GEOGRAPHICAL VARIATION OF THE PLUMAGE POLYMORPHISM IN THE EASTERN REEF HERON (*EGRETTA SACRA*)[1]

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Abstract. I investigated the distribution of white and dark morphs of the Eastern Reef Heron (*Egretta sacra*) on several coasts and islands in central to southwestern Japan, eastern Australia, and French Polynesia. Both morphs preferred white beaches to dark beaches. Every local population contained some dark herons, however, the range of the white morph was restricted. The white morph population increased in proportion to the distance from the equator in Japan. It was plentiful in the Great Barrier Reef in Australia and was common in Polynesian islands. The distribution of the white morph coincides with the presence of coral reefs, from which white beaches are derived. Only the dark morph was seen outside this range. None of several hypotheses proposed so far explains the observed polymorphism and its geographic variation.

Key words: Color polymorphism; plumage color; geographic variation; coral reefs; Eastern Reef Heron; Egretta sacra.

INTRODUCTION

Given that conspicuousness and crypticity are subject to natural selection, the coexistence of white and dark conspecifics presents an interesting paradox. Such "white-or-dark" type of plumage polymorphism is known in several avian species such as the Parasitic Jaeger *Stercorarius parasiticus* and relatively common in the Ardeidae (egrets and herons). Four to six species, depending on the taxonomy, are known to be polymorphic within some local populations, independent of age and sex (Mock 1980, Hancock and Kushlan 1984): the Great Blue Heron *Ardea herodias,* the Reddish Egret *Egretta rufescens,* the Little Egret *E. garzetta,* the Madagascar Reef Heron *E. dimorpha,* the Western Reef Heron *E. gularis,* and the Eastern Reef Heron *E. sacra.* All except the Great Blue Heron live almost exclusively in coastal habitats.

There are several hypotheses regarding plumage polymorphism in Ardeidae. Murton (1971) proposed that white herons, which he thought less conspicuous prey than dark ones, use "stand and wait" or "wade slowly and surprise" foraging

techniques while dark herons forage in a more active manner. This hypothesis was questioned by Recher (1972) who did not find any difference in foraging behavior between the two morphs of the Eastern Reef Heron (Recher and Recher 1972). Instead, Recher and Recher suggested that physiological adaptation to hot coastal habitats may have played an important role; white birds may be favored in hot areas because of less absorption of sunlight. Walsberg et al. (1978), however, showed that white plumage may actually absorb more heat than dark plumage. Balanced selection forces between risk of predation (Caldwell 1986) and the advantage of "hunting camouflage" (Craik 1944) for white birds may contribute to maintain polymorphisms in Ardeidae. It is obvious that more quantitative data on the morph ratios and other aspects are required to test such hypotheses (see Mock 1980).

The Eastern Reef Heron is a western Pacific coastal heron that exhibits two distinctive color morphs: white and dark. On the basis of censuses in several Polynesian islands, Holyoak (1973) found a close correlation between morph ratios and beach colors, the white morph being more prevalent on islands with predominantly white beaches.

I investigated the distribution of the polymorphic Eastern Reef Herons and their habitats at more localities across a wider range than did Holyoak, including southern Japan and several

TABLE 1. Study areas and the numbers of Eastern Reef Herons observed in Japan (A), Australia (B) and French Polynesia (C).

(A) Japan

No.	Study area	Location N	E	Dates	Hours	Morphs Dark	White	Total no. of herons
J1.	Mikunichô	35°15′,	136°07′	28–29 Mar. 1987	12	12	0	12
J2.	Kii Peninsula	33°30′,	135°45′	9–13 May 1988 13–14 June 1988	64	16	0	16
J3.	South Kyushu[1]	31°00′,	130°40′	22 Feb. 1988	4	—	—	0
J4.	Kuchierabu Is.[2]	30°28′,	130°10′	21 Feb. 1988	4	1	0	1
J5.	Tanega Is.	30°44′,	131°00′	22–23 Feb. 1988	27	19	0	19
J6.	Yaku Is.	30°25′,	130°35′	20 Feb. 1988	3	2	0	2
J7.	Tokara Arch.[3]	29°10′,	129°13′	18–20 Feb. 1988	36	2	2	4
J8.	Amami Ôshima	28°22′,	129°30′	13–20 June 1987	74	35	20	55
J9.	Yoron Is.	27°10′,	127°27′	16–17 Feb. 1988	12	7	5	12
J10.	Okinawa Is.	26°12′,	127°40′	6–8 Feb. 1988 2–5 June 1988	55	31	55	86
J11.	Aguni Is.	26°35′,	127°14′	9 Sep. 1988	8	8	3	11
J12.	Aka Is.	26°11′,	127°17′	11 Sep. 1988	10	4	2	6
J13.	Miyako Is.	24°48′,	125°17′	15–16 Feb. 1988	13	15	10	25
J14.	Minna Is.	24°45′,	124°42′	7 Sep. 1988	6	3	19	22
J15.	Tarama Is.	24°39′,	124°42′	6 Sep. 1988	8	21	25	46
J16.	Ishigaki Is.	24°21′,	124°08′	9–11 Feb. 1988	22	14	32	46
J17.	Kohama Is.	24°21′,	123°59′	4 Sep. 1988	7	2	4	6
J18.	Iriomote Is.	24°10′,	123°45′	12–13 Feb. 1988	18	14	26	40
J19.	Yonaguni Is.	24°28′,	123°00′	10 Feb. 1988	3	1	5	6

(B) Australia

No.	Study area	Location S	E	Dates	Hours	Morphs Dark	White	Total no. of herons
A1.	Green Is.	16°43′,	146°00′	4–5 Feb. 1988	10	12	84	96
A2.	Fitzroy Is.	16°54′,	146°00′	15 Dec. 1989	5	2	2	4
A3.	Wilson Is.	23°20′,	151°54′	20 Dec. 1988	2	—	—	0
A4.	Heron Is.	23°27′,	151°55′	13–15 Nov. 1988	12	46	137	183
A5.	Lord Howe Is.	31°28′,	159°09′	23–25 Nov. 1988	7	—	—	0

(C) French Polynesia

No.	Study area	Location S	W	Dates	Hours	Morphs Dark	White	Total no. of herons
P1.	Raiatea	16°50′,	151°30′	2 Dec. 1989	2	—	—	0
P2.	Borabora	16°30′,	151°45′	3 Dec. 1989	4	9	2	11
P3.	Tuamotu Arch.	15°00′,	147°40′	23 Nov.–9 Dec. 1989	10	9	16	25

[1] Consists of two localities, about 30 km apart.
[2] Includes Io and Take Islands.
[3] Consists of nine small islands.

other Pacific islands in the Southern Hemisphere. My data indicate great geographic variations in morph ratios and that the distribution of the white morph coincides with that of coral reefs. I report these results with discussion on the possible selection force contributing to maintain the color polymorphism.

STUDY AREA AND METHODS

Censuses were carried out by one to five person(s) for a total of 438 hr during 61 days from March 1987 through December 1989 in 19 localities in Japan, five in Australia and three in French Polynesia (Table 1). Two census methods were employed. 1. The observer(s) walked or drove at a speed of about 1 km/hr along the coasts (or all the areas on islands that were reasonably small), and recorded the numbers of the color morphs (white or dark) and their habitats (also white or dark). 2. When it was not possible to land or walk along a coast, we counted Reef Herons that were flushed from the coasts as our boat passed 50–150 m away.
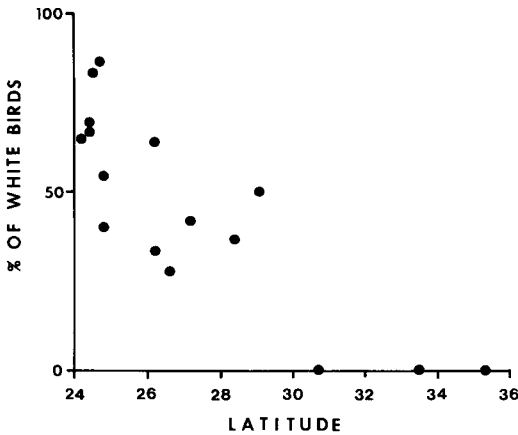
Habitat color was divided into two categories.

FIGURE 1. The correlation between latitude and the proportion of white Eastern Reef Herons in Japan. Kendall's rank correlation test: $n = 16$, $S = 71$, $P = 0.001$ when all data are used; $n = 13$, $S = 32$, $P = 0.051$ when northern three localities, where all herons were dark, are excluded.
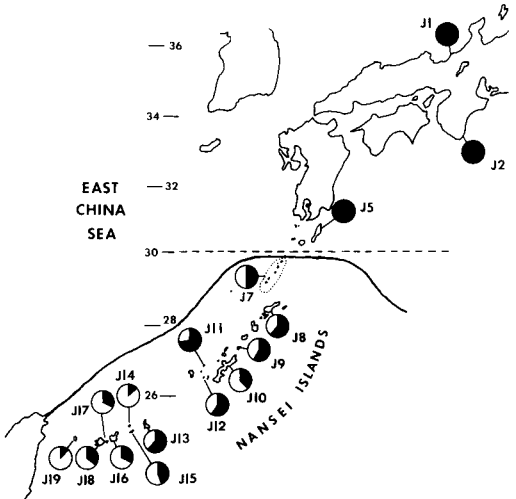

FIGURE 2. The distribution of color morphs of *E. sacra* in Japan with isothermal lines for the coldest monthly sea surface temperature (20°C, Feb. 1956–1985). The numbers coincide with those in Table 1. The broken line is Watase Line (see text). The circles indicate the proportion of white and dark morphs in each locality as blank and shaded parts, respectively. See Table 1 for sample sizes.

"Dark beaches" consisted of dark rocks and/or sands. "White beaches" consisted of limestones or white sands (sometimes with scattering dark rocks). Habitat color was recorded on maps when the bird censuses were made; beach lengths were measured from the maps. In any of the northern localities in Japan (J1–J6 in Table 1), no white beaches were found, while no dark beaches were observed in Australia and Polynesia. However, there was one special circumstance on Heron Island. Although dark fringed substrates surrounded this island, Reef Herons did not feed on these areas. This apparently was due to heavy tourist use. In this paper, therefore, Heron Island is classified as a white beach on which the herons fed.

At three localities in Japan, two in Australia, and one in Polynesia, fewer than four herons (Table 1) were observed, so these were excluded from further analyses. Most correlation analyses were made for data from the Nansei Islands, Japan (the Tokara Archipelago, Amami Islands, and Okinawa Islands: J7–J19 in Table 1) because these islands provided variations in both beach types and bird color.

RESULTS

DISTRIBUTION OF THE TWO MORPHS

In all, I counted 415 Eastern Reef Herons in Japan, 283 in Australia, and 36 in French Polynesia (Table 1), with 208 (50.1%), 221 (78.1%), and 18 (50%) white morphs.

The proportion of the white morph decreased as latitude increased in Japan (Fig. 1). The correlation was weak when northern localities with only dark herons were excluded.

The sample size in the Southern Hemisphere was too small to make a similar correlation analysis. The proportion of the white morph was high in both Green (A1), Fitzroy (A2) and Heron (A4) Islands in the Great Barrier Reef, Australia: 87.5%, 50.0% and 74.9%, respectively. Eastern Reef Herons were plentiful there; the total number of herons (283) found in these small islands (0.3 and 0.17 km²) is more than 77% of that in many of the Nansei Islands, where intensive censuses were made. In Polynesia, we found 11 Reef Herons with two (18.1%) white morphs in Borabora and 25 herons with 16 (64.0%) white ones in Rangiroa. All beaches we examined in Australia and Polynesia were white.

Every local population contained some dark Eastern Reef Herons, whereas the range of the white morph was restricted. Takara Island in the Tokara Archipelago (J7) was the northern limit of white Eastern Reef Herons (Fig. 2). All 50 birds were the dark morph in the north of the Watase Line, a biogeographic boundary that runs through the Tokara Straits at the latitude of 30°N; while 208 (56.9%) birds out of 365 herons were
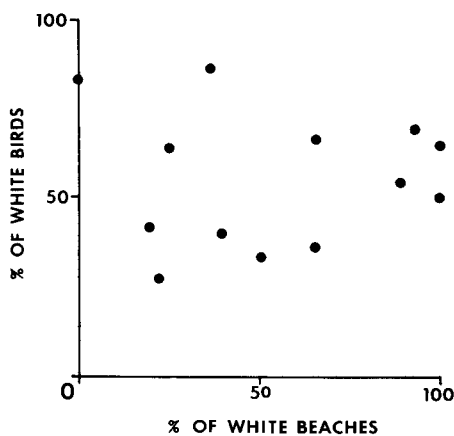
FIGURE 3. The correlation between the proportion of white beaches and that of white Eastern Reef Herons. Kendall's rank correlation test: $n = 16$, $S = 42$, $P = 0.059$ when all data are used; $n = 10$, $S = 15$, $P = 0.180$ when localities that do not contain either dark beaches or white ones are excluded.

the white morph in 13 islands in the south of the line (Fig. 2).

The proportion of white herons was not significantly correlated with that of white coasts in Japan (Fig. 3), whether including or excluding localities that lacked either dark beaches or white beaches.

HABITAT CHOICE BY THE TWO MORPHS

Table 2 summarizes the numbers of Reef Herons observed in the Nansei Islands with respect to beach colors. In three islands (Amami-Ōshima [J8], Okinawa [J10] and Miyako [J13]) out of the 10 islands where both white and dark beaches exist, herons of both colors were significantly more abundant on white beaches than on dark ones. The same tendency was found in four of the other seven islands, although the difference was not statistically significant. The frequencies of the two beach types were almost identical on one island. More herons were observed on dark beaches than white ones in Aguni (J11) and Kohama (J17) Islands, though these differences were not significant. This may be because most of the white beaches in Aguni Island were too narrow with steep cliffs nearby for herons to forage, and Kohama Island was censused when the white beaches looked like mud flats that are not preferable habitats for Eastern Reef Herons. When all records for the 13 islands are pooled, more

Reef Herons were observed on white beaches than on dark ones ($\chi^2 = 23.222$, $P < 0.001$).

Eastern Reef Herons show no preference for beach habitats that match their plumage. The proportion of white birds did not differ between white and dark beaches within each island (Table 3). White morphs were seen on dark beaches in 10 of 11 islands and, conversely, dark morphs were seen on white beaches in all 12 islands. The same is true even if the data source is restricted to the 10 islands where there are both types of beaches. On the basis of pooled data, 56.7% of Eastern Reef Herons seen on white beaches and 57.5% of ones on dark beaches were the white morph ($\chi^2 = 0.019$, $P = 0.890$).

DISCUSSION

Several birds exhibit a "white-or-dark" type of polymorphism, independent of sex and age, within populations as does the Eastern Reef Heron. Genetical studies have shown that these polymorphisms are usually controlled by two alleles, with various extent of dominance, at a single locus (the Antarctic Giant Petrel *Macronectes giganteus*: Shaughnessy 1970, the Parasitic Jaeger: O'Donald and Davis 1959, the Lesser Snow Goose *Chen caerulescens caerulesens*: Cooke and Mirsky 1972, the Little Shag *Phalacrocorax melanoleucos brevirostris*: Dowding and Taylor 1987). Using family analysis, Naik and Parasharya (1983) suggested that the polymorphism in the Western Reef Heron is also determined by a single pair of alleles with the gene for dark being incompletely dominant over the gene for white. It seems likely, therefore, that the observed phenotypic variation in plumage color in the Eastern Reef Heron is based on genotypic variation similar to that of other white-or-dark birds.

What evolutionary mechanism contributes to maintaining the phenotypic polymorphism within local populations of Reef Herons and what are the selective advantages, if any, of being either white or dark? Because individuals of each morph are quite uniform, the status signaling hypothesis (Rohwer 1977) and the individual recognition hypothesis (Shields 1977) are not applicable to the Eastern Reef Heron.

This study revealed a consistent geographic variation in morph ratios. The boundary between the region where both color morphs occur and the region where only the dark morph occurs

TABLE 2.   The distributions[1] of beach color and the two color morphs of *E. sacra* in the Nansei Islands.

Locality[2]	Dark beaches						White beaches				
	Length (km)	Morphs		Total no. of herons	Birds/ km		Length (km)	Morphs		Total no. of herons	Birds/ km
		Dark	White					Dark	White		
J7	—	—	—	—	—	*	4.6	2	2	4	0.87
J8	67.0	6	2	8	0.12	*	126.6	29	18	47	0.37
J9	16.0	3	4	7	0.44		3.9	4	1	5	1.28
J10	184.7	14	29	43	0.23	*	62.0	17	26	43	0.69
J11	7.0	7	3	10	1.43		2.0	1	0	1	0.50
J12	6.1	2	1	3	0.49		6.2	2	1	3	0.48
J13	41.5	2	0	2	0.05	*	27.0	13	10	23	0.85
J14	0.7	0	2	2	2.86		5.7	3	17	20	3.51
J15	10.5	12	15	27	2.57		6.1	9	10	19	3.11
J16	5.5	0	1	1	0.18		75.6	14	31	45	0.60
J17	4.7	1	3	4	0.85		9.0	1	1	2	0.22
J18	—	—	—	—	—		50.6	14	26	40	0.79
J19	12.4	1	5	6	0.48		—	—	—	—	—
Total	356.1	48	65	113	0.31	*	379.3	109	143	252	0.66

[1] It was tested whether the distribution differed from expected value on the basis of the beach length, using the binomial test or χ²-test. Asterisks = $P < 0.05$; the others = N.S.
[2] The numbers coincide with those in Table 1.

is in the Tokara Strait (the Watase Line) in Japan (Fig. 2). Eastern Reef Herons of both types live south of the Watase Line, and only dark herons live north of it. Kiyosu (1978) reported that all 81 Reef Herons found in Honsyu, north up to Aomori (40°49′N, 140°49′E), were the dark morph. The Watase Line also corresponds with the northern limit of coral reefs (Takahashi 1988). That is, coral reefs develop well in the south of the Nansei Islands, decrease drastically from Amami Ôshima to Takara Island, and vanish in the north of the Tokara Strait (Takahashi 1988).

The same pattern has been found in the Southern Hemisphere. MacDonald (1973) describes that "the white morph gets increasingly common towards north and rare towards south." Both morphs have been recorded in the Great Barrier Reef and Caledonia (Mayr and Amadon 1941, this study), while only dark morphs have been seen farther in the south, between Sydney (33°52′S, 151°12′E) and the Victorian-Border (H. F. Recher, pers. comm.), Tasmania and New Zealand (Falla et al. 1970). In short, the white morph of Eastern Reef Herons apparently increases in proportion as the distance from the equator increases towards both north and south, although the documentation for the southern hemisphere remains a bit sketchy. This pattern coincides with the distribution of coral reefs, from which white beaches are derived.

Non-adaptive polymorphism can be an out-

come of recent merging of two formerly allopatric populations as in the Lesser Snow Goose (Cooke et al. 1988) or maintained by immigration of individuals with a phenotypic preference for marginal habitats where another competitive phenotype has a selective advantage. In the Ardeidae, all the three coastal species are polymorphic (the Western Reef Heron, the Eastern Reef Heron, and the Reddish Heron). White morphs are generally predominant at lower latitudes, as observed in this study, except in the Red Sea (see Palmer 1962, Mock 1980, Hancock and Kushlan 1984 for brief reviews). Such con-

TABLE 3.   Beach color preference of the two color morphs of *E. sacra* in the Nansei Islands. Islands where only dark or white beaches exist are excluded.

Locality[1]	Percent of white birds	
	Dark beaches	White beaches
J8	25.0	38.3
J9	57.1	20.0
J10	67.4	60.4
J11	30.0	0.0
J12	33.3	33.3
J13	0.0	43.5
J14	55.6	52.6
J15	100.0	85.0
J16	100.0	68.9
J17	75.0	50.0

[1] The numbers coincide with those in Table 1.

sistent geographic variation seems to favor adaptive explanations to non-adaptive ones.

Murton (1971) presented a hypothesis that white and dark morphs in herons are maintained because the white forms are less visible to prey and have an advantage in situations demanding stealth or surprise while the dark morphs have an advantage in scaring or flushing prey out of hiding or into movement. Recher (1972), however, argued that Murton's hypothesis is unlikely since there is no difference in foraging behavior between the two morphs of the Eastern Reef Heron (Recher and Recher 1972). In addition, interspecific comparison of foraging behavior among North American herons does not provide any correlation between foraging techniques and body color (Kushlan 1978).

Recher (1972) suggested that the dimorphisms may have a physiological rather than an ecological reason; white herons hunting on hot coasts may be better able to regulate their body temperature than dark ones. This hypothesis coincides with the result of the present study, the negative correlation between the latitude and the proportion of the white morph (but see Holyoak 1973 for an exception). Ellis' (1980) laboratory experiment indicates that metabolism and solar radiation may combine to amplify heat stress in hot climates in dark herons.

Matching with different habitats may seem straightforward as an explanation of polymorphism. Holyoak (1973) examined the relationship between beach color and the morph ratios in Eastern Reef Herons in French Polynesia. There were highly significant differences between the morph ratios of islands with beaches of different colors, those islands with light coral beaches had far more white herons. The white morph was absent from coasts with no coral, as in New Zealand and southern Australia, and present wherever white coral beaches are within easy reach. These findings were not confirmed by this study because the correlation between habitat color and morph ratios was not significant. The current study, furthermore, revealed that individual herons did not choose habitats of their own color. Therefore, the observed geographic variation in morph ratios requires explanations at the population level such as frequency-dependent selection or immigration.

Given that habitat matching plays an important role in maintaining the polymorphism in herons, the advantage of habitat matching should

also be explained. Caldwell's (1986) experiment showing that white heron models attracted more predators than blue models suggests that morphs matching their backgrounds are at less risk from predation. Alternatively, it has been shown that the white underparts of herons and seabirds facilitate foraging because of their inconspicuousness to aquatic prey against the bright sky (Mock 1980, Götmark et al. 1986, Götmark 1987). The balanced selection of these two selection pressures may contribute to maintain two morphs in herons.

None of the above fully explains polymorphism in Ardeidae. Because all the three typically polymorphic herons are marine birds, changes in activity patterns with tides may be important. It thus is interesting that Eastern Reef Herons are active at night as well as in the daytime (Itoh, pers. obs.), considering that nocturnal species in Ardeidae have dark plumage. To test any of these hypotheses, further intensive studies are needed.

ACKNOWLEDGMENTS

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