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GEOGRAPHICAL VARIATION IN *DEMIGRETTA SACRA* (GMELIN)

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The study of the geographical variation of color phases has received considerable attention in recent years, because of the belief that such studies might shed light on the question of species formation. The widespread Reef Heron, *Demigretta sacra*, which occurs in a gray and in a white phase, lends itself very well to such a study, particularly since the Whitney South Sea Expedition gathered magnificent material of this species on nearly all of the island groups of the Pacific. Miss Cardine Bogert measured most of this material some years ago, but was prevented from completing this task. Her notes were of considerable value in the preparation of the present report. In addition to 640 specimens in the Amer. Mus. Nat. Hist., a series of 72 birds in the U. S. National Museum and a specimen in the Mus. Comp. Zoöl., Cambridge, were also examined. We are grateful to the curators of these institutions for permission to report on this material.

[1] Previous papers in this series comprise American Museum Novitates, Nos. 115, 124, 149, 322, 337, 350, 356, 364, 365, 370, 419, 469, 486, 488, 489, 502, 504, 516, 520, 522, 531, 590, 609, 628, 651, 665, 666, 709, 714, 820, 828, 912, 915, 933, 939, 947, 977, 986, 1006, 1007, 1056, 1057, 1091, 1116, and 1133.

I.—SIZE VARIATION

A tabulation of the measurements of our specimens reveals that *Demigretta sacra* can be divided into two races on the basis of size. This division is independent of any geographical variation of color phases. The wing and tarsus measurements in the appended tabulation are based on fully adult specimens except where stated.

TABLE OF MEASUREMENTS OF *Demigretta sacra*

LOCALITY GROUP 1	NUMBER MEASURED	WING LENGTHS	MEAN
New Zealand	2	277 (imm.), 278 mm.	
Australia	3	280, 283, 283	
New Guinea and nearby islands, Bismarck Archipelago	22	271, 272, 275, 276, 279...295, 297, 302, 305, 306	(288)
East Indies	53	268, 270, 270, 271, 271...295, 295, 295, 296, 308	(282)
Coast of Asia: Malay to China	10	272, 274, 280, 281, 282, 293, 294, 297, 300, 303	(288)
Philippine Islands	14	271, 273, 275, 276, 277...284, 285, 286, 292, 293	(282)
Marianne and Caroline Islands	30	268, 270, 270, 271, 272...296, 297, 297, 298, 309	(284)
Union, Samoa, Tonga Islands	17	270, 270, 273, 275, 275...294, 294, 298, 304, 306	(285)
Marquesas Islands	31	270, 270, 270, 271, 272...295, 295, 297, 298, 301	(284)

Locality	Number Measured	Wing Lengths	Mean
Group 1			
Tuamotu Archipelago	27 ♀	270, 270, 270, 270, 271...279, 280, 281, 283, 285 (274)	
	39 ♂	279, 280, 282, 285, 285...297, 298, 299, 301, 301 (292)	(283)
Austral Islands	18	270, 272, 273, 277, 277...292, 294, 295, 302, 302	(286)
Society Islands (type locality *D. sacra*)	15	272, 280, 280, 281, 288...295, 297, 297, 300, 302	(290)
Group 2			
Japan and Nansei Islands	2 ♀	287, 293 (290)	
	11 ♂	295, 297, 302, 302, 305... 311, 312, 313, 314, 317 (307)	(299)
Solomon Islands	33	270, 274, 275, 278, 279... 308, 309, 309, 310, 313	(294)
Swallow, Banks, Santa Cruz, New Hebrides Islands	11	272, 272, 285, 285, 288... 296, 302, 316, 316, 318	(296)
Fiji Islands	34	275, 276, 278, 280, 283... 307, 307, 310, 311, 315	(297)
Group 3			
New Caledonia	2 ♀	322, 329(325.5)	
	2 ♂	332(sub-adult type *E. brevipes*), 338(335)	(330)
Loyalty Islands	2	♀ 320; ♂ 343	(332)

Locality	Number Measured	Tarsus Lengths (selected groups)	Mean
Andaman Islands	1	67	
Thailand and Malay Peninsula	7	67, 69, 69, 70, 73, 78, 79	(72)
Sumatra and coastal islets	6	64, 68, 69, 70, 74, 74	(70)
Celebes	9	67, 67, 68, 71, 75, 77, 78, 81, 82	(74)
Australia and New Zealand	9	65, 71, 72, 74, 75, 75, 77, 78, 81	(74)
Japan and Nansei Islands	3 ♀	74, 77, 82 (78)	
	11 ♂	77, 78, 80, 81, 84, 84, 85, 87, 88, 88, 90 (84)	(81)
Solomon Islands	34	67, 70, 70, 70, 72...82, 84, 85, 85, 86	(78)
Fiji Islands	33	72, 73, 73, 74, 75...85, 85, 88, 92, 92	(81)
Society Islands	18	67, 70, 70, 73, 73...79, 79, 79, 79, 82	(76)
Tuamotu Archipelago	36 ♀	65, 66, 66, 66, 66...73, 74, 74, 74, 74 (70)	
	37 ♂	71, 71, 72, 72, 73...80, 80, 80, 81, 82 (76)	(73)
Loyalty Islands	2	85, 92	(89)
New Caledonia	5	83, 87, 88, 89, 96 (type *E. brevipes*)	(89)

Study of this large series of measurements of *Demigretta sacra* permits the following conclusions:

I.—Over most of its range the size of the Reef Heron (as reflected in the wing length) is quite uniform and without significant variation (see Group 1 in the table of wing lengths).

II.—The populations placed in Group 2 in the table are of somewhat larger average size. The following percentages of each component of this group exceed the maximum wing length (309 mm.) of the "normal" birds in Group 1: Japan and Nansei Islands—23% (45% of males); Solomon Islands—7%; New Hebrides and adjacent islands—27%; Fiji Islands—12%. Obviously none of these approaches the degree of distinctness necessary for racial separation. The series from the Society Islands (type locality of *A. sacra* Gmelin is Tahiti, S. I.) averages 290 mm. in wing length, which happens to be about the average between the extremes of Groups 1 and 2.

III.—The birds from New Caledonia and the

Loyalty Islands (Group 3) are much larger than any of the other populations. Their separation as a distinct race by earlier systematists, though generally overlooked or ignored by recent writers, must be upheld.

IV.—The size trends just discussed are not so well reflected in the tarsal measurements. Perhaps this is merely because it is a smaller unit, and hence more affected by small errors in taking the measurement.

It will be noted that the tarsus shows no increase in length in the Malayan and Indian Ocean regions of the range, and hence no trend toward the long-legged species of *Egretta*, some of which were formerly included in *Demigretta*. The tarsus of *sacra* throughout its range is only about 26% of the wing length. In the species of *Egretta* the corresponding percentages are about as follows: *gularis*—33%; *eulophotes* (from Hartert, Vögel Pal. Fauna, II, p. 1241)—33%; *dimorpha*—35%; *schistacea*—38%; *garzetta*—38%. Also related to the length of the legs in *Egretta*, perhaps, is the fact that the bare area of the tibia is over half of the tarsus length (54–64% in various species), while in *Demigretta sacra* it is only about 45%. *Egretta* also has longer and somewhat more specialized plumes.

On the other hand, *Demigretta* shows great similarity to *Egretta* in many respects. Each of the three dimorphic species of the latter genus has, in the gray phase, a white gular stripe and white on the edge of the wing, just as in gray *D. sacra*. We have sub-adult white phase *E. gularis* with scattered gray feathers suggesting that they were mottled gray and white in the juvenal plumage. This also is exactly like the Reef Heron (see beyond). This group of herons, then, shows a rather gradual specialization from the dimorphic, simply plumed, short-legged *D. sacra* (or stock close to it) to the always white, elaborately plumed, long-legged *Egretta garzetta*. But since there is, as noted above, in several characters a small gap between *D. sacra* and all the species of *Egretta*, we are retaining *Demigretta* as a monotypic genus.

The two races of the Reef Heron to be recognized are as follows:

(a) Demigretta sacra sacra (Gmelin)

Ardea sacra Gmelin, 1789, Syst. Nat., I, pt. 2, p. 640.—(Tahiti).

Subspecific Characters.—Size small; wing length of majority of adults between 270–280 mm. in females, and 290–300 mm. in males. As noted above a few localities have populations of slightly larger size. Large males from these areas may have a wing length of as much as 315 mm. or even slightly more (see table).

Range.—Coasts of Asia from Korea to the Malay Peninsula; Andamans, Nicobars, East Indies; islands of western Pacific from Japan south to New Zealand and Australia; south Pacific islands, except New Caledonia and the Loyalty Islands.

Remarks.—From New Zealand we have one adult and three immature specimens. It is obvious after comparison of even this scanty material that the New Zealand Reef Herons belong to the nominate race and not to the larger form of New Caledonia. This suggests that New Zealand was colonized via Australia or the Kermadec Islands and not via New Caledonia.

After the map had been printed, information was received from the New Zealand Ornitholog. Soc. (due to the kindness of Charles A. Fleming) which proves a more extensive breeding range of the species. Reef Herons breed commonly on the South Island of New Zealand as far south as the Banks Peninsula and are regular (with nesting records) as far south as Dunedin. They may breed on Stewart Island where they have been observed in every month of the year.

(b) Demigretta sacra albolineata (G. R. Gray)

Ardea (*Herodias*) *albolineata* G. R. Gray, 1859, Proc. Zool. Soc. London, p. 166.—(Isle of Pines, off coast of New Caledonia).

Egretta brevipes Verreaux and Des Murs, 1862, Rev. Mag. Zool., p. 130.—(New Caledonia, type in Amer. Mus. Nat. Hist.; *cf.* Mayr, Auk, 1933, p. 206.)

Subspecific Characters.—Size large, wing more than 320 mm. (see table); weights averaging heavier: 604–872 gms. (New Caledonia, ♂ 851, ♀ 604, 710, 737; Uvea, Loyalty Islands, ♂872, ♀628) as against 550–700 gms. in *D. s. sacra* (Solomon Islands: Santa Anna, ♂ 625, ♀ 550; Malaita, ♂ 700; Rennell, ♂ 675, ♀ 625).

Range.—New Caledonia and the Loyalty Islands.

Remarks.—Gray described *Ardea albolineata* as "closely allied to *A. sacra* Gm... the white (throat stripe) is wider and extends less down the throat, and the tarsi are rather longer..." The amount of white

on the throat of this species is known to be subject to individual variation. As to the greater length of tarsus, however, Sharpe (Cat. Birds Brit. Mus., 26, p. 144) listed the type of *albolineata* as an immature with tarsus of 3.45 inches (88 mm.). He gave the length of tarsus of an adult male also from the Isle of Pines, New Caledonia, as 3.85 inches (98 mm.). These are considerable in comparison with the tarsal measurements of 147 other skins of the Reef Heron from all parts of its range listed by Sharpe. The two longest of these are each 3.4 inches (86 mm.); only fourteen skins had a tarsus of over 3 inches. In other words, the tarsus of an adult from New Caledonia was much longer (12 mm.) and that of the immature type of *albolineata* slightly longer (2 mm.) than the maximum tarsus lengths of 147 specimens from other localities.

A few other measurements of *albolineata* have been recorded in the literature. Sarasin (Vögel Neu Caled., 1913, p. 65) lists a New Caledonian male with the (trans.) "very significant measurements of wing 320, tarsus 94, culmen 100." However, this wing length is small rather than large for a male of *albolineata*. Brasil (Rev. Franc. d'Orn., 4, p. 199) records a pair from Lifu Island, Loyalties, as ♂, wing 345, tarsus 95; ♀, wing 310, tarsus 88. In general the data from the literature confirm our findings concerning the distinctly larger size of the Reef Herons of New Caledonia and the Loyalty Islands.

A series from the nearby New Hebrides is somewhat intermediate but as a group clearly belongs with the smaller race, *D. s. sacra*.

II.—PLUMAGES OF *DEMIGRETTA SACRA*

All the plumages of this Reef Heron are alike in both races and in both sexes, though the ornamental plumes may tend to be proportionately longer in males than in females of the same age. From examination of many moulting specimens, it was found that the post-juvenal moult begins on the head, neck and upper back. The wing and tail quills moult last after the entire body plumage, or most of it, has been replaced. Moult seems to begin in both the inner and outer primaries at the same time, so that the central ones are replaced last. As this species seems to have a prolonged breeding season (dates of six sets of eggs, from Polynesia: Jan., March, April, Sept., Oct., Nov.), it is difficult to establish the relative age of specimens, and hence to determine the age at which birds acquire their first adult plumage. However, the extreme fading and wear present in many immature specimens suggests that the juvenal plumage may be retained for almost a year, as is known to be the case in some other species of Ardeidae.

As in many herons, the ornamental plumes are only partly developed in the first adult plumage of *D. sacra*. Adults retain the plumes to a greater or lesser extent at all seasons of the year. Only 18 per cent of 447 adults have the head plumes fully developed (i.e., with long lanceolate tips about 70 mm. long). The probable explanation is that such plumes are not acquired in the first adult plumage, and that even in older individuals they are more apt to be worn off (or lost in skinning!) than the back and breast plumes, which are exactly like them in general structure. There is no evidence for the existence of an eclipse plumage between breeding seasons.

COLOR PHASES

Demigretta sacra occurs in the three following phases. Well-known plumages have not been fully re-described, except in so far as is necessary to show their significance.

(1) GRAY PHASE.—In this phase there is usually a white gular stripe and a few white feathers along the edge of the wing. The reference of specimens to the "gray phase" is not meant to deny the presence of these marks. The unfaded juvenal plumage of a gray nestling (Marquesas Islands) is blackish on the upper parts, head and breast (except throat stripe); the under parts are slightly lighter grayish black.

The juvenal plumage may become very faded and brownish through wear and bleaching. A juvenal from the Loyalty Islands has two of the rectrices tipped with white; this is presumably an individual variation. The adult plumage, in the gray phase, is essentially the same as the juvenal, except that the bluish-gray ornamental plumes are present. Moreover, the entire adult plumage, especially the mantle, acquires a certain amount of bluish-gray "bloom." This condition, which is most pronounced in fully adult birds, is lost with wear, and the plumage then assumes a blackishness like that of the unfaded juvenal.

(2) WHITE PHASE.—The juvenal plumage of this phase is white, usually with some gray markings. We have only one pure white nestling (Ningpo, China), but probably they are less rare than this would indicate. The gray usually is found as mottlings, streaks, etc., on white feathers, but in heavily marked specimens there is as much gray as white and many completely gray feathers. A normal juvenal (down still adhering to head) from the Reef Islands is white with about six gray or partly gray feathers scattered on the under parts; on the crown and back such feathers are more common; the wing quills all have gray markings near their tips, and some of the tertials are almost entirely gray; the two outer pairs of tail feathers are white, but the others are marked with gray. Another from the same island has more extensive gray areas. The juvenal plumage of the white phase may be said to vary from pure white to a condition in which gray and white are present in equal amounts.

In the post-juvenal moult, as shown by close examination of many skins, white adult feathers appear. Often the body becomes entirely white before the juvenal, gray-marked remiges, which are the last areas to moult, are gone. Not infrequently, however, a few gray or gray-marked feathers reappear in the first adult plumage. These feathers, which are usually six or less in number, most frequently occur among the dorsal plumes as shown by fifty adults in this condition. That most of these birds are in first adult plumage is indicated in two ways: (1) Some of them have not completed the post-juvenal moult. (2) The ornamental plumes are poorly developed. Only one of the fifty has well-developed head plumes; this exception is evidently an older individual; it has only one gray feather. We may say, then, that the mottled juvenals of the white phase become white or almost white in the first adult plumage, and pure white (with very rare exceptions) in the next plumage thereafter.

(3) MOTTLED PHASE.—In this group we include only those that are mottled as adults, for as just shown the juvenal plumage of the white phase is usually mottled. Mottled adults are not unusual in Fiji and they occur rarely in the Solomon, Marshall and Caroline Islands, and perhaps elsewhere. Our large series seems to prove that they are entirely lacking over large parts of the range, such as eastern Polynesia. The mottled adults, as shown below, stay in this condition permanently. They represent a distinct and rare type of coloration.

Our seven mottled adults may be briefly described as follows: The lightest individual is from the Fijis; it is mostly white with gray feathers scattered over the under parts; two of the tail feathers are gray, and there are markings on one primary; the back, tertials and greater wing-coverts are about fifty per cent gray. Four other Fijian birds are quite similar with white head and neck; under parts gray with scattered white and mottled feathers; most or all of the remiges with extensive gray areas. A specimen from Santa Anna Island, Solomons (the nearest island of this group to Fiji), is similar but darker with the body mostly gray, head and neck white, and remiges about half white. The remaining skin (from Malaita Island, Solomons) is all gray, except for one white primary, a white feather or two in the breast and head plumes, and a few white feathers along the ulnar region of the wing, on the under surface of the wing, and in the under tail-coverts. In addition to these specimens we have seen an adult in mottled plumage in the M. C. Z., at Cambridge, from Arno Marshall Islands.

All of the seven mottled birds described appear to be fully adult, and four of them

have the long head plumes which suggest that they are in at least the second adult plumage. One of them, No. 207698 from Fiji, is especially important as the wing is in full moult and the new feathers are mottled like the old ones. It seems almost certain, then, that the mottled adult condition is permanent, and hence differs completely from the white phase in which gray occurs only in immatures or (to a slight extent) in sub-adults.

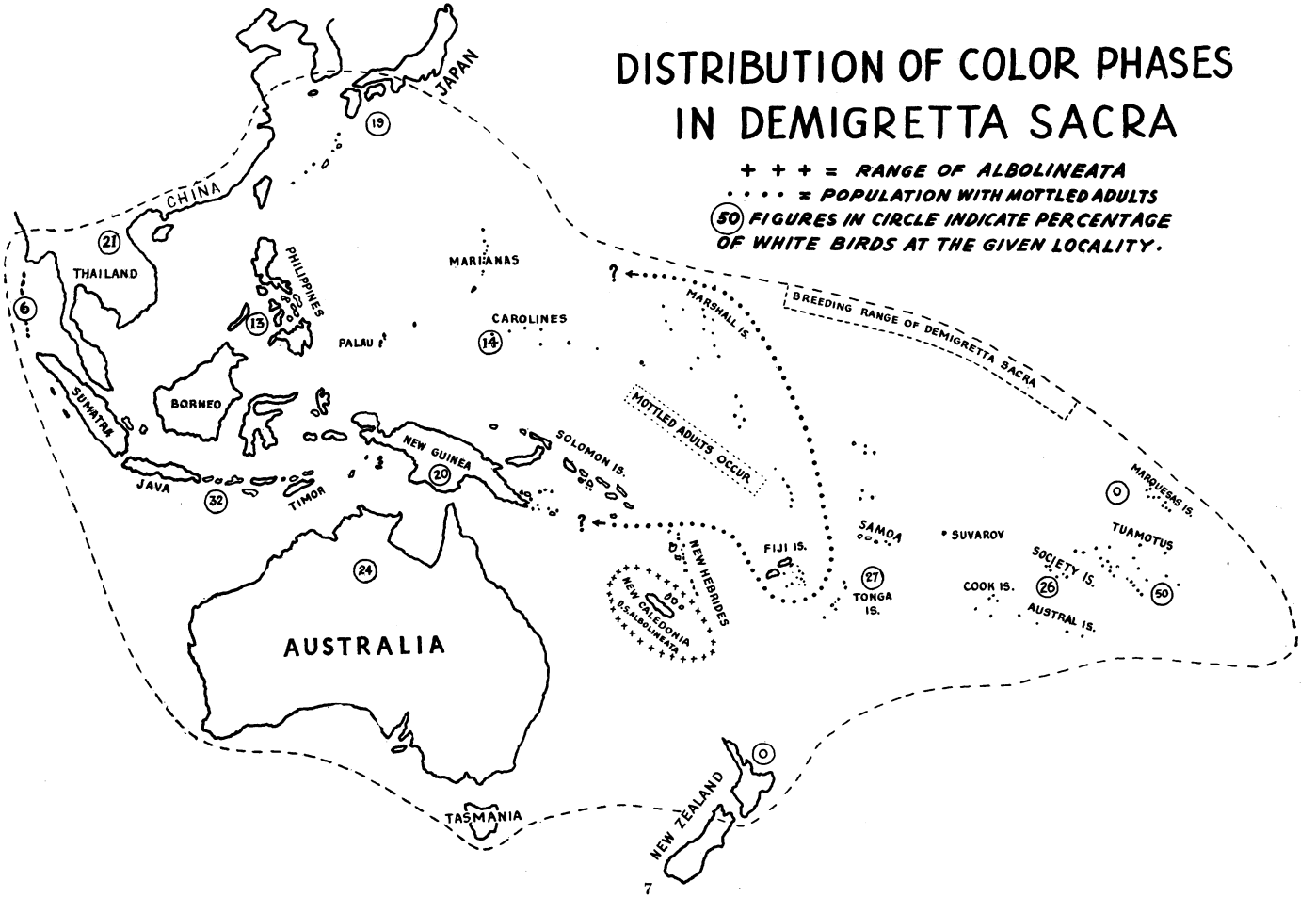
Because of the rarity of this phase we lack material to determine its immature stages as fully as is possible in the other two phases. Four specimens, however, seem of significance. No. 530027 from the Caroline Islands is an unusually heavily mottled juvenal, with the back mostly gray. The post-juvenal moult has just begun, and among new white feathers coming in on the back are some gray and mottled ones. This was found in none of the others and suggests that this was to become a mottled adult, though possibly one of the sub-adult white phase, with a few gray feathers. Another immature from the Carolines (No. 530031) is more important. This was a dark juvenal, mostly gray with white feathers scattered in the body feathers, under tail-coverts and primaries. It has also begun the post-juvenal moult and is acquiring white, mottled and gray feathers on the head, neck and back, and some new gray feathers on the throat and breast. This specimen was certainly moulting into a mottled adult. A third juvenal (Bougainville Is., Solomons) would be called a gray phase juvenal, if it were not that one primary in one wing and two primaries and two secondaries in the other have white blotches. The moult is somewhat further along in this individual and all of the new body feathers are gray. However, it is quite possible that when the wing and tail moulted some white would have appeared and produced a bird like the very dark adult described above from Malaita Island.

The three juvenals just described are unique in two respects: (1) Although having some white in their plumage they are predominantly gray. (2) In the post-juvenal moult numerous gray and (in two cases) mottled and white feathers are appearing. This suggests that the mottled phase, like the white phase, is mottled in the juvenal plumage, but with gray rather than white predominating. An additional Fijian specimen corroborates this belief. It is in sub-adult mottled plumage with many juvenal feathers still present. Such juvenal body feathers as remain are almost entirely gray, while the primaries are mottled heavily. Hence the juvenal plumage must have been mostly gray with scattered white areas. Without more knowledge of the juvenal plumages of the mottled phase, it is impossible to say if they can always be separated from the most heavily mottled juvenals of the white phase; perhaps not.

SUMMARY.—We may now summarize the plumage sequences of *Demigretta sacra* as follows:

PHASE	JUVENAL PLUMAGE	FIRST ADULT PLUMAGE	FULLY ADULT PLUMAGE
Gray	All gray	All gray	All gray
Mottled	Predominantly gray, mottled with white (so far as known)	Mottled gray and white	Mottled gray and white
White	White, usually mottled with up to 50% (or more?) of gray	White, frequently retaining a very few gray feathers	All white, very rarely with a gray feather or two

The geographical distribution of the three color phases is shown in the following table. In addition to the large series examined, a few supplemental records have been taken from the literature as follows: Sharpe, Cat. Birds Brit. Mus., 26, pp. 142, 274; Sarasin, Vögel Neu Caled., p. 65; Oliver, Birds New Zealand, p. 363. Field counts made by the Museum's collector, Mr. Macmillan, are also included. As this table is based chiefly on museum specimens it must be remembered that discriminatory collecting of the white phase has undoubtedly made their frequency of occurrence, as


DISTRIBUTION OF COLOR PHASES
IN DEMIGRETTA SACRA
+ + + = RANGE OF ALBOLINEATA
. . . . = POPULATION WITH MOTTLED ADULTS
(50) FIGURES IN CIRCLE INDICATE PERCENTAGE
OF WHITE BIRDS AT THE GIVEN LOCALITY.
JAPAN
19
CHINA
21
THAILAND
6
PHILIPPINES
13
MARIANAS
CAROLINES
14
PALAU
MARSHALL IS.
BREEDING RANGE OF DEMIGRETTA SACRA
MOTTLED ADULTS OCCUR
SUMATRA
BORNEO
NEW GUINEA
20
SOLOMON IS.
JAVA
32
TIMOR
24
AUSTRALIA
NEW HEBRIDES
NEW CALEDONIA
D'ENTRECASTEAUX IS.
FIJI IS.
SAMOA
SUVAROV
27
TONGA IS.
COOK IS.
26
AUSTRAL IS.
SOCIETY IS.
TUAMOTUS
50
MARQUESAS IS.
0
TASMANIA
NEW ZEALAND
0

expressed in the table, greater than the proportion actually existing in nature. The white birds are conspicuous, and they are also comparatively rare, hence they receive undue attention from the collector. In New Caledonia, for example, Mr. Macmillan collected four gray specimens, and mentions (MS.) seeing at least five others. He saw no white ones and learned that they were unknown even to the natives. Yet in the New Caledonian literature we found reference to four white and only two gray specimens! For localities where large numbers of records were available, however, the results expressed in the table are probably not much in error. Thus Rensch (Mitt. Zool. Mus. Berlin, 1931, 17, p. 501) saw 28% white birds (5 of 18) on Lombok, Sumbawa and Flores Islands, which is not a great deviation from the 32% white for the East Indies determined in the table without using Rensch's data.

In the following table, records of mottled birds given in the literature were not used, because it is usually not stated whether they were adults or immatures. Since it is important to base the percentages upon as large numbers as possible, juvenals are included in the figures given for the museum collection. As noted in the previous discussion, gray phase juvenals are like the adults, while white phase juvenals have some gray in the plumage. In the relatively small part of the range where the mottled phase (as shown by adults) occurs, the juvenals must be identified with much care. However, the occurrence in this area alone of a few very heavily mottled juvenals, one or two of which are moulting into a mottled adult plumage, indicates that the juvenal plumages of the white and mottled phases are probably quite distinct. The only two specimens which seemed of more or less uncertain status are accompanied by a question mark in the table.

A = Specimens in the A. M. N. H. collections.
B = Specimens from other collections or reported in the literature.
C = Percentage of this phase.

THE GENETIC BASIS.—A single pair of alternative color characters like white against colored has generally a simple mode of inheritance. It has been suggested by Stresemann (1926, Journ. f. Ornith., 74, p. 381) that the white color in the Reef Heron is due to a single recessive. In this case heterozygous individuals would have wild

DISTRIBUTION OF COLOR PHASES OF *DEMIGRETTA SACRA*

Locality	Gray Phase			White Phase			Mottled Phase		
	A	B	C	A	B	C	A	B	C
Society Islands	23	—	74	8	—	26	—	—	—
Marquesas "	45	—	100	—	—	—	—	—	—
Tuamotu "	87	—	51	85	—	49	—	—	—
Austral "	25	—	86	4	—	14	—	—	—
Suwarrow, Keppel, Samoa, Tonga, Union Islands	51	—	73	19	—	27	—	—	—
Fiji Islands	24	—	62	9	—	23	6	—	15
Swallow, Bank, Reef, Santa Cruz, New Hebrides Islands	11	—	65	6	—	35	—	—	—
New Zealand	4	Many	99+	—	1	—	—	—	—
Australia	7	22	76	5	4	24	—	—	—
New Guinea region	16	—	80	4	—	20	—	—	—
Bismarck Archipelago	13	—	81	3	—	19	—	—	—
Solomon Islands	36	—	69	13	—	25	2, 1 (?)	—	6
Marshall, Caroline, Marianne, Palau Islands	27	—	54	20	—	40	1, 1 (?)	1	6
Philippine Islands	5	9	87	—	2	13	—	—	—
East Indies	51	41	68	24	20	32	—	—	—
Andaman, Nicobar Islands	1	49	94	—	3	6	—	—	—
Asia: Malay to China	3	27	79	1	7	21	—	—	—
Japan and Nansei Islands	11	15	81	4	2	19	—	—	—
New Caledonia	5	7	71	1	4	29	—	—	—
Loyalty Islands	4	100	100	—	—	—	—	—	—

type coloration. This interpretation is based on the observation that even apparently homozygous white birds are more or less gray in their immature plumage, and it is, therefore, to be expected that the white color factor is even less potent in heterozygous condition. This view is substantiated by the fact that white is nearly always a recessive character in birds.

If the white phase had exactly the same selective value as the gray phase, and if the white gene were as common as the gray (wild type) one, we would expect a balanced population consisting of 75% gray birds (25% homozygous gray and 50% heterozygous) and 25% white ones (homozygous white). Actually the white phase is generally much rarer. This is particularly true in the New Zealand region, in the islands of the Indian Ocean (Andamans, Nicobars), in the New Caledonia-Loyalty Islands area and in the Marquesas Islands.

There is some slight evidence that in the subtropical parts of the range the white phase is somewhat rarer than in the tropical. Exceptions are presented by several populations; the white phase is common in the Japanese region, while the gray phase prevails in such typically tropical districts as the Indian Ocean and the Marquesas Islands.

Even in the islands where collections indicate a 3:1 ratio the white birds are actually rarer in nature, for they are more conspicuous and, therefore, more frequently collected. The Tuamotu Islands are the only place where the white birds are, apparently, as frequent as the gray ones. This is the more remarkable since the white phase is completely absent in the neighboring Marquesas Islands. Both of these groups of islands are isolated and on the periphery of the range. Hence it is possible that both groups were settled by a single pair of birds and that the present populations are descendants of these original colonists without much dilution by subsequent immigrants. If we assume that the white color is caused by the recessive gene *c* in homozygous condition, it would then follow that both ancestors of the Marquesas Islands population were of the constitution *CC*, while in the case of the Tuamotus one of the pair had the constitution *Cc*, the other *cc*.

It is possible to explain in a similar manner the varying proportions of white and gray birds in the various localities of the range. For most regions there are not enough data available to permit accurate charting of the exact percentages of the white phase, such as was done, for example, by Southern for the Bridled Guillemot (*Uria aalge*). If neither allele has a selective advantage over the other, and if the mutation rate is low, the composition of any given population will depend very much on the genic composition of the founders of the population (Hardy's formula), except for a few additional subsequent immigrants. If the population is very small, random elimination might change the proportions even without selection and mutation entering the picture (Sewall Wright). For a discussion of these questions from the point of view of the geneticist see Dobzhansky (Genetics and the Origin of Species, 1937, pp. 121–132).

The presence of a white phase is a common phenomenon among herons. It apparently does not influence pair formation. There is no evidence that birds of the same type of coloration are more frequently mated with one another than would be expected in random assortment. As noted already, three species of the very closely related genus *Egretta* also occur in a gray and in a white phase. In the other two species of this genus, *E. garzetta* with its races, and *E. eulophotes*, the wild type (gray) phase has completely disappeared. (See also Steinbacher, 1936, Ornith. Monatsber., 44, pp. 19–22.)

The Mottling Factor.—As stated above the phenomenon of color variation in *Demigretta sacra* over most of its range can be explained by the assumption of a single pair of alleles *C* and *c*. The only exception to this statement is provided by the mottled adults which we found in Fiji, the Solomon Islands and Micronesia. To account for these an additional genetic factor must be postulated. It is, of course, impossible to determine the actual nature of this factor without breeding experiments. It might be an additional allele of the albino

series, or a separate gene. Neither can it be determined whether the factor is dominant over white or not. On the basis of the Fijian material in our collections, the hypothesis works well that the mottling is produced by a gene *M*, which would produce mottling if present in homozygous condition (*MM*) in a bird heterozygous for wild color (*Cc*). Making the additional, and as stated above very probable, assumption that wild color is dominant over white, we would expect a 5:2:1 ratio of Wild type: White: Mottled in a population in which the two genes and their alleles were of equal frequency. This is almost exactly the ratio which we find among a series of 39 adults from Fiji. It is composed of 24 gray (wild type), 9 white and 6 mottled birds, as compared with the expected ratio of 24.4, 9.75 and 4.9. The just presented hypothesis is, of course, only one of several possibilities.

The mottled birds from Fiji, the Solomons and Micronesia are somewhat different from one another, as described above, and it is probable that additional modifiers are involved, such as have been found in every well-analyzed investigation on spotting genes in vertebrates. What the geographical distribution of the mottling factor in *Demigretta sacra* is, is hard to say. We have found it only in the above-characterized area (Fiji to Micronesia). Unfortunately, other observers have not made a clear distinction between piebald young and adults. The descriptions and records of spotted birds from the Malayan region, from Japan and from Australia are, therefore, without significance until it is proved that such specimens are fully adult.

LIST OF SPECIMENS IN AMER. MUS. NAT. HIST.

Demigretta sacra sacra

SOCIETY ISLANDS: Tahiti, 8♂, 12♀; Huahine, 1♂, 1(?); Mopelia, 3♂; Moorea, 2♂, 2♀; Raiatea, 1♂; Tetiaroa, 1♀.

AUSTRAL ISLANDS: (unspecified), 1♂, 1♀; Rimitara, 2♂, 1♀; Rurutu, 3♂, 6♀; Tubuai, 1♂, 2♀; Ravaivai, 6♂, 6♀.

TUAMOTU ARCHIPELAGO: Tikahau, 6♂, 6♀; Matahiva, 6♂, 9♀; Rangiroa, 2♂, 5♀; Makatea, 1♀; Kaukura, 5♂, 3♀; Toau, 1♂, 4♀; Niau, 1♀; Fakarava, 1♂, 3♀; Faite, 6♂, 2♀; Tahanea, 1♂, 8♀; Manihi, 5♀; Ahii, 3♂, 2♀; Takaroa, 5♂, 2♀, 1(?); Apataki, 1♂, 2♀, 1(?); Aratika, 1♂, 3♀, 1(?); Taiaro, 1♂, 1♀; Kauehi, 1♂; Raraka, 5♂, 1♀; Katiu, 5♂; Hiti, 2♀; Tuanake, 1♂; Makemo, 3♂, 1♀; Taenga, 2♂, 1♀; Raroia, 6♂, 6♀; Takume, 4♂, 3♀; Fakahina, 1♀; Nihiru, 2♂; Hao, 2♀; Ahunui, 4♂; Vanavana, 2♂, 1♀; Tenararo, 2♂, 1♀; Tenarunga, 2♂, 2♀; Maturei-Vavao, 2♂, 1♀; Mureia, 1♂; Marutea, 3♂, 1♀; Mangareva, 2♂, 1♀; Timoe-Atoll, 1♂, 1♀.

MARQUESAS ISLANDS: Eiau, 7♂, 3♀; Fatuhiva, 1♀; Fatuhuku, 1♂, 1♀; Hivaoa, 2♂; Nukahiva, 16♂, 6♀; Uahuka, 2♂, 2♀, 1(?); Uapu, 1♂, 2♀.

SUWARROW (SUVÁROV): 7♂, 4♀, 2(?).

UNION ISLANDS: Fakaofo, 2♂, 3♀; Hono, 1♀; Nassau, 1♂.

SAMOAN ISLANDS: Ofu, 1♂, 1♀; Olosinga, 2♂, 2♀, 1(?); Rose, 1♀; Tutuila, 1♂, 5♀.

KEPPEL ISLAND: 1♂, 3♀.

TONGA ISLANDS: Fanuaika, 1♂, 1♀; Toku, 1♂.

FIJI ISLANDS: Turtle, 1♂; Fulanga, 1♂, 1♀; Marambo, 1♂; Kambara, 2♀; Namuka Ilau, 1♀; Komo, 2♀; Mothe, 1♀; Lakemba, 1♀; Matuku, 2♂, 1♀, 1(?); Totoya, 1♂, 1♀; Moala, 3♀; Vanua Vatu, 1♂; Naiau, 2♂; Thithia, 1♀; Mango, 2♂; Avea, 1♂, 1♀; Vanua Mbalavu, 2♂; Thikombia, 2♀; Vatanua, 1♀; Ngele Levu, 1♂; Wakaya, 1♂, 2♀; Mbatiki, 1♀; Vatu Leile, 1♂.

NEW HEBRIDES: Efate, 1♂, 3♀; Erromanga, 2♀.

BANKS ISLANDS: Valua, 1♀.

REEF ISLANDS: Lomlom, 4♂, 2♀.

SWALLOW ISLANDS: Nepani, 1♀.

SANTA CRUZ ISLANDS: Santa Cruz, 1♀; Tucopia, 1♂, 1♀.

MARIANNE ISLANDS: Guam, 3♂, 6♀; Saipan, 2♀.

PALAU ISLANDS: 3♂, 2♀.

CAROLINE ISLANDS: Ponape, 1♂, 1(?); Kusai, 9♂, 15♀; Ruk, 2♂, 2♀; Tah, 1♀, 1(?).

SOLOMON ISLANDS: Ontong Java, 1♂; Bougainville, 2♂, 2♀; Faisi, 1(?); Whitney, 1♂, 1♀; Shortland, 1♂, 1♀; Choiseul, 1♀; Arnarvon, 1♀; Gijunabena, 1♀; Ysabel, 1♂, 1♀, 1(?); Vella Lavella, 2♂, 1♀; Kulambangra, 1♀; New Georgia, 2♀; Narova, 1♀; Vangunu, 1♂; Gatukai, 1♀; Tetipari, 1♂, 3♀; Malaita, 1♂; Guadalcanar, 2♂, 1♀; San Cristobal, 1♂; Santa Anna (Auaraha), 3♂, 3♀; Rennell, 2♂, 1♀.

BISMARCK ARCHIPELAGO: Ahu-Ninigo Group, 1♀; Manus, 2♂, 1♀; New Hanover, 2♂; Lihir, 1♂, 1♀; Boang (Tanga Group), 1♂; New Britain, 3♂, 2♀; St. Matthias, 1♂; Long, 1♂.

COASTAL ISLANDS OF NEW GUINEA: Waigeu, 1♂; Salawati, 2♂; St. Aignan, 3♂, 1♀;

Karkar, 1♂; Jobi, 1♀, 1(?); Daru, 1♂; Sudest, 1♂, 1♀; Woodlark, 1♀; Goodenough, 1♂; Kiriwina (Trobriands), 1♂, 2♀; Gawa (Marshall Bennett), 1♂; Rossel (Louisiades), 1♂.

NEW ZEALAND: 1♂, 2♀, 1(?).

AUSTRALIA: New South Wales-Namoi River, 1♂. Queensland-Capricorn Islands, 1♂, 1♀; Cooktown, 1♂ (type *cooktowni* Mathews); Utingu, 1♂; Cape York, 1♂. Northern Territory-Buchanan Island, 1♂ (type *buchanani* Mathews). Western Australia-Point Torment, 1♂ (type *tormenti* Mathews); Lewis Island, 1♀; Point Cloates, 1♂, 1♀; Yardie Creek, 1♀.

ANDAMAN ISLANDS: 1(?).

GREATER SUNDA ISLANDS: 4♂, 9♀, 2(?).

LESSER SUNDA ISLANDS: 13♂, 11♀, 2(?).

TANIMBAR, KEI ISLANDS: 6♂, 3♀, 3(?).

MOLUCCAS, TALAUT ISLANDS: 4♂, 4♀.

CELEBES REGION: 2♂, 4♀, 6(?).

PHILIPPINE ISLANDS: Cagayan Sulu, 1♂; Cayoagan (near Samar), 1♀; Cebu, 1♀; Palawan, 1♂, 1♀.

NANSEI ISLANDS (RIU KIU): 8♂, 2♀, 2(?).

JAPAN: 1♂, 1♀, 1(?).

CHINESE REGION: China, 1♂; Hainan, 1♂.

BURMA: 2♀.

Demigretta sacra albolineata

NEW CALEDONIA: 2♂, 4♀.

LOYALTY ISLANDS: Mare, 2♂; Uvea, 1♂, 1♀.