A TWO-EGG CLUTCH OR POLYGYNY? TWO WHITE-PHASE CHICKS IN THE NEST OF A SOUTHERN GIANT PETREL *MACRONECTES GIGANTEUS* AT MACQUARIE ISLAND

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SUMMARY

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Females of the order Procellariiformes most often produce single-egg clutches. At Macquarie Island (54°S, 159°E) in 1959 during a field study of Southern Giant Petrels *Macronectes giganteus*, four or five nests (0.14–0.18% of all nests) contained two eggs or two chicks (Warham 1962). This species occurs in two plumage forms, a dark phase and a white phase. Inheritance of these forms is controlled by a single autosomal gene with two alleles, with white phase dominant to dark phase. At Macquarie Island in 1959, one nest contained two white-phase chicks brooded by a white-phase adult, which Warham (1962) believed resulted from a two-egg clutch rather than from polygyny. Analyses using probabilities based on the inheritance pattern of plumage phases in Southern Giant Petrels and the frequency of white-phase birds at Macquarie Island in 1959 indicate that it was almost seven times more likely that the two white-phase chicks in the nest brooded by a white-phase adult resulted from a clutch of two eggs rather than from polygyny.

Key words: sub-Antarctic, color phase dimorphism, population genetics, allele frequencies

INTRODUCTION

Females of the order Procellariiformes most often produce single-egg clutches (Tickell & Pinder 1966, Tickell 1970), although two-egg clutches have been observed in the Northern Fulmar *Fulmarus glacialis* (Fisher 1952) and in some albatrosses, such as Wandering Albatross *Diomedea exulans* and *Thalassarche* spp. (Tickell & Pinder 1966). Two-egg clutches have also been observed in the Southern Giant Petrel *Macronectes giganteus*, a large, surface-nesting member of the Procellariidae that breeds in the sub-Antarctic and Antarctic (Patterson *et al.* 2008). This species occurs in two color morphs: a dark phase in which adults have gray plumage on most of the body and pale plumage on the head and neck, and a white phase in which nearly all the plumage is white except for some dark feathers scattered throughout the plumage. The color phase of chicks is apparent soon after hatching (Warham 1962).

Plumage phase in Southern Giant Petrels is controlled by a single autosomal gene with two alleles, and with white phase (W) dominant to dark phase (w; Shaughnessy 1970, Shaughnessy & Conroy 1977). White-phase birds can be homozygous dominant (WW) or heterozygous (Ww), and all dark-phase birds are homozygous recessive (ww). As a consequence, matings of two dark-phase birds produce dark chicks only, and matings of two white-phase birds produce white chicks or dark chicks, as do matings of a white-phase bird and a dark-phase bird.

At Macquarie Island (54°S, 159°E) in 1959 during a field study of Southern Giant Petrels, four or five nests, representing 0.14–0.18 % of all nests, contained two eggs or two chicks (Warham 1962). In one of those nests, Warham (1962, his Fig. 2) photographed two white-phase chicks brooded by a white-phase adult. He believed that all nests having two eggs or two chicks resulted from two-egg clutches rather than polygyny, and presented three reasons for that conclusion: (1) the improbability of an adult giant petrel leaving its egg without losing it to Brown Skuas *Stercorarius antarcticus lonnbergi*; (2) the territoriality of Southern Giant Petrel breeders, which threaten other birds that approach; and (3) the discovery of two white-phase chicks brooded by a single white-phase female when, by implication, white-phase Southern Giant Petrels were uncommon. Tickell & Pinder (1966) commented on these observations; in the absence of knowledge of the genetics of plumage phase in Southern Giant Petrels, they were not convinced that Warham's observations constituted evidence for excluding polygyny.

Warham's reasons for supporting the two-clutch proposal are not considered here. Rather, I compare probabilities of obtaining two white-phase chicks in a nest in which a single white-phase adult is observed, by using the inheritance pattern of color-phase dimorphism in Southern Giant Petrels and the frequency of the color phases at Macquarie Island.

METHODS

The probabilities of white-phase chicks and dark-phase chicks resulting from matings of combinations of birds of various phenotypes were calculated using p as the frequency of the white allele (W) and q as the frequency of the dark allele (w), with $p + q = 1$. Actual values for p and q were then substituted based on the frequency of white-phase Southern Giant Petrels at Macquarie Island in 1959 provided by Warham (1962). Two situations are considered here: first, when there is one white-phase female parent (a double-egg clutch) and, second, when there are two female parents (polygyny), with at least one being white-phase.

The comparison begins with consideration of a single white-phase female producing a white-phase chick when mated with a male of unknown genotype. Then, the probability of a single dark-phase female producing a white-phase chick was calculated under the same conditions. For each of these situations, the probability of producing a single chick of each phenotype was calculated, followed by the probabilities for two chicks in single nests containing various combinations of chick phenotypes.

If the white-phase adult brooding the two chicks in Warham's (1962) photograph was a male, then the probabilities of obtaining two white-phase chicks under the two situations would be identical. Thus, the comparison can be made only on the assumption that the adult seen on the nest was female.

Expectations with a single chick at a nest

A white-phase female of genotype WW will always produce a white-phase chick, irrespective of the male's genotype. A heterozygous female will produce a white-phase chick with probability $(p + 0.5q)$ and a dark-phase chick with probability $0.5q$ (Table 1). Among white-phase females, the two genotypes WW and Ww occur with frequencies of $p/(1 + q)$ and $2q/(1 + q)$, respectively. Thus, the probability of a white-phase female producing a white-phase chick is given by

$$\frac{p}{1+q} \cdot 1 + \frac{2q}{1+q} \cdot (p + 0.5q) = \frac{1+pq}{1+q} .$$

TABLE 1
Expected probability[a] of Southern Giant Petrel chicks of two phenotypes (white- and dark-phase) from a heterozygous white-phase female (Ww) mated to a male of unknown phenotype

Parents' genotype		Probability of the mating	Probability of chick phenotypes	
Female	Male		White-phase	Dark-phase
Ww	WW	p^2	p^2	0
Ww	Ww	$2pq$	$1.5\ pq$	$0.5\ pq$
Ww	ww	q^2	$0.5\ q^2$	$0.5\ q^2$
Total		1	$p + 0.5\ q$	$0.5\ q$

[a] Probabilities generated by manipulation of those in Li (1955, Table 4).

TABLE 2
Expected probability of Southern Giant Petrel chicks of two phenotypes (white- and dark-phase) from a dark-phase female (ww) mated to a male of unknown phenotype

Parents' genotype		Probability of the mating	Probability of chick phenotypes	
Female	Male		White-phase	Dark-phase
ww	WW	p^2	p^2	0
ww	Ww	$2pq$	pq	pq
ww	ww	q^2	–	q^2
Totals		1	p	q

The probability of a white-phase female producing a dark-phase chick is

$$\frac{p}{1+q} \cdot 0 + \frac{2q}{1+q} \cdot \frac{q}{2} = \frac{q^2}{1+q} .$$

The probability that a dark-phase female (ww) will produce a white-phase chick is p, and the probability that it will produce a dark-phase chick is q (Table 2). These four situations are summarized in Table 3.

Expectations with two chicks at a nest

With two chicks at a nest, there are three possible combinations of phenotypes for the chick-pair: two white-phase chicks, a white-phase chick with a dark-phase chick, and two dark-phase chicks. The probability of a single white-phase female mated to a male of unknown genotype giving rise to a single white-phase chick is $\frac{1+pq}{1+q}$, from Table 3.

The probability of producing two white-phase chicks from the mating of a white-phase female to a male of unknown genotype is the square of the probability of producing a single white-phase chick, namely:

$$\left(\frac{1+pq}{1+q}\right)^2 \qquad \text{(equation 1).}$$

This refers to the first of the two options that Warham (1962) suggested, namely a single adult female producing a double clutch that leads to two white-phase chicks. This probability is

TABLE 3
Expected probability of Southern Giant Petrel chicks of two phenotypes (white- and dark-phase) in nests with a single adult female mated to a male of unknown phenotype

Parents' phenotype (probability)		Probability of chick phenotypes		
Female	Male	White	Dark	Total
White-phase $(1\text{-}q^2)$	Unknown	$\frac{1+pq}{1+q}$	$\frac{q^2}{1+q}$	1
Dark-phase (q^2)	Unknown	p	q	1

TABLE 4
Expected probability of two Southern Giant Petrel chick pairs of the two phenotypes (white- and dark-phase) in nests of double-egg clutches with a single adult female mated to a male of unknown phenotype

Female's phenotype	Probability of chick phenotypes		
	2 white	1 white, 1 dark	2 dark
White-phase	$\left(\frac{1+pq}{1+q}\right)^2$	$\frac{q^2\ (1+pq)}{(1+q)^2}$	$\frac{q^4}{(1+q)^2}$
Dark-phase	p^2	pq	q^2

presented in Table 4 (top left in the body of the table), along with the other possible combinations of adult female phenotype and chick phenotype.

Warham's other option was two adult females on the nest, one of which was white-phase (i.e., polygyny). The probability that the second female was also white-phase is $(1 - q)^2$, and the probability that she was dark-phase is q^2 (Table 5). The probability of obtaining two white-phase chicks if the second female is white-phase is $\left(\frac{1 + pq}{1 + q}\right)^2$, and if the second female is dark-phase, it becomes $\frac{1 + pq}{1 + q} \,.\, p$, using probabilities generated in the column of Table 3 headed "White." These probabilities hold, irrespective of whether the females were fertilized by one or two males. Thus, the probability of obtaining two white-phase chicks in the nest with two female parents (one of which is white-phase) is given by

$$(1 - q^2)\left(\frac{1 + pq}{1 + q}\right)^2 + q^2\left(\frac{1 + pq}{1 + q}\right) . \, p,$$

which reduces to $p(1 + pq)$ (equation 2).

This is the probability for Warham's second option.

RESULTS AND DISCUSSION

Probabilities can be calculated from equations (1) and (2) using the frequencies of white-phase birds that Warham (1962) observed at rookeries on Macquarie Island in 1959, namely, 44 white-phase birds among 557 birds. He used the term "rookeries" when referring to colonial breeders, Southern Giant Petrels, rather than to solitary breeders, which have since been recognized as Northern Giant Petrels *M. halli* (Bourne & Warham 1966). Thus, the frequency white-phase adults was 0.07899, and the frequency of dark-phase adults (q^2) was 0.92101; hence $q = 0.9597$ and $p = 0.0403$. A similar frequency for white-phase birds on Macquarie Island (0.07894) was reported for nestlings banded between January and March 1955 (Howard 1956). It is likely that this referred to Southern Giant Petrels, because the period during which the nestlings were banded was appropriate for this species and inappropriate for Northern Giant Petrels, which at Macquarie Island breed several weeks before Southern Giant Petrels.

Based on the phenotypic frequencies recorded in 1959, if the white-phase adult that Warham (1962) observed on the nest was a female, the probability that the two white-phase chicks resulted from a single female becomes 0.2809 (from equation 1) and the probability that they resulted from two females is 0.0419 (from equation 2). Thus, it is 6.7 times more likely that there was only one female on the nest rather than two (i.e., polygyny). These calculations do not exclude the possibility of polygyny in the situation at Macquarie Island. Rather, they show that two white-phase chicks in a nest are more likely to have resulted from a clutch of two eggs than from polygyny. It would be of interest to have more observations of plumage phases of Southern Giant Petrels at two-chick nests, especially if the color phase and sex of both adults could be determined.

The frequency of white-phase Southern Giant Petrels is lower at most breeding islands in the sub-Antarctic and Antarctic than at Macquarie Island (Shaughnessy 1971). In such situations, and based on the above calculations, two chicks in a single nest would be even more likely to result from two-egg clutches than from polygyny than at Macquarie Island. For example, if the frequency of white-phase birds at breeding colonies were 0.03 (rather than 0.07899, as used above), a two-egg clutch would be 17 times more likely than polygyny, and if the frequency of white-phase birds were 0.02, a two-egg clutch would be 25 times more likely than polygyny.

There are three particular mating combinations involving polygyny that could lead to two white-phase chicks in a nest; these are included in the second scenario presented above. First, Tickell & Pinder (1966) suggested two dark-phase (i.e., "normal" in their terminology) Southern Giant Petrel females fertilized by one white-phase male could give rise to two white-phase chicks: this event has a probability of $(p \,.\, q^2)^2$. With the frequency of white-phase adults at Macquarie Island observed in 1959, that probability would be equal to 0.0014. Second, two white-phase chicks could result from matings of a white-phase male with two females, one white-phase and one dark-phase, with a probability of $(p^2 \,.\, (1 + 2q)) \,.\, (p \,.\, q^2)$. At Macquarie Island, this event would happen with a probability of 1.42×10^{-5}. Finally, two white-phase chicks could also be in a nest in which the adult male and two adult females were all white-phase; such an event would occur with a probability of $(p^2 \,.\, (1 + 2q))^2$. At Macquarie Island, this event would happen with a probability of 2.25×10^{-5}.

A two-egg clutch of Southern Giant Petrels was also reported by Prévost (1953) in one nest of 110 to 120 nests observed at Îles des Pétrels in Terre-Adélie, but Prévost did not report how many adults were at that nest. Two-egg clutches have also been observed at Anvers Island, Western Antarctic Peninsula, over the last 25 years by Donna Patterson-Fraser (pers. comm.). Five nests were observed frequently, and only two parents were seen in each. Observations of these five nests indicate that the contents most likely resulted from two-egg clutches rather than from polygyny, which accords with predictions reported here.

TABLE 5

Expected probability of Southern Giant Petrel chick pairs of two phenotypes (white- and dark-phase) in nests with two adult females (one known to be white-phase, the other of unknown phenotype) mated to a male of unknown phenotype

Phenotype of second female (probability)	Probability of chick phenotypes		
	2 white	1 white, 1 dark	2 dark
White $(1 - q^2)$	$(1 - q^2) \,.\, \left(\frac{1 + pq}{1 + q}\right)^2$	$(1 - q^2) \,.\, 2q^2 \,.\, \frac{(1 + pq)}{(1 + q)^2}$	$(1 - q^2) \,.\, \frac{(q^4)}{(1 + q)^2}$
Dark (q^2)	$q^2 \,.\, \left(\frac{1 + pq}{1 + q}\right) . \, p$	$q^2 \,.\, \left(\frac{1 + 2pq}{1 + q}\right) . \, q$	$q^2\left(\frac{q^3}{1 + q}\right)$

In summary, these analyses using probabilities based on the inheritance pattern of plumage phase in Southern Giant Petrels and the frequency of white-phase birds at Macquarie Island in 1959 indicate that it was almost seven times more likely that the two white-phase chicks that Warham (1962) recorded on a nest brooded by a white-phase adult resulted from a clutch of two eggs than from polygyny.

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REFERENCES

BOURNE, W.R.P. & WARHAM, J. 1966. Geographical variation in the giant petrels of the genus *Macronectes*. *Ardea* 54: 45-67.

HOWARD, P.F. 1956. Banding of giant petrels at Heard Island and Macquarie Island – II. *Emu* 56: 401-404.

FISHER, J. 1952. *The Fulmar*. London, UK: Collins.

LI, C.C. 1955. *Population Genetics*. Chicago, IL: University of Chicago Press.

PATTERSON, D.L., WOEHLER, E.J., CROXALL, J.P., ET AL. 2008. Breeding distribution and population status of the Northern Giant Petrel *Macronectes halli* and Southern Giant Petrel *M. giganteus. Marine Ornithology* 36: 115-124.

PRÉVOST, J. 1953. Note sur l'écologie des pétrels de Terre Adélie. *Alauda* 21: 205-222.

SHAUGHNESSY, P.D. 1970. The genetics of plumage phase dimorphism of the southern giant petrel *Macronectes giganteus*. *Heredity* 25: 501-506.

SHAUGHNESSY, P.D. 1971. Frequency of the white phase of the southern giant petrel, *Macronectes giganteus* (Gmelin). *Australian Journal of Zoology* 19: 77-83.

TICKELL, W.L.N. 1970. Biennial breeding in albatrosses. In: HOLDGATE, M.W. (Ed.) *Antarctic Ecology*. London, UK: Academic Press. pp. 551-557.

TICKELL, W.L.N. & PINDER, R. 1966. Two-egg clutches in albatrosses. *Ibis* 108: 126-129.

WARHAM, J. 1962. The biology of the giant petrel *Macronectes giganteus. Auk* 79: 139-160.