray	yellow	rufous
brassi	absent	medium	medium	ash gray	gray	white	rufous

evidence for hybridization in every sample collected by him in 1950 in the Hagen, Wahgi, and Wilhelm mountains. It is thus evident that wattle-birds and black-bills hybridize along the broad front between the Oranje Mountains (Mt. Goliath) and the Herzog Mountains, wherever they have come into contact (fig. 2).

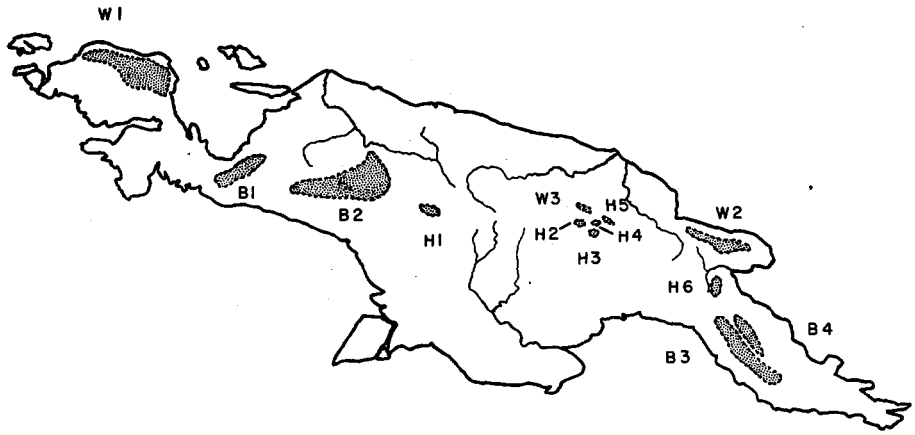

Fig. 2. Distribution of the known populations of honeyeaters of the *Melidectes leucostephes-belfordi* group. W = wattle birds; W_1 = *M. leucostephes* (Arfak Mts.); W_2 = *M. b. foersteri* (Saruwaged Mts.); W_3 = *M. b. rufocrissalis* (Schraderburg, Sepik Mts.). B = black-bills; B_1 = *M. b. joiceyi* (Weyland Mts.); B_2 = *M. b. kinneari* (Nassau, Oranje Mts.); B_3 = *M. b. brassi* (southeast New Guinea, low altitudes); B_4 = *M. b. belfordi* (southeast New Guinea, high altitudes). H = hybrid populations; H_1 = Mt. Goliath (*griseirostris*); H_2 = Mt. Hagen; H_3 = Mt. Kubor; H_4 = Wahgi Mts.; H_5 = Bismarck Mts.; H_6 = Herzog Mts. (*stresemanni*).

HYBRID INDEX

It has become customary within the last twenty-five years to express degrees of hybridity quantitatively. Following a suggestion made independently by various authors, perhaps first by Meise (1936), it is convenient to tabulate a hybrid index in such a manner that a typical individual of one parental strain scores 0, and a typical individual of the other parental strain 100. Nine differences between black-bills and wattle-birds were selected and given values, ranging from zero in the black-bills according to their importance up to 5, 10, 15, or 20 in the wattle-birds. The proper selection and scoring of these characters was by no means simple because some of them are affected by age, sex, season, and preservation. Still, we believe that our quantitative approach permits a more precise recording of the differences between the populations and of the hybridity of individual specimens than any other, more subjective method. The nine characters used are the following:

A. *Throat wattle* (0–15 points). Absence of a wattle is scored as zero, a large wattle as 15. Errors are introduced by the fact that females and immatures have on the average smaller wattles. Also, the wattles tend to shrivel up in dried skins which makes the scoring more difficult. Birds from the Lake Habbema region (*kinneari*) and from southeast New Guinea are almost consistently zero on this character. The Mount Goliath "black-bills" include several birds scoring "1" and one female scoring 7. The Schraderberg series, which theoretically should be 15, has: males, 10–15 (14.0) and females, 5–15 (9.1).

B. *Gape wattle* (0–10 points). Variability here is similar to that in the throat wattle.

C. *Naked area around eye* (0–5 points). This area is largely feathered in black-bills (0) and extensively naked in wattle-birds (5). Whatever naked area there is in black-bills is blue in life. The naked area in wattle-birds often appears yellow in the dried skin.

D. *Color of superciliary* (0–15 points). A white superciliary is scored 0; a bright lemon yellow superciliary is scored 15. All birds from Schraderberg score 15 on this character except one with 13.

E. *Color of posterior ear coverts* (0–5 points). White coverts are scored 0, yellow coverts 5.

F. *Color of forehead* (0–20 points). The forehead is black (0) in typical black-bills, extensively white (20) in wattle-birds. The feathers of the forehead in some specimens are completely coated by a mixture of nectar and pollen, which makes the scoring of such birds difficult.

G. *Bill-wing ratio* (0–15 points). Birds in which the bill is less than 27.7 per cent of the wing are scored 0; birds in which the bill is more than 33.3 per cent are scored 15. The correlation between this ratio and the apparent degree of hybridity is by no means perfect, but closer than either wing length or bill size alone.

H. *Color of bill* (0–10 points). A black bill is scored 0, a gray bill 10. In intermediate specimens the method of preservation sometimes seems to have affected the amount of grayness.

I. *Feathering at base of maxilla* (0–5 points). In black-bills the area between gape and nostrils is usually fully feathered (0); in wattle-birds it is often largely bare (5).

For the purpose of scoring, all birds were laid out in a single series in the sequence in which they showed the expression of a given character. The labels were not consulted and the specimens recorded until all specimens had been classified. This procedure was repeated for each character.

THE ANALYSIS OF POPULATIONS

BLACK-BILLS

(1) *kinneari* (Lake Habbema-Idenburg River) (B_2 on map).

Hybrid index—males, 2, 3, 8; females, 5, 9, 10.

The slight deviation from 0 is almost entirely contributed by the bill-wing ratio (G), namely 24 of the total 37 points in the six specimens. There is no indication in this population of the presence of wattle-bird genes.

(2) *brassi* (Mt. Tafa, Angabunga River, southeast New Guinea) (B_3 on map).

Hybrid index—males, 3, 4, 10; females, 1, 4, 4.

The slight deviation from a theoretical zero value is no indication of hybridism.

WATTLE-BIRDS

rufocrissalis (Schraderberg, Sepik Mountains) (W_3 on map).

Hybrid index—males, 87, 89, 90, 90, 96, 96, 100; females, 81, 83, 84, 85, 86, 88, 98; median, 88.5.

The material is in part poorly prepared and difficult to score. There is no evidence that the deviations from a theoretical 100 score are due to gene flow from black-bill populations.

HYBRID POPULATIONS

(1) *griseirostris* (Mount Goliath) (H_1 on map).

Hybrid index—males, 30, 32, 35, 35, 36; females, 21, 38; median, 35.

The index shows a distinct influence of wattle-bird genes not only in the gray bill but also in the development of the wattles, the bare areas on the bill and around the eye, and occasional indications of yellow in superciliary and ear coverts.

(2) Mount Hagen (2500-3500 meters), collected by E. T. Gilliard (H_2 on map).

Hybrid index—males, 7, 9, 31; females, 7, 9, 9, 10, 54; median, 9.

This is a very interesting series. Six of eight specimens are virtually pure black-bills, two others are hybrids, one even closer to the wattle-birds than to the black-bills.

(3) Mount Kubor (? 1800 meters), collected by E. T. Gilliard (H_3 on map).

Hybrid index—female, 76.

Closer to the wattle-birds but with evident gene flow from the black-bills, leading to reduction of gape and throat wattle.

(4) Mount Wilhelm, Bismarck Mountains (2900-3300 meters), collected by E. T. Gilliard (H_5 on map).

Hybrid index—males, 9, 37; females, 17, 23.

These birds are close to black-bills, but some have definite wattle-bird traits. One bird, for instance, has a large throat wattle and much white on the forehead.

(5) Wahgi Mountains, above Nondugl (1620-2300 meters), collected by E. T. Gilliard (H_4 on map).

Hybrid index—males, 32, 65, 67, 76, 81, 84, 88; females, 59, 80, 81; median, 78.

Some of these specimens appear to be virtually pure wattle-birds, but at least half of the specimens are evident hybrids, one bird being definitely a "black-bill." The forehead varies from black to almost completely white. A male from Yandara (northern slope of the Bismarcks) has an index of 82.

(6) *stresemanni* (Herzog Mountains) (1400-2100 meters) (H_6 on map).

(*a*) Dawong (Mayr collection) (see Mayr, 1931).

Hybrid index—males, 41, 52; females, 27, 39, 40, 50, 55.

(*b*) Mount Misim (Stevens collection) (see Greenway, 1935).

Hybrid index—males, 25, 38, 39, 48, 61, 64; females, 32, 35, 52; median, 40.5.

Both series (*a* and *b*) are similar in their variability and are samples from an evident hybrid population. Curiously, however, the forehead is black in all birds. In most other characters the birds are closer to wattle-birds than to black-bills. About 35 per cent of the birds have superciliary and ear coverts largely white.

CORRELATION BETWEEN CHARACTERS

An examination of phenotypes is at best a poor substitute for a genetic analysis. However, since it is impossible to analyze these mountain birds genetically, at least a few remarks may be made on the probable genetic basis.

The first important fact is that a bird which shows hybridism in one character usually also indicates hybridism in several other characters.

The second is that the amount of hybridism is not the same in all characters. For instance, a female from the Hagen Mountains (A.M.N.H.) has full wattle-bird characters with respect to bill color (10), bill feathering (5), and color of the superciliary (15); is near the wattle-birds in the color of the ear coverts (4), is intermediate in the naked ocular area (3) and the gape wattle (6), and closer to the black-bills in the forehead coloring (5), the throat wattle (2), and the bill-wing ratio (4). A similar situation prevails with most specimens from the hybrid population, as is evident from table 3.

The third important fact is that every character seems to have a multifactorial basis. Every stage of intermediacy is represented in most of the hybrid populations for most of the characters. There are a few notable exceptions. One, as stated, is that all birds from the Herzog Mountain have a black forehead, no matter how close to a wattle-bird they may be in other characters. Another is that all birds from Mount Goliath have a gray bill no matter how purely "black-bill" they are in all other characters.

Table 4 indicates clearly that the various characters by no means show the same degree of intermediacy in the various populations. The bill, for instance, is grayer in all five hybrid populations (1, 2, 4, 5 and 6 above) than expected according to the "mean hybridity" of the respective population. The forehead, on the other hand, has less white in all five populations than should be expected on the basis of "mean hybridity." The throat wattle also scores lower than expectation in all five populations. Gape wattle and naked ocular area score higher in all populations except the Wahgi Mountains. There is no regularity (nor great deviations from expectation) with respect to the color of the ear coverts and the feathering at the base of the bill. Finally, there are two characters which deviate from expectancy, according to whether the population as a whole is more wattle-bird or more black-bill. The bill-wing ratio is above expectation in the three

Table 3

Characters of All Examined Specimens from Five Hybrid Populations

Locality	Sex	Altitude	15 Bill/wing	15 Throat wattle	10 Gape wattle	5 Ocular area	5 Ear coverts	15 Superciliary	20 Forehead	10 Bill color	5 Bill feathering	100 Total
		Maximal scores for each of nine characters										
Mt. Goliath	♂	?	8	1	8	2	1	1	0	10	1	32
	♀	?	9	7	6	3	1	1	0	10	1	38
	♂	?	9	1	4	3	1	1	0	10	1	30
	♂	?	12	0	4	4	0	0	0	10	5	35
	♀	?	0	1	4	3	1	1	0	10	1	21
	♂	?	11	1	3	3	3	3	0	10	1	35
	♂	imm. ?	10	1	5	3	3	3	0	10	1	36
		Median	9	1	4	3	1	1	0	10	1	35
Mt. Hagen	♂	8200	3	4	7	4	1	0	3	4	5	31
	♀	8200	4	2	6	3	4	15	5	10	5	54
	♀	11000	4	0	3	0	0	0	0	2	1	10
	♀	11000	3	0	3	3	0	0	0	0	0	9
	♂	8200	3	0	3	1	0	1	0	1	0	9
	♂	8200	4	1	1	1	0	0	0	0	0	7
	♂	8200	4	0	1	0	0	0	0	2	0	7
	♂	8200	6	0	0	0	0	0	0	2	1	9
		Median	4	0	3	1	0	0	0	2	1	9
Mt. Wilhelm	♂	9500	5	10	4	1	1	0	12	3	1	37
	♀	11000	4	0	4	2	0	1	0	3	3	17
	♀	11000	6	0	2	1	3	5	3	3	0	23
	♂	9500	4	2	1	1	1	0	0	0	0	9
		Median	4.5	1	3	1	1	1	2	3	1	20
Wahgi Mts.	♂	6000	15	13	10	4	5	15	15	10	1	88
	♂	6500	11	11	9	3	5	15	15	10	5	84
	♂	6000	9	13	9	5	5	15	10	10	5	81
	♂	6500	9	12	8	5	3	5	10	10	3	65
	♀	6500	13	5	8	4	5	15	15	10	5	80
	♂	6500	11	11	8	5	4	13	0	10	5	67
	♂	5300	12	10	7	3	4	10	15	10	5	76
	♂	7500	8	8	6	2	1	1	0	3	3	32
	♀	6500	12	13	5	4	5	15	12	10	5	81
	♀	6500	8	0	4	1	3	1	0	4	1	22
		Median	11	11	8	4	4	14	11	10	5	78
Herzog Mts.	♂	Mt. Misim	6	7	9	4	1	1	0	10	1	39
	♂	Mt. Misim	6	2	8	4	4	13	0	10	1	48
	♂	Mt. Misim	7	11	8	4	5	15	0	10	1	61
	♂	Dawong	4	13	7	4	3	10	0	10	1	52
	♂	Mt. Misim	6	9	7	3	1	1	0	10	1	38
	♂	Mt. Misim	4	1	5	2	1	1	0	10	1	25
	♂	Mt. Misim	6	15	6	5	4	13	0	10	5	64
	♂	Dawong	4	2	6	0	4	10	0	10	5	41
	♀	Dawong	6	0	6	0	1	1	0	10	3	27
	♀	Dawong	2	2	6	3	3	13	0	10	1	40
	♀	Mt. Misim	8	10	6	4	3	10	0	10	1	52
	♀	Mt. Misim	5	6	5	2	3	1	0	10	0	32
	♀	Dawong	8	5	5	3	4	15	0	10	0	50
	♀	Dawong	2	2	5	2	4	13	0	10	1	39
	♀	Mt. Misim	6	9	4	3	1	1	0	10	1	35
	♀	Dawong	4	10	4	4	5	15	0	10	3	55
		Median	6	6.5	6	3	3	10	0	10	1	40.5

black-bill populations and below expectancy in the two wattle-bird populations. The superciliary stripe, on the other hand, is below expectation in the three black-bill populations and above it in the two wattle-bird populations.

Table 4

Observed Medians in Per Cent of Complete Wattle-bird Characters

	Forehead	Throat wattle	Superciliary	Ear coverts	Bill feathering	Mean hybrid index	Bill/wing	Ocular area	Gape wattle	Bill color
Mt. Goliath	0	6.7	6.7	20	20	34.8	60	60	40	100
Mt. Hagen	0	0	0	0	20	13	26.7	20	30	20
Mt. Wilhelm	10	6.7	6.7	20	20	19.3	30	20	30	30
Wahgi Mountains	55	73.3	93.3	80	100	81.7	73.3	80	80	100
Herzog Mountains	0	43.3	66.7	60	20	50	40	60	60	100

The curves of variation of nearly all these populations are strongly skewed. Since the mean gives in such cases an entirely distorted picture of the character of the population, the median was chosen to indicate the central tendencies. Table 4 was calculated in a manner illustrated by the following example. The median for gape wattle of the Mount Goliath population is 4. This is 40 per cent of the value 10 found in a "pure" wattle-bird. Or, the median for forehead color in the Wahgi population is 11. This is 55 per cent of the value 20 found in a "pure" wattle-bird, and so forth (see table 4). The results of table 4 are shown graphically in figure 3.

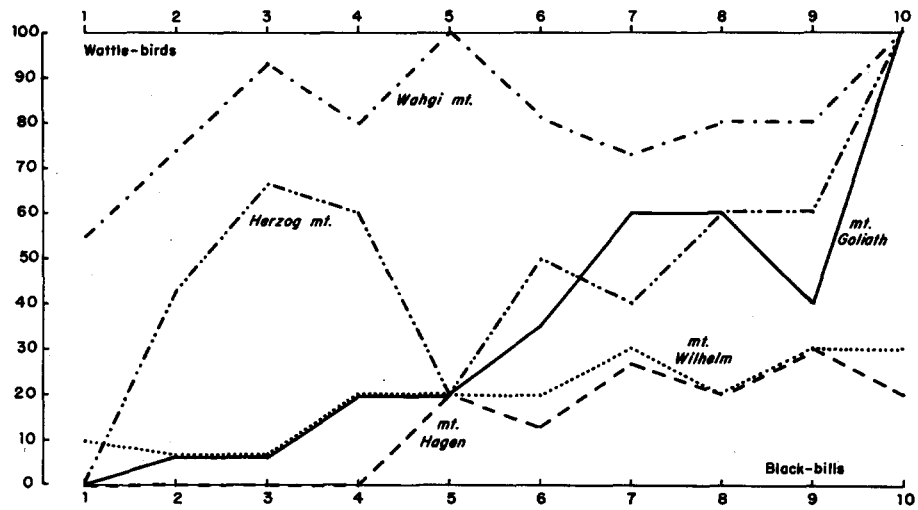

Fig. 3. Pictorial presentation of the data in table 4. Ordinate (0–100) indicates per cent of complete wattle-bird characters. Points 1–10 on abscissa indicate following characters: 1 = forehead, 2 = throat wattle, 3 = superciliary, 4 = ear coverts, 5 = bill feathering, 6 = mean hybrid index, 7 = bill/wing ratio, 8 = bare skin in ocular area, 9 = gape wattle, 10 = bill color. For further explanation, see text.

Precisely what the data presented in table 4 mean is difficult to determine. It is probable that the genes producing the various hybrid characteristics are coupled with physiological properties, which are subject to local selection. This may account for the gray bills in the Mount Goliath population and the black forehead of the Herzog Moun-

tain population. Also, comparatively few wattle-bird genes may be sufficient to pass the threshold for the "gray bill" character, while a very high concentration of wattle-bird genes may be required for the character "white forehead." The other deviations might all be explained in terms of "modifier complexes" or "genetic background," but it would be futile to do so in absence of any concrete evidence.

VARIATION AND ALTITUDE

The wattle-birds are, on the whole, inhabitants of the low mountains (1500-2000 meters), the black-bills of high mountains (2500-3400 meters). Where the black-bills

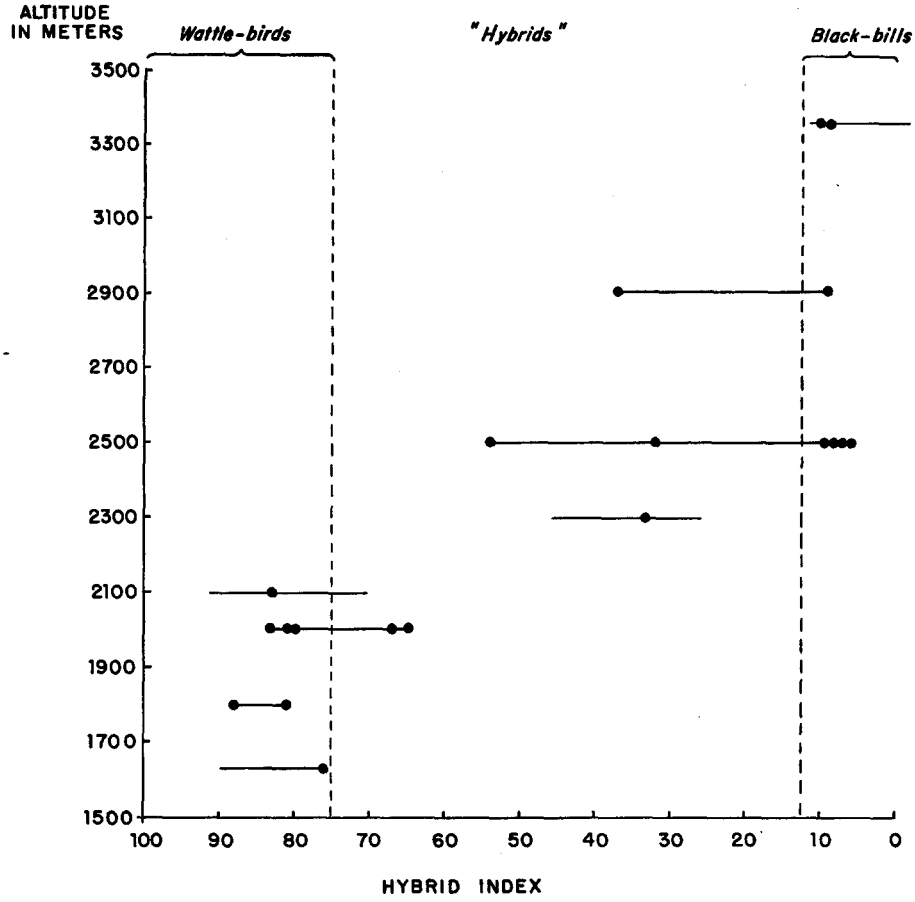

Fig. 4. Decrease of hybrid index with increase in altitude. Each point denotes a specimen collected in the Hagen-Bismarck area at the stated altitude.

are absent, as in the Saruwaged Mountains, the wattle-birds may ascend to an altitude of 2000-3400 meters. In southeastern New Guinea and apparently also in the Weyland and Oranje mountains, where the wattle-birds are absent, the black-bills descend as low as 1800 or even 1600 meters.

Collections made in the hybrid zone are not sufficiently well labeled to yield conclusive information, but there is much evidence that the hybrid index decreases with increasing altitude (fig. 4). The higher the altitude, the closer the birds resemble black-bills, on the average.

Gilliard obtained three large samples in the Hagen-Bismarcks region. The Mount Hagen sample collected at 2700-3500 meters has a median hybrid index of 9, six of eight birds being almost pure black-bills. The Mount Wilhelm (Bismarck Mountains) sample, collected about 140 kilometers farther east at the equally high altitude of 2900-3300 meters, has a median hybrid index of 20, also close to the black-bills. However, a series collected about half way between these two localities on the Wahgi Mountains, which connect the Bismarcks with the Hagen Mountains, but at the low altitude of 1600-2300 meters had a median hybrid index of 78, only 10 points below the median of 88.5 found in a pure wattle-bird series (*rufocrissalis*).

Specimens were collected at different altitudes on Mount Hagen, on Mount Wilhelm, and on the Wahgi Mountains, but most of these specimens were obtained by native hunters at unknown altitudes and brought to the base camp. No reliable correlation between hybrid index and altitude can therefore be established for a single mountain. However, the two specimens from Mount Hagen, which have the highest index were collected at the lower camp (2500 meters), and the only specimen in the Wahgi Mountains that was collected above 2000 meters had by far the lowest hybrid index (32). It is the only specimen from the Wahgi Mountains which is closer to the black-bills than to the wattle-birds. What little is definitely known about altitudinal variation on a single mountain thus fully supports the hypothesis that there is a close inverse relation between altitude and hybrid index. This is further supported by the only specimen from the Kubor Mountains collected at 1800 meters, which has a hybrid index of 76, and a single specimens from Yandara (2100 meters), north slope of the Bismarcks, with an index of 82. Both of these birds from low altitudes have essentially the characters of wattle-birds.

ORIGIN OF THE HYBRID POPULATIONS

The black-bills and the wattle-birds are allopatric, but where they come into contact they form highly variable hybrid populations. The most plausible interpretation of this situation is that wattle-birds and black-bills have attained their distinctness in geographical isolation, and have come into contact only rather recently. It would seem of interest to try to reconstruct the areas of isolation and to speculate on the nature of the isolating barriers.

The map (fig. 2) shows that two of the wattle-bird populations (W_1, W_2) are completely isolated, while the third (W_3) is on an incompletely isolated northern spur of the central ranges. The hybrid zone extends from Mount Goliath (H_1) in the west to the Herzog Mountains (H_6) in the east. Most of the hybrid populations are near the northern slopes of the central ranges, but the presence of hybrid populations on Mount Goliath (H_1) and on Mount Kubor (H_3) indicates the southward penetration of wattle-bird genes. Most puzzling is the fact that apparently pure black-bill populations occur both east and west of the hybrid zone: *joiceyi* (B_1), *kinneari* (B_2), *brassi* (B_3) (southeast New Guinea, lower altitudes), and *belfordi* (B_4) (southeast New Guinea, higher altitudes). These four subspecies are very similar to each other, differing only in size and minor details of coloration.

The present day distribution thus does not furnish a clear picture. 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.

There is much in the distribution of New Guinea birds to indicate that part of northern New Guinea was once isolated from the remainder of the island. This fact has been commented on by several authors, for instance, Hartert *et al.* (1936). Northern New

Guinea is the home of many endemic species and subspecies of birds, some of which have subsequently spread into the Vogelkop, to the south coast of New Guinea (opposite the head of Geelvink Bay) or into southeast New Guinea, without, however, losing their essential status as endemics of northern New Guinea.

Species indigenous to northern New Guinea are *Casuarius unappendiculatus, Talegalla jobiensis, Rallicula rubra, Goura victoria, Eos duivenbodei, Psittaculirostris edwardsii, Monarcha rubiensis, Poecilodryas brachyura, Manucodia jobiensis, Drepanornis bruijni, Paradisaea minor, Xanthomelus (aureus) bakeri, Philemon brassi.* Very distinct subspecies or subspecies groups of non-passerines endemic in northern New Guinea are *Ptilinopus iozonus finschi, Ptilinopus viridis salvadorii, Megaloprepia magnifica septentrionalis, Ducula pinon jobiensis, Gallicolumba rufigula septentrionalis, Trugon terrestris mayri, Charmosyna pulchella rothschildi, Micropsitta pusio beccarii, Probosciger aterrimus stenolophus, Geoffroyus geoffroyi (pucherani* group), *Alisterus chloropterus moszkowskii, Chaetura novaeguineae bürgersi, Alcyone azurea ochrogaster, Alcyone pusilla laetior, Melidora macrorhina jobiensis,* and *Halcyon nigrocyanea quadricolor.* There are even more such cases among the passerine birds, but it would lead too far to list them all.

Too little is as yet known about the geology of New Guinea to permit a decision as to whether northern New Guinea was once a real island, separated by water, or merely an ecological island separated by vegetational barriers. It is possible, for instance, that during an arid period in the late Tertiary a belt of grasslands separated the forest country in north New Guinea from similar country in central and south New Guinea. Such a grassland barrier might have permitted species formation. Perhaps the barrier was a combination of a marine basin in the Sepik-Mamberano Valleys and unsuitable habitat in a possible land bridge east of Geelvink Bay. Any further speculation would be pointless until more is known about the geological and phytogeographical history of New Guinea.

DISCUSSION

Various kinds of hybridization phenomena are known in birds and other animals. Sympatric hybridization between individuals of different populations, which otherwise behave like good species, occurs occasionally, as in birds of paradise, grouse, and ducks, but seems without evolutionary significance.

Frequent cases of allopatric hybridization, in which populations formerly isolated now interbreed in a contact zone, have also been recorded in the literature. Since acquisition of reproductive isolation and morphological divergence are not closely correlated, we find every degree of morphological difference between the hybridizing populations. The mere fact of random interbreeding is usually accepted—by definition—as proof of conspecificity, although as a taxonomist one is reluctant to unite into a single species such strikingly different forms as *Astrapia stephaniae* and *A. mayeri* (Mayr and Gilliard, 1952).

Hybridization in the *Melidectes belfordi* group belongs in this category. There appears to be random interbreeding between wattle-birds and black-bills wherever they come into contact. What distinguishes this from previously described examples of allopatric hybridization in birds is the position of the hybrid belt. Normally the hybrid zone is a geographical line (east to west, or north to south). Here the hybrid belt is in an altitudinal zone.

As stated, wattle-birds prefer lower altitudes (1600-2000 meters), black-bills higher altitudes. When these two kinds of birds met in the same mountain ranges, the black-bills became superimposed over the wattle-birds, with a hybrid belt forming in inter-

mediate altitudes. It appears from the analysis of the populations in the Hagen-Wahgi mountains that each altitudinal belt has its characteristically composed population. The explanation for the fact that there has not been a complete merging of the two ancestral populations into a single homogeneous one at all altitudes is presumably the following. The morphological characters of wattle-birds are apparently associated with genes having a selective advantage at low altitudes, the black-bill characters with such having a high selective value at high altitudes. Accordingly, in the hybrid zone there is a gradient on each mountain from prevailingly wattle-birds at lower altitudes to prevailingly black-bills at higher altitudes. Similar situations have been described by botanists for altitudinally representative "species" of plants. Selection thus prevents the complete obliteration of the two original gene complexes.

The argument might be raised that the "hybrid belt" is not due to hybridization at all but is simply an altitudinal character gradient. A study of altitudinal variation in the areas where only one of the two types (black-bills *or* wattle-birds) occurs proves conclusively the fallacy of this assumption. For instance, in areas where wattle-birds are absent black-bills have not only a much greater vertical range but also fail to show any variation of color or structure with altitude. The only altitudinal variation in these areas is one of size (table 5). In southeast New Guinea there is a rather sharp break between

Table 5

Altitudinal Variation of Wing Length of Black-bills (*Melidectes belfordi*)

Western Oranje Range (from Rand, 1942)			Southeastern New Guinea (from Rand, 1936)		
Altitude (in meters)	Male	Female	Altitude (in meters)	Male	Female
3600	144–150	121–127	3680	147–153	140
3225	136–151	128, 134			
2800	138–151	125–135	2800	139	127, 131
2200	133	125	2400		139
2150	140, 142	127, 128	2000	140–144	127–131
1800	133–144	116–127	1600	132–144	123–137

brassi (1600-2800 meters) and *belfordi* (± 3680 meters); in the Oranje Ranges there is no sharp break anywhere, but an indication of a step in the increase of size between 2200 and 2800 meters. In spite of greatly increased altitudinal range, the birds are thus at all altitudes of the black-bill type.

The analysis of hybridism in the *Melidectes belfordi* group adds some new aspects to the known diversity of hybridism among birds. Although lacking the perplexing complications of hybridization as found in *Passer* (Meise, 1936), *Terpsiphone* (Chapin, 1948), and *Pipilo* (Sibley, 1950), the situation in *Melidectes* again shows that morphological divergence and acquisition of a sterility barrier may be independent of each other. It also emphasizes the fact that morphological characters are the product of gene complexes which at the same time control physiological characters of considerable adaptive value.

TAXONOMIC QUESTIONS

Like all borderline cases the *Melidectes leucostephes-belfordi* group is difficult to deal with from the point of view of taxonomy. Although including all the birds in a single superspecies, recent ornithologists have almost unanimously maintained *leucostephes* (Arfak) as a separate species, while combining the other wattle-birds and the black-bills into a single species. Is this logical? If one wants to recognize species, should one

not put all wattle-birds in one species and all black-bills in another? But what to do then with all the populations between Oranje and Herzog mountains? The complete lack of reproductive isolation wherever wattle-birds and black-bills come into contact indicates that they should not be treated as two separate species in spite of the morphological differences. The current solution to place all populations (except the widely isolated *leucostephes*) into a single species is presumably the most sensible compromise.

An equally great, if not greater, quandary exists on the subspecies level. The four generally recognized subspecies of black-bills (*belfordi, brassi, kinneari,* and *joiceyi*) are less different than the various hybrid populations from mounts Hagen, Wilhelm, and Wahgi are from each other. And, intergrading populations at different altitudes of the same mountain are more different from each other than the recognized subspecies of black-bills. Yet it would be absurd to distinguish the populations in the hybrid area as different subspecies, much though they may differ from each other in the average phenotype (= median hybrid index). The most sensible solution of this difficulty is probably to list these populations simply as *Melidectes belfordi,* with locality and altitude stated in parentheses.

SUMMARY

Two subgroups of honeyeaters of the *Melidectes leucostephes-belfordi* group are allopatric in New Guinea, but interbreed freely in a broad area of contact in the mountains of central New Guinea. The two groups, which may be called "wattle-birds" and "black-bills," differ in many characters, such as proportions of the bill, color of the bill, extent of feathering on base of bill and around the eye, presence (or absence) and size of gape and throat wattles, and color of the forehead, superciliary, and ear-coverts. By scoring these characters a hybrid index can be calculated, ranging from 0 in an extreme black-bill to 100 in an extreme wattle-bird. An analysis of the hybrid index shows that there are now known six hybrid populations: Mt. Goliath (east Oranje Mountains), Hagen Mountains, Wahgi Mountains, Bismarck Mountains, Kubor Mountains, and Herzog Mountains. Some of them are closer to black-bills (Hagen, Bismarcks), others to wattle-birds (Wahgi, Herzog), but all show extreme variability. A specimen showing indications of hybridism in one character usually shows also signs of hybridism in others. The degree of intermediacy of characters indicates that they have a multifactorial basis. In the hybrid zone populations of low altitudes show a prevalance of wattle-bird characters, birds of high altitudes a prevalence of black-bill characters. Outside the hybrid zone black-bills and wattle-birds may range from 1600 meters to 3300 meters without vertical variation of morphological characters except size.

The data indicate that black-bills and wattle-birds attained morphological distinctness but not reproductive isolation in geographical isolation. When these two kinds of honeyeaters met after the breakdown of extrinsic isolation, they interbred freely. However, since their respective gene complexes had become correlated with a preference for and higher viability at different altitudes, there is now different genetic composition at different altitudes, presumably maintained by selection. The great extent of the hybrid area, from Mt. Goliath (139° 5′ E) to the Herzog Mountains (147° E), indicates that it is not a very recent condition.

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LITERATURE CITED

Chapin, J. P.
1948. Variation and hybridization among the paradise flycatchers of Africa. Evol., 2:111-126.
Greenway, J. C.
1935. Birds from the coastal range between the Markham and the Waria rivers, northeastern New Guinea. Proc. New England Zoöl. Club, 14:98-99.
Hartert, E., K. Paludan, Lord Rothschild, and E. Stresemann
1936. Die Vögel des Weyland-Gebirges und seines Vorlandes. Mitt. Zool. Mus. Berlin, 21:165-240.
Mayr, E.
1931. Die Vögel des Saruwaged- und Herzoggebirges (N. O. Neu-Guinea). Mitt. Zool. Mus. Berlin, 17:713-714.
1941. List of New Guinea birds. American Museum of Natural History, New York, 260 pp.
Meise, W.
1936. Zur Systematik und Verbreitungsgeschichte der Haus- und Weidensperlinge, *Passer domesticus* (L.) und *hispaniolensis* (T.). Jour. für Ornith., 84:633.
Rand, A. L.
1936. Altitudinal variation in New Guinea birds. Amer. Mus. Nov., no. 890:1-4.
1942. Results of the 1938–1939 New Guinea Expedition. Bull. Amer. Mus. Nat. Hist., 79:425-515.
Sibley, C. G.
1950. Species formation in the red-eyed towhees of Mexico. Univ. Calif. Publ. Zoöl., 50:109-194.
Stresemann, E.
1923. Dr. Bürgers' ornithologische Ausbeute im Stromgebiet des Sepik. Arch. f. Naturg., 89 A: 55-56.

American Museum of Natural History, New York, New York, June 2, 1952.