

GENETICS OF POLYMORPHISM IN THE LITTLE SHAG

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ABSTRACT

A genetic model is presented to explain plumage polymorphism in the Little Shag (*Phalacrocorax melanoleucos brevirostris*). Parent-offspring data from an Auckland colony show that expression of the three morphs (white-throated, smudgy and pied) is primarily controlled by two alleles at a single genetic locus. The allele specifying 'dark' (*D*) shows incomplete dominance over that specifying 'pied' (*d*).

Comparison of morph frequencies with calculated genotype frequencies reveals that about 40% of white-throated birds are homozygous dominant (*DD*), the rest of the white-throated birds and all smudgy birds are heterozygous (*Dd*), and pied birds are homozygous recessive (*dd*).

The population mates non-assortively and the Hardy-Weinberg law correctly predicts the frequencies of black and pied offspring from crosses.

Morph frequencies (and allele ratios) show a gradient from north to south in New Zealand, dark birds being more common in the south. The main factor maintaining this cline may be climatic.

INTRODUCTION

Genetic polymorphism is defined as 'the occurrence together in the same habitat of two or more discontinuous forms, or "phases", of a species in such proportions that the rarest of them cannot be maintained merely by recurrent mutation' (Ford 1965). Plumage polymorphism is well known in birds, and in most cases that have been analysed genetically two alleles of a single gene are known to be responsible for the different phenotypes (morphs) observed. Familiar examples are the black and pied morphs of the Fantail (*Rhipidura fuliginosa*) (Caughley 1969), the white and dark morphs of the Southern Giant Petrel (*Macronectes giganteus*) (Shaughnessy 1970) and the yellow-crowned and orange-fronted morphs of the parakeet *Cyanoramphus auriceps* (Taylor *et al.* 1986).

In these examples one allele shows complete genetic dominance over the other and no intermediate morphs occur. In other birds one allele may be incompletely dominant, and so heterozygous individuals (those carrying both alleles) may have intermediate phenotypes. Examples are the dark, intermediate and pale morphs of the Arctic Skua (*Stercorarius parasiticus*) (Berry & Davis 1970) and the pied, intermediate and black morphs of the Variable Oystercatcher (*Haematopus unicolor*) (Baker 1973).

The Little Shag, which is the New Zealand subspecies of the Little Pied Cormorant of Australia (*P. m. melanoleucos*) displays two distinct morphs (white-throated and pied) as well as variable intermediates (smudgy). In this paper we present a genetic model to explain this polymorphism, using data from the study described by Taylor (1987, this issue).

RESULTS

The parent-offspring data shown in Table 1 were collected at the Hobson Bay, Auckland, colony during the 1977-1978 and 1978-1979 breeding seasons. Offspring were either totally black or pied, that is, black above and white below (Taylor 1987, this issue).

Juvenile plumages

It seems likely that pied juveniles develop into pied adults and that black juveniles develop into either white-throated or smudgy adults. That smudgy adults develop from black juveniles seems probable because the plumage of smudgy adults is usually much more like that of white-throated adults than that of pied adults. That is, the white of face and throat extends only to the upper breast of most smudgy birds. The genetic analysis presented below supports this conclusion; smudgy and pied birds combined make up 49% of the population. The Hardy-Weinberg law states that this proportion will be constant from one generation to the next. However, only 13 of 62 (21%) of the juveniles in Table 1 are pied. This difference is highly significant ($\chi^2 = 17.6$, $\nu = 1$, $P < 0.001$).

White-throated and smudgy birds combined make up 68% of the population and 49 of 62 (79%) of the juveniles in Table 1 are totally black. This difference is not significant ($\chi^2 = 2.9$, $\nu = 1$, $P = 0.1$) and supports the theory that black juveniles develop into both white-throated and smudgy adults.

TABLE 1 — Parent-offspring data for the Hobson Bay colony of Little Shags (1977-1979)

Parental mating combination	Number of pairs	Offspring	
		Dark	Pied
Wh x Wh	11	17	0
Wh x Sm	8	11	0
Wh x Pd	16	19	6
Sm x Sm	1	1	1
Sm x Pd	6	1	5
Pd x Pd	1	0	1
Totals	43	49	13

(Wh = white-throated, Sm = smudgy, Pd = pied)

Genetic model

Our model proposes that polymorphism in the Little Shag is controlled by two alleles (designated *D* and *d*) of a single gene. From the predominance of dark offspring evident in Table 1, our first hypothesis was that 'dark'

is dominant over 'pied'; white-throated birds being homozygous dominant (DD), smudgy heterozygous (Dd) and pied homozygous recessive (dd).

Such a hypothesis would require, however, that all the offspring of matings of the two homozygous forms (white-throated x pied) be heterozygous i.e. scored 'dark', but 6 of the 25 offspring were pied.

We therefore proposed that white-throated birds consist of both homozygous dominant (DD) birds and heterozygous birds and that pied birds are homozygous recessive (dd). Probably all smudgy birds are heterozygous (Dd) – of the eight smudgy parents in smudgy x smudgy and smudgy x pied crosses in Table 1, seven must have been heterozygous (because they produced pied offspring) and the eighth could have been.

All the data in Table 1 fit this interpretation. That 'pied' is not dominant can be demonstrated by considering the offspring of the white-throated x pied crosses in Table 1. At one extreme, all pied birds would be homozygous dominant (PP) and all offspring of Wh x Pd matings would be pied. At the other extreme, all pied birds would be heterozygous (Pp) and black and pied offspring would occur in equal numbers. Of the 25 offspring of Wh x Pd matings, 19 were black. 'Pied' is therefore clearly not dominant over 'dark'.

We therefore tested the hypothesis by using the Hardy-Weinberg model to calculate genotype frequencies and so to predict the ratio of black to pied offspring in crosses. This model requires that the population is at genetic equilibrium (we have no evidence that it is not) and that the population mates non-assortively.

Non-assortive mating

The 84 pairs formed at the Hobson Bay colony during the 1978-1979 season were tested for non-assortive mating and the results are shown in Table 2. The 84 pairs consisted of 86 white-throated, 28 smudgy and 54 pied birds. Phenotype frequencies were thus:

$$\text{white-throated} = 0.512, \text{ smudgy} = 0.167, \text{ pied} = 0.321$$

These frequencies were used to calculate the number of pairs of each mating combination that would be expected if pairing were random.

There is good agreement between observed and expected values ($\chi^2 = 5.10$, $\nu = 5$, $0.5 > P > 0.3$) and mating is thus shown to be random as to plumage type.

Genotype frequencies

In the Hardy-Weinberg model, the frequency of the allele D is designated p and the frequency of d is q , where $p + q = 1$. Genotype frequencies are calculated from the binomial $p^2 + 2pq + q^2$, using the frequency of homozygous recessive (pied) birds, 0.321, as q^2 . Thus $q = 0.566$ and $p = 0.434$. Genotype frequencies are therefore:

$$\begin{aligned} p^2 &= 0.188 = DD \text{ (homozygous dominant)} \\ 2pq &= 0.491 = Dd \text{ (heterozygous)} \\ q^2 &= 0.321 = dd \text{ (homozygous recessive)} \end{aligned}$$

We can now calculate the numbers of black and pied offspring to be expected from each of the mating combinations shown in Table 1. As an

TABLE 2 — Non-assortive mating in the Hobson Bay colony of Little Shags

Mating combination	Observed number of pairs	Expected number of pairs	$\frac{(\text{Observed} - \text{expected})^2}{\text{Expected}}$
Wh x Wh	18	22.01	0.73
Wh x Sm	14	14.36	0.01
Wh x Pd	36	27.64	2.53
Sm x Sm	3	2.35	0.18
Sm x Pd	8	8.99	0.11
Pd x Pd	5	8.65	1.54
	84	84.00	$\chi^2 = 5.10$

example, we will consider the 16 white-throated x pied crosses, which yielded 25 offspring. White-throated birds are a mixture of *DD* and *Dd* and all pied birds are *dd*. The proportion of Wh x Pd crosses that are *DD* x *dd* therefore

$$= \frac{DD}{DD + Dd} = \frac{0.19}{0.19 + 0.49} = 0.28$$

All offspring from these crosses will be *Dd* and therefore black. The proportion of Wh x Pd crosses that are *Dd* x *dd*

$$= \frac{Dd}{DD + Dd} = \frac{0.49}{0.19 + 0.49} = 0.72$$

Offspring from these crosses will be *Dd* and *dd* in equal numbers and therefore half will be black and half pied.

The expected and observed numbers of black and pied offspring from Wh x Pd crosses are shown in Table 3.

The differences between expected and observed are not significant ($\chi^2 = 1.08$, $\nu = 1$, $P = 0.3$).

The numbers of black and pied offspring to be expected from all other mating combinations were also calculated and the results are summarised in Table 4.

The differences between observed and expected numbers for the first three combinations (Wh x Wh, Wh x Sm and Wh x Pd) are not significant ($P = 0.22$, 0.25 and 0.3 respectively).

The sample sizes of the other three combinations are too small to analyse. Finally, the differences between observed and expected totals in Table 4 are also not significant ($\chi^2 = 1.4$, $\nu = 1$, $P = 0.24$).

The lack of significance in all cases provides strong support for the proposed model.

TABLE 3 — Expected and observed phenotype frequencies among 25 offspring of Wh x Pd matings

Parental genotypes	Frequency of crosses	Offspring phenotype			
				Black	Pied
<u>DD</u> x <u>dd</u>	0.28 x 25 =			7.0	0.0
<u>Dd</u> x <u>dd</u>	0.72 x 25 =			9.0	9.0
	Expected =			16.0	9.0
	Observed =			19	6

TABLE 4 — Summary of the expected and observed phenotype frequencies among offspring of all crosses

Crosses	Total offspring	Black offspring		Pied offspring	
		Exp	Obs	Exp	Obs
Wh x Wh	17	14.8	17	2.2	0
Wh x Sm	11	9.0	11	2.0	0
Wh x Pd	25	16.0	19	9.0	6
Sm x Sm	2	1.5	1	0.5	1
Sm x Pd	6	3.0	1	3.0	5
Pd x Pd	1	0.0	0	1.0	1
Totals	62	44.3	49	17.7	13

Gradient of genotype frequencies

The frequency of dark and pied morphs varies in different parts of New Zealand, the pied morph being more common in the north (see Taylor, this issue). Assuming these populations to be at equilibrium, we can calculate genotype and allele frequencies as before, from the frequency of homozygous recessive (pied) birds. The results are shown in Table 5.

TABLE 5 — Calculated genotype and allele frequencies for the Little Shag in different parts of New Zealand

Location	Frequency of pied morph ⁽¹⁾	Genotype frequencies			Allele frequencies	
		<u>DD</u>	<u>Dd</u>	<u>dd</u>	p	q
Far North	60%	0.05	0.35	0.60	0.22	0.78
Auckland (this study)	32%	0.19	0.49	0.32	0.43	0.57
Rest of North Island	15%	0.38	0.47	0.15	0.61	0.39
South Island	8%	0.51	0.41	0.08	0.72	0.28

(1) Data from Taylor (1987)

There is a clear gradient of allele frequencies from north to south, reflecting the observed morph cline.

DISCUSSION

Our evidence supports the conclusion that plumage polymorphism in the Little Shag is controlled by two alleles at a single genetic locus, the allele specifying 'dark' being incompletely dominant. This genetic evidence also supports the current classification of *P. melanoleucos* in New Zealand as a single subspecies.

On comparing the phenotype (morph) frequencies observed in Auckland with the calculated genotype frequencies, we find that about 60% of the Auckland birds scored white-throated must, in fact, be heterozygotes. A similar situation has been described for the Arctic Skua where dark, intermediate and pale morphs occur. "... a large proportion (45% according to O'Donald) of birds classified as Dark are in fact heterozygotes" (Berry & Davis 1970). 'White-throated' Little Shags having any extension of white on to the upper breast or a few white feathers on the flanks or belly are therefore likely to be heterozygotes (and should probably be scored as smudgy).

We do not know what mechanism controls how much black develops on the underparts of heterozygotes. There may be additional genetic effects at other loci, as Baker (1973) suggested for the Variable Oystercatcher, or environmental effects or a combination of both. Heterozygotes of the Little Shag, however, seem to vary less than do intermediate Variable Oystercatchers. About two-thirds of heterozygous Little Shags in Auckland

are similar in appearance to white-throated birds. That is, they are class A or B in Figure 2 of Taylor (this issue). About one-third are smudgy, i.e. class D.

The factors maintaining this polymorphism need further study. The 'dark' phenotype has presumably evolved since the Little Shag arrived in New Zealand because the Australian subspecies *P. m. melanoleucos* is pied. The large difference in allele ratios in different parts of New Zealand (Table 5) suggests that one or more selective forces are constantly in operation. One obvious suggestion is that these are climatic. The dark morphs may be at an advantage in areas of lower temperature because the greater amounts of solar heat absorbed by an all-dark bird would reduce the amount of energy expended on the maintenance of body temperature.

Perhaps morph frequencies are altered locally by the occasional arrival of Little Shags from Australia, but large numbers would probably be needed to have a significant effect. Such immigrants would have to be more common in the north than in the south if invasion plays a part in maintaining the cline.

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SHORT NOTE

Homing ability of the House Sparrow

The House Sparrow (*Passer domesticus*) is a social species that is throughout New Zealand. Sparrows are highly sedentary birds, 92% of recoveries of banded sparrows in Great Britain being within 2 km of their banding site (Summers-Smith 1963). In Illinois the longest movement of 89 sparrows recaptured from 1785 banded was 3.2 km (Will 1973). In New Zealand, 97% of 2237 recoveries of individual banded sparrows were at their banding site. Twelve birds were recovered within 15 km, 35 birds from 15-30 km, 15 birds from 30-100 km and six birds further than 100 km from their banding site. The recoveries include one bird at 236 km and one at 317 km. We report here movements of House Sparrows of up to 5.7 km in returning to their original capture site after escaping from an aviary.