FURTHER DATA ON THE INHERITANCE OF PLUMAGE PHASES OF THE SOUTHERN GIANT PETREL *Macronectes giganteus*

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ABSTRACT. Family data relating to the inheritance of the plumage phase dimorphism in southern giant petrels, *Macronectes giganteus*, at Signy Island (lat. 60°43′S., long. 45°38′W.), South Orkney Islands, are analysed. The data are in accord with the hypothesis originally suggested for these birds at Macquarie Island that the dimorphism is controlled by two autosomal allelic genes with white phase dominant to dark.

It is proposed that totally white birds with pink feet are homozygous white. The observed proportion of white-phased birds that were totally white at Signy Island in 1969 (2·85 per cent) was close to that expected (2·77 per cent) on this model. The proportion of totally white birds from matings between two white parents is predicted to be slightly greater than 0·25 in populations that include the white phase.

THE southern giant petrel, *Macronectes giganteus*, occurs in two distinct colour phases: white, in which the birds are completely white except for a few black feathers; and dark, in which the plumage varies from dark brown to grey with a pale head, neck and breast. Family data collected at Macquarie Island (lat. 54°S., long. 159°E.) indicated that the dimorphism was controlled by two autosomal allelic genes with white phase dominant to dark (Shaughnessy, 1970). At Signy Island (lat. 60°43′S., long. 45°38′W.), South Orkney Islands, Conroy (1972) collected family data relating to the inheritance of colour phases. These data are analysed in this note.

A third colour phase of southern giant petrels, with totally white plumage and pink feet, was reported from Signy Island by Conroy (1972). The mode of inheritance of this third phenotype is also discussed here.

FAMILY DATA RELATING TO THE PLUMAGE DIMORPHISM

Most of the pertinent data (Table I) are from Conroy (1972, table XXX). There, 22 chicks from dark × white matings were included. These were produced from 15 pairs; the single chicks of seven of the pairs were also included in the second year's observation. Because the method of analysis used requires that the offspring be independent samples from the given type of mating, siblings cannot be included. Consequently, for each of these seven pairs, only the chicks from the first year's observation have been included in the present analysis.

TABLE I. FAMILY DATA FOR PLUMAGE PHASE INHERITANCE IN *Macronectes giganteus* AT SIGNY ISLAND. OBSERVED (O) AND EXPECTED (E) NUMBERS OF PROGENY ON THE HYPOTHESIS THAT PLUMAGE PHASE IS CONTROLLED BY TWO AUTOSOMAL ALLELIC GENES WITH DARK PHASE DOMINANT TO WHITE (MODEL I)

Type of mating	*Chick phenotypes*				*Number of chicks*	χ^2_1	*Probability*
	Dark		*White*				
	O	E	O	E			
Dark × dark	250	238·1	0	11·9	250	12·5	$P < 0·001$
Dark × white	6	11·7	9	3·3	15	—	$P < 0·0001$*
White × white	0	0	1	1	1	—	—

* Probability calculated using the binomial distribution.

The two hypotheses considered by Shaughnessy (1970) are re-examined in the light of these new data. These are that plumage phase is controlled by two autosomal allelic genes with, first, dark phase dominant to white, and secondly, white phase dominant to dark. The

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expected distribution of progeny on the basis of these hypotheses has been set out by Li (1955, table 4) in terms of the frequency (q) of the allele for the recessive phenotype among breeding birds.

The estimate of the frequency of the white phase among adult birds at Signy Island (7·82 per cent, from Conroy (1972, table XXIV)) enables estimates of allele frequencies to be obtained.

i. Model I: dark phase is dominant to white phase.
The estimate of the frequency of the recessive allele is:

$$(0{\cdot}0782)^{\frac{1}{2}} = 0{\cdot}2796.$$

The observed and expected numbers of progeny from each type of mating on this model are shown in Table I.

ii. Model II: white phase is dominant to dark phase.
The estimate of the frequency of the recessive allele is:

$$(0{\cdot}9218)^{\frac{1}{2}} = 0{\cdot}9601.$$

The observed and expected numbers of progeny from each type of mating on this model are shown in Table II.

TABLE II. FAMILY DATA FOR PLUMAGE PHASE INHERITANCE IN *Macronectes giganteus* AT SIGNY ISLAND. OBSERVED (O) AND EXPECTED (E) NUMBERS OF PROGENY ON THE HYPOTHESIS THAT PLUMAGE PHASE IS CONTROLLED BY TWO AUTOSOMAL ALLELIC GENES WITH WHITE PHASE DOMINANT TO DARK (MODEL II)

Type of mating	*Chick phenotypes* *Dark* O	E	*White* O	E	*Number of chicks*	χ^2_1	*Probability*
Dark × dark	250	250	0	0	250	—	—
Dark × white	6	7·3	9	7·7	15	0·48	$0{\cdot}70 < P < 0{\cdot}80$
White × white	0	0·2	1	0·8	1	—	—

It is apparent from Tables I and II that the family data are in agreement with the hypothesis that plumage phase is controlled by two autosomal allelic genes with white phase dominant to dark, but not with the alternative hypothesis that dark phase is dominant to white.

The tests performed in Tables I and II are based on the assumption that there is no differential selection between the two phases. No evidence for differential mortality could be found at Macquarie Island by Shaughnessy (1970). On the other hand, Conroy (1972) has presented evidence for a difference in mortality rate between the two phases in immature birds at Signy Island, and observed a higher frequency of white phase among nestlings (9·37 per cent) than adults (7·82 per cent). In the analysis of family data in Tables I and II, the observed frequency of white phase among adult birds is used. If, however, the observed frequency of white phase among nestlings is used, the expectations and probabilities are slightly affected, but the conclusion regarding the inheritance of plumage phases remains unaltered.

Thus the family data from the Signy Island study support the conclusion reached from the earlier study of inheritance of the plumage phase dimorphism in southern giant petrels at Macquarie Island, namely, that white phase is dominant to dark phase. In the earlier study, two anomalous families were observed in which white chicks resulted from matings between dark parents. The family data from the Signy Island study also support the contention of Shaughnessy (1970) that those anomalous families do not detract from the conclusion that white phase is dominant to dark phase, but resulted from another cause (e.g. modifying genes, or infidelity or fostering on the part of one of the presumed parents).

INHERITANCE OF TOTALLY WHITE BIRDS

Warham (1962) reported pale-footed nestlings of the southern giant petrel at Macquarie Island. We suspect that these were representatives of the same colour phase that Conroy

(1972) reported from Signy Island. Although these chicks have pink feet, they are not albinos, since their irises are the dark colour typical of other chicks. Here we refer to this third phenotype as "totally white". Warham (1962) suggested that chicks of this phenotype resulted from matings between two white-phased adults. Since white phase is dominant to dark, the offspring of such matings could be either homozygous white, heterozygous or even homozygous dark phase. Here we propose that totally white birds are homozygous white, while the more common white birds which have a few dark feathers in their plumage are heterozygous. Note that the term "white phase" includes both heterozygous and homozygous white birds according to this interpretation, while the term "totally white" refers only to homozygous white birds.

From this model of the inheritance pattern of white birds, two predictions can be made: one concerning population data, the other concerning family data. First, the proportion of white-phased birds expected to be totally white is

$$\frac{p^2}{p^2+2pq}, \text{ i.e. } \frac{p}{1+q},$$

where p and q are the frequencies of the alleles for white phase and dark phase, respectively, and $p+q = 1$. The manner in which this proportion varies with the frequency of white phase in populations is shown in Fig. 1a. Since in all populations examined to date white-phased birds are uncommon, occurring with frequencies up to 15 per cent (Shaughnessy, 1971), the graph indicates that totally white birds will comprise only a small percentage of the white phase (up to 4 per cent). Of 1,000 chicks inspected during the 1969 breeding season at Signy Island, 105 (10·5 per cent) were found to be white phase. Three of these were totally white, being 2·85 per cent of the white-phased birds (with standard error 1·63 per cent), which is very close to the predicted figure of 2·77 per cent (standard normal deviate = 0·05, $P = 0{\cdot}96$).

Secondly, totally white chicks can only be produced from matings between two white-phased adults. The proportion of totally white chicks expected from such matings is

$$\frac{1}{(1+q)^2}.$$

The manner in which this proportion varies with the frequency of the white phase in populations is shown in Fig. 1b, which indicates that slightly more than 25 per cent of chicks from white × white matings are expected to be totally white in known populations of the southern giant petrel. An exception is populations from which the white phase is absent, from which totally white chicks must also be absent. At present there are no family data concerning totally white chicks with which to compare this prediction.

It is hoped that these predictions will stimulate other observers of southern giant petrels to record the frequency of totally white birds with pale-coloured feet in populations, and to note the plumage phase of offspring from matings between white-phased adults.

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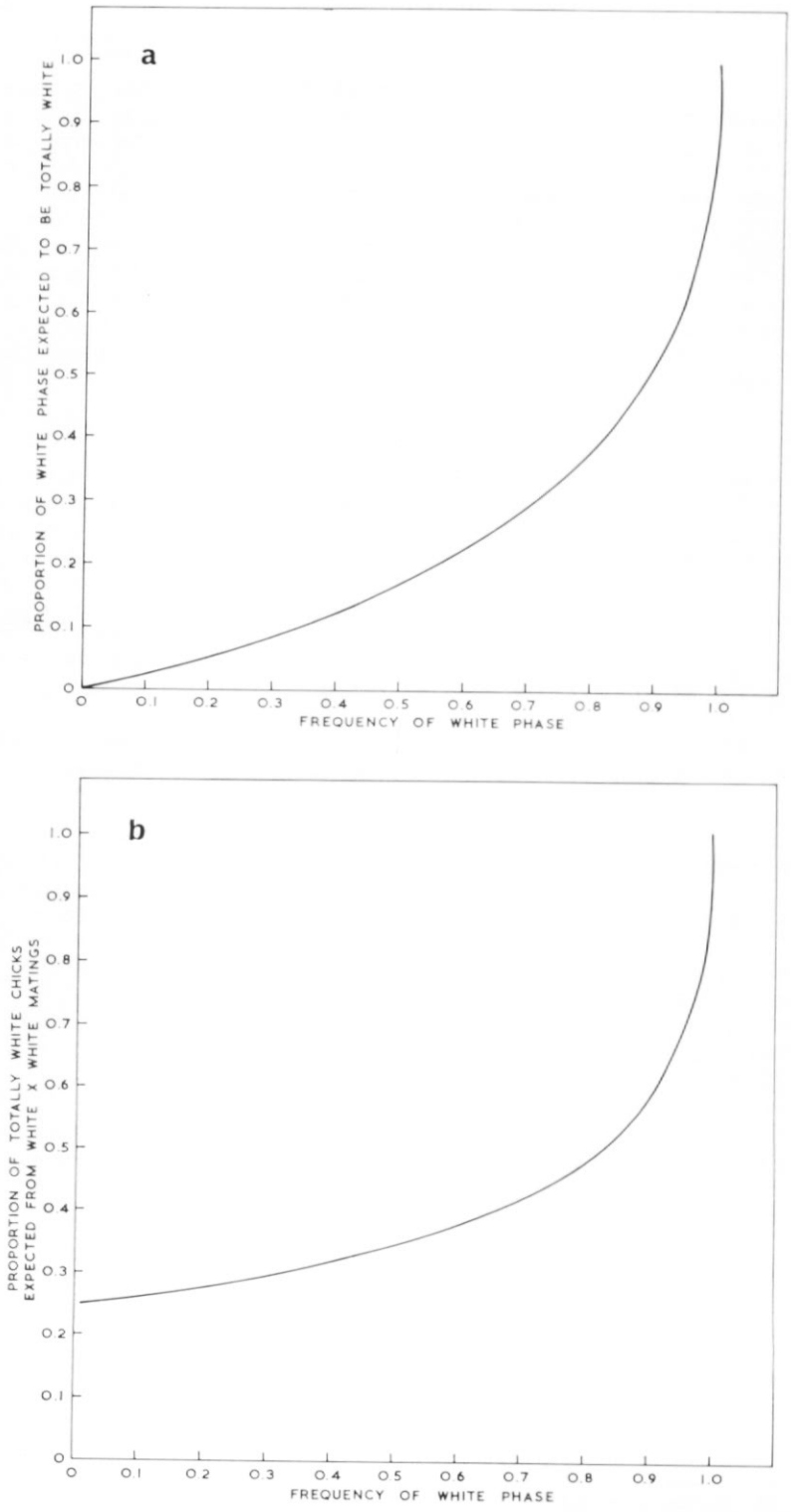

Fig. 1. The manner in which the frequency of totally white southern giant petrels expected in (a) population data and (b) family data varies with the frequency of white-phased birds in the population.