GENETICS OF PLUMAGE VARIABILITY IN THE VARIABLE OYSTERCATCHER
(Haematopus unicolor)

By ALLAN J. BAKER
Department of Zoology, University of Canterbury

ABSTRACT

The Variable Oystercatcher *(Haematopus unicolor),* which has melanistic, pied and intermediate phases, was studied in the field in New Zealand from 1969 to 1972 inclusive. Parents and their progeny were colour-banded, and the development of plumage with age was checked for non-genetic variation. The parent-offspring data can be most simply explained by a genetic model involving a major gene (W) whose dominance is modified only in the heterozygous condition. In the model, the pied condition is homozygous dominant (WW), the melanistic condition is homozygous recessive (ww), and all intermediate-plumaged birds are heterozygous Ww. The wide range of plumage variability in the intermediate phase seems most likely explained by the action of polygenic modifiers acting cumulatively at a number of loci, and specifically on the Ww genotype. Gene frequencies and genotype frequencies are in Hardy-Weinberg equilibrium, indicating that selection does not operate against the heterozygote to form an isolating mechanism between the homozygous pied and melanistic phases. The three phenotypes are therefore best considered as colour phases of one species, *H. unicolor.*

INTRODUCTION

Oystercatchers are dimorphic through much of their world range, being either pied or wholly black. The melanistic forms have been particularly troublesome to taxonomists (see Stresemann 1927) especially since they do not often occur sympatrically with pied forms. Thus the acid test of interbreeding of these forms (and the consequent evaluation of genic differences that it permits) is rarely available for systematic studies. Black and pied forms are sympatric and interbreed in only three known locations; *Haematopus bachmani* (black) and *H. palliatus palliatus* (pied) interbreed in the Gulf of California (Bancroft 1927), *H. ater* (black) and *H. palliatus durnfordi* (pied) in Golfo San Jose, Argentina (Jehl *et al.* 1973), and *H. unicolor* (black and pied) in New Zealand (Buller 1888). Interbreeding of pied and black phases of *H. unicolor* was first suspected by Buller (1873), and later Rothschild (1899) considered an intermediate-plumaged bird from such crosses sufficiently distinctive to warrant full species rank *reischeki.* The systematic confusion which followed this move (see Falla 1939; Oliver 1955; Falla *et al.* 1966) has resulted from a lack of knowledge of the interbreeding and inheritance of the colour phases.

NOTORNIS 20: 330-345 (1973)

In New Zealand, crosses of black and pied phases of *H. unicolor* produce progeny of extremely variable plumage, and it was this variability that led to the coining of the vernacular (R. B. Sibson, pers. comm.). The purpose of this paper is to describe this plumage variability and to give a broad outline of its inheritance as a step towards clarifying systematic relationships of the colour phases.

METHODS AND MATERIALS

Wintering birds were trapped by projecting a cannon-net over roosting flocks, and breeding birds were trapped at the nest using an automatic drop-trap (Baker in press) set over the eggs. Because Northland is the only part of New Zealand in which all colour phases are well represented (Baker 1973), most trapping was concentrated there. Sampling localities and sample details are listed in Table 1. Trapping was carried out over the period 1969 to 1971 inclusive. Each of the trapped birds was colour-banded, and photographs were taken of the alar bar on the wing, the ventral plumage, and the rump patch of all pied and intermediate phase birds (see Fig. 3).

Inheritance of colour phases was studied by examining broods from various parentages. Data were gathered on 57 such broods involving a total of 108 chicks. Progeny phenotypes were recorded at hatching, as black chicks have brown bellies, pied chicks have white bellies, and intermediate chicks have a mixture of brown and white down on the belly (see Figs. 1 & 2). This primary classification

Table 1. Samples of Variable Oystercatchers used in this study.

Locality	Latitude (°S) and	Longitude (°E)	Date	N
Te Werahi Bay	34° 27'	172° 41'	Jan. 1971	4
Ninety Mile Beach	34° 30'	172° 40'	Jan. 1971	10
Great Exhibition Bay	34° 38'	173° 03'	Jan. 1971	4
Kowhai Beach, Houhora	34° 46'	173° 09'	Jan. 1971	4
Rangaunu Bay	34° 50'	173° 12'	Jan. 1971	2
Takou Bay	35° 06'	173° 56'	Jan. 1970	2
Waipu Beach	36° 00'	174° 28'	Jan. 1970	8
Waipu Beach	36° 00'	174° 28'	May 1970	27
Waipu Beach	36° 00'	174° 28'	Jan. 1970	2
Waipu Beach	36° 00'	174° 28'	May 1971	9
Somes Island	41° 16'	174° 51'	Nov. 1970	4
Kaikoura Peninsula	42° 24'	173° 41'	Dec. 1969	2
Jackson Bay	43° 58'	168° 40'	Dec. 1970	2
			Total	80

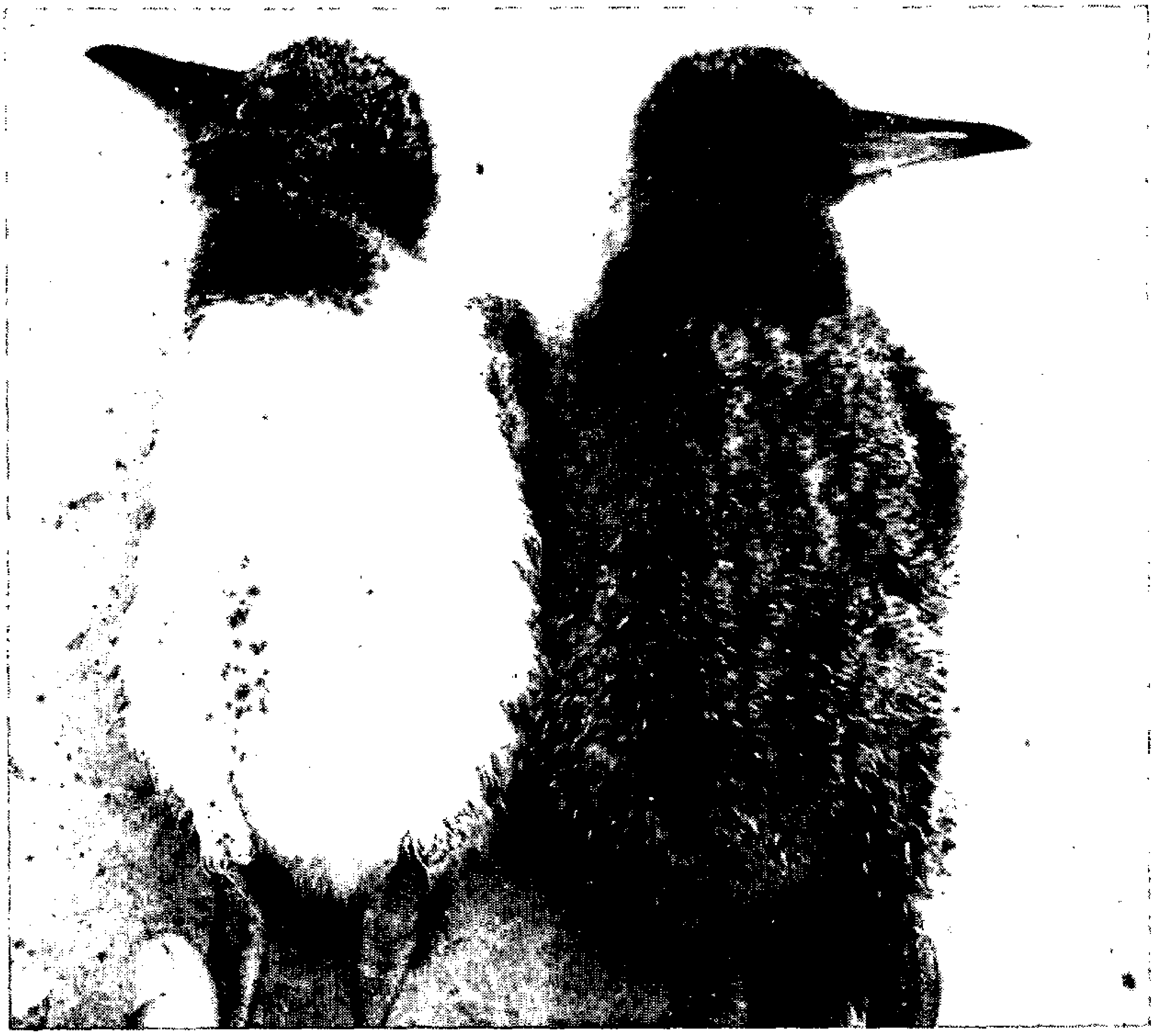

FIGURE 1 — Pied and black phase Variable Oystercatcher chicks aged about 14 days.

is only approximate, however, as there is no detectable difference between the downy plumages of black and very black intermediate chicks, and also between pied and very pied intermediates. The degree of intermediacy in the plumage of the intermediate phase birds cannot be gauged until the chicks have gained their juvenile feathers at the age of approximately six weeks. I have been able to follow only 12 juveniles through to their second year plumage, but in all cases there was no detectable change in plumage variability with age.

The frequencies of the colour phases in Northland were recorded in the 1969-1970 and 1970-1971 breeding seasons, though the major part of the Northland census was accomplished with the aid of personnel of the OSNZ Northland field trip in January 1971.

RESULTS

Plumage variability:

It has been tacitly assumed in the past that plumage variation between the extremes of pied and black is continuous, as for example in the statement of Oliver (1955): " There is no fixed pattern, every

FIGURE 2 — Intermediate phase Variable Oystercatcher chicks aged about 21 days. Note the dark down amongst the white of the undersurface.

individual being differently marked." The range of plumage variation in breast, rump and alar bar patterns of birds captured during this study is shown in Figure 3. Although these patterns do not include all those evident in live-trapped or museum specimens, they do cover the observed range of variation with the exception of some very pied individuals. In the extreme condition, pied birds are similar to the South Island Pied Oystercatcher *(H. o. finschi)*, with white areas in front of wing, and a white rump patch extending up onto the back in a bright wedge. I have observed two of these birds, and

FIGURE 3 — Variation in the plumage patterns of the breast, alar bar on the wing, and rump patch of Variable Oystercatcher, ranging from pied (1) to black (10) phases. See text for explanation of numbers.

3

4

5

6

7

8

9

10

one was recently reported from D'Urville Island (Mrs Marion Lane, pers. comm.). The corresponding loss of white parts in the breast, rump and alar bar patterns from pied through to black indicates that there is effective linkage between the genes controlling these traits. To facilitate the description of plumage variability in sections beyond, the phenotypes in Figure 3 were classified as follows: pied (1), very pied intermediate (2 & 3), pied intermediate (4), intermediate (5 & 6), black intermediate (7 & 8), very black intermediate (9), and black (10). All the phenotypes from 2 through to 9 can be referred to collectively as the " intermediate phase."

Inheritance of plumage variability: Parent-offspring data:

Parent-offspring data can be most easily presented initially by lumping all parti-coloured phenotypes under the intermediate phase, and thus dealing with only three colour phases as in Table 2. The most noticeable feature of these data is that the extremes of black and pied both breed true. Although the sample sizes are small for these phenotypes, similar findings have been reported previously by Oliver (1955). It therefore seems likely that black and pied phases are homozygous for the genes controlling plumage variability. The parental cross of black and pied phases produced only intermediate phase offspring, though it is noteworthy that six of the 16 chicks were near the pied end of the intermediate phase. The F_1 cross of intermediate by intermediate yielded F_2 progeny of all three phenotypes, showing that the genes involved had segregated and recombined independently in a typical Mendelian manner. Again, it is noteworthy that there is a large representation of pied phenotypes. The backcross of black and intermediate phases produced only black and intermediate progeny, and the other backcross of pied and intermediate produced only intermediate and pied progeny.

Genetic model:

Quite clearly then, these data can be simply explained by two autosomal allelic genes at a single genetic locus, with black and pied being homozygous and the intermediate phase being heterozygous. This hypothesis can be tested using the Hardy-Weinberg Law of population genetics. Where three phenotypes (WW, Ww and ww) are distinguishable, the maximum likelihood estimate of the frequency (p) of W is given by

$$p = \frac{2a + b}{2N}$$

where a = the number of homozygous WW individuals, b = the number of heterozygous Ww individuals, and N = the total sample size (see Li 1955: 12). Using the data of Table 2 for the mating combinations,

$$p = \frac{40 + 56}{228} = 0.421$$

$$\text{and } q = 1 - p = 0.579$$

Table 2. Parent-offspring data for the Variable Oystercatcher

Mating Combination	Inferred Genotype	N	Progeny Black (ww)	Intermediate (Ww)	Pied (WW)
Black x black	ww x ww	10	20	-	-
Black x intermediate	ww x Ww	11	6	14	-
Intermediate x intermediate	Ww x Ww	20	6	16	14
Intermediate x pied	Ww x WW	5	-	5	3
Pied x pied	WW x WW	4	-	-	7
Pied x black	WW x ww	7	-	17	-
			32	52	26
	Totals	57		108	

The observed phenotypes in the progeny and those expected from Hardy-Weinberg proportions are shown in Table 3. The lack of significance of the X^2 values attests to the agreement of observed and expected numbers, and supports the hypothesis that the three colour phases are controlled by two autosomal allelic genes.

Unfortunately, it is not possible to elucidate dominance relations of the two alleles from these data because of the phenotypic variability in the heterozygote, and so the data in Table 2 were subdivided further to provide critical information on the inheritance of this variability (see Table 4).

Table 3. Observed and expected frequencies of 108 offspring phenotypes assuming Hardy-Weinberg equilibrium where $p = 0.421$ and $q = 0.579$.

Phenotype	Genotype	H/W proportions	Observed frequency	Expected frequency	X^2-value	P
Pied	WW	p^2	26	19.1	1.83	$0.5 > p > 0.1$
Intermediate	Ww	2pq	52	52.7	0.01	$p < 0.9$
Black	ww	q^2	32	36.2	0.55	$0.5 > p > 0.1$

Table 4. Additive effects of "piedness" in parent-offspring data.

N	Mating Combination	Phenotypes of intermediate phase offspring: very black	black	intermediate	pied	very pied
4	Black x very black intermediate	+	+			
2	Very black intermediate x very black intermediate	+	+	+		
3	Black intermediate x black intermediate		+	+	+	
6	Intermediate x intermediate			+	+	●
3	Pied intermediate x pied intermediate				+	+
2	Very pied intermediate x very pied intermediate					+

It is apparent from this analysis that as the amount of "piedness" in the mating phenotypes increases then so does the amount of "piedness" increase in the progeny phenotypes. Moreover, this effect seems to be additive, so that the " pied " allele becomes increasingly dominant over the " black " allele on progression from a black intermediate through to a pied intermediate. Thus it is reasonable to assume that in the intermediate (Ww) phase the dominance of W is influenced by additive genic effects at other loci. Genes which control the phenotypic expression of a heterozygote by altering dominance relations of the major genes are referred to as specific modifiers, specific in the sense that they modify only the heterozygote (Sinnott *et al.* 1950). If the modifiers were present as a polygneic complex of say five genes, then the intermediate phenotypes might be represented as in Table 5. Thus the modifiers would act additively in determining the degree of dominance of the major gene W, as is common in these polygenic systems (Sinnott *et al. op cit.*). The intermediate phenotypes could therefore range between the extremes of black or pied, even though they all had the same basic genotype for the major gene. The actual number of modifiers involved in controlling dominance is likely to be greater than five, since there are more phenotypes discernable than are listed in the simplistic example above.

Table 5. Hypothetical model of the action of modifier genes on the major gene for colour phase.

Phenotype	Condition at major locus	Condition at modifier loci
Black	ww	no action irrespective of condition
Very black intermediate	Ww	M_1
Black intermediate	Ww	M_1 M_2
Intermediate	Ww	M_1 M_2 M_3
Pied intermediate	Ww	M_1 M_2 M_3 M_4
Very pied intermediate	Ww	M_1 M_2 M_3 M_4 M_5
Pied	WW	no action irrespective of condition

Implications of genetic equilibrium:

The maintenance of genetic equilibrium in successive generations of *H. unicolor* as indicated by the Hardy-Weinberg proportions in the offspring has several important implications for an interpretation of interbreeding of the colour phases in this species. Hardy-Weinberg equilibrium conditions are as follows: the breeding population must be large; the population must mate at random; and, mutation, selection

Table 6. Relative frequencies of the three colour phases of the Variable Oystercatcher in Northland.

	Phenotype		
	Black	Intermediate	Pied
Numbers in Northland	258	267	179
		704	
Per cent occurrence	36.7	37.9	25.4
		100.0	

and migration must be absent or have reached their own equilibria. Are these conditions really met for the *H. unicolor* data above, or are they merely fortuitous accidents of sampling design ?

The Northland population of *H. unicolor* probably involves at least 200 pairs; I have observed 101 pairs in less than half the known Northland breeding range. A breeding population of this size would seem to be large enough to preclude deviations from equilibrium due to sampling error. Whether or not the colour phases breed at random can be ascertained by comparing observed mating frequencies with those expected on the basis of the relative frequencies of the colour phases in Northland. The relative frequencies of the three colour phases in Northland are shown in Table 6. Although there is almost certainly some misclassification of phenotypes in this table (with very black intermediates being classified as black and very pied hybrids being classified as pied) resulting in an under-representation of the intermediate phenotype, it is doubtful whether this source of error would effect significantly phenotype frequencies in view of the large overall sample size. Observed and expected frequencies of 101 Northland mating combinations, the phenotypes of which were determined

Table 7. Observed and expected frequencies of 101 mating combinations in Northland.

Mating combination	Observed frequency	Expected frequency assuming random mating	X^2-value	P
Black x black	17	13	1.23	$0.5 > p > 0.1$
Pied x pied	7	7	0.00	$p > 0.975$
Pied x black	14	18	0.89	$0.5 > p > 0.1$
Intermediate x intermediate	22	15	3.27	$0.1 > p > 0.05$
Black x intermediate	24	28	0.57	$0.5 > p > 0.1$
Pied x intermediate	17	20	0.45	$0.9 > p > 0.5$

by careful inspection by the author, are shown in Table 7. Expected frequencies were calculated (using the data of Table 6) as follows: the mating frequency of WW crosses is given by:

WW (♂♂) x WW (♀♀) = (179/704) x (179/704
= 0.065

For 101 pairs we would expect 101 x 0.065 pied matings i.e. approximately 7 pairs. None of the differences between observed and expected frequencies are significant, indicating that mating is random with respect to colour phase. Variable Oystercatchers are non-migratory (Oliver 1955; Falla *et al.* 1966), and once they form pairs they tend to localize in an area and occupy the same territory from year to year. Evidence for selection and mutation is lacking too (Baker 1972), so it can be concluded that conditions under which the Hardy-Weinberg law applies are fully met.

DISCUSSION

The parent-offspring data are in agreement with the hypothesis that plumage colour phases are controlled primarily by two autosomal allelic genes, with the dominance relations of the pied and black alleles in the heterozygote being modified by genes at other loci. However, some previously published parent-offspring data apparently do not conform to this hypothesis, the most notable exception being that recorded by Buller (1888) in which two pied chicks were seen following two black adults. It is not clear from Buller's account whether the black adults were actually the parents of these chicks, and it is also possible that one or both of these adults may have been very black hybrids. During the 1970 OSNZ Northland field trip I received a report from several ornithologists in the party that two black adults had a brood of one black and one pied chick. On investigating this personally I found that both parents had tiny amounts of white near the vent, and thus were very black intermediates. With this mating combination pied and black chicks are to be expected. Other instances in which " pied " chicks are reported from black x intermediate matings (e.g. Falla 1939; Brathwaite 1950) may also be due to misclassification of parental or offspring phenotypes. The only other explanation of these data is that the modifiers can produce black and pied birds at the phenotypic extremes of the basic Ww genotype. If this were so then two pied parents could produce black offspring (which has never been recorded) and two black parents could produce pied offspring (only one unsubstantiated report).

Where major effects such as black versus white or black versus pied are involved, the genetic mechanism involved is usually simple and involves very few major genes, usually a pair (see Southern 1945; O'Donald & Davis 1959; Cooke & Gooch 1968; Munro *et al.* 1968; Caughley 1969; Berry & Davis 1970; Shaughnessy 1970; and Craig 1972). However, in these cited cases, the colour phases are sharply discontinuous and are referred to as polymorphism. Polymorphism has been defined precisely by Mayr (1963: 670) as " the simultaneous occurrence of several *discontinuous* phenotypes or genes in a population, with the frequency of the rarest type higher than can be maintained by recurrent mutation." Since the variation in intermediate phase phenotypes of *H. unicolor* ranges between the extremes of black and pied (thereby giving a continuous span of phenotypes), the use of polymorphism (OSNZ 1970) to describe this variability may be unwise. Continuous variation is usually indicative of an underlying polygenic system of genetic control, where a series of genes each with minor and cumulative effects are involved (Mather 1949). In *H. unicolor* the variation seems to be restricted to the genotype heterozygous for the major gene, and is most easily explained by modifiers acting specifically on the genotype heterozygous for the major gene (Dunn 1937).

The existence of Hardy-Weinberg equilibrium in gene frequencies and genotype frequencies of the three colour phases has taxonomic implications. If the heterozygous intermediate colour phase was of lower fitness than the two homozygous phases, then disequilibrium would ensue and the heterozygote would drop to a very low frequency. Thus the extremes of black and pied would be effectively reproductively isolated, which would require the recognition of these two phases as semispecies as suggested by Oliver (1955), and they should be accorded full species rank (Short 1969). The occurrence of equilibrium proportions of the intermediate phase genotype in the Variable Oystercatcher argues against such an interpretation, and therefore it must be concluded that the three phenotypes are best considered as colour phases of one species *(H. unicolor)*, as is advocated by the Checklist Committee (OSNZ 1970).

ACKNOWLEDGEMENTS

This study was made during the tenure of a Wildlife Scholarship from the Wildlife Branch, Department of Internal Affairs. I am most grateful to Wildlife personnel for field assistance, particularly B. D. Bell, D. V. Merton, C. J. R. Robertson, L. R. Moran, C. R. Veitch, and Dr J. A. Mills.

My wife more than anyone made this study possible with sterling field support and encouragement. I would like to thank the members of the 1970 OSNZ Northland field trip for their immense help in locating breeding pairs and in censusing the Aupori Peninsula, particularly A. T. Edgar, T. R. Calvert and D. E. Crockett. The research was supervised by Dr J. Warham to whom I express my gratitude. Dr C. McGowan, Dr J. C. Barlow and G. Shields read the manuscript and made helpful suggestions for improvement.

LITERATURE CITED

BAKER, A. J. 1972. Systematics and affinities of New Zealand oystercatchers. Unpublished Ph.D. thesis, University of Canterbury. Pp. 1-134, text - figs 1-25, tables 1-28, pls 1-14.

——— 1973. Distribution and numbers of New Zealand oystercatchers. Notornis 20 (2): 128-144, text - figs 1-8, table 1.

——— in press. Criteria for aging and sexing New Zealand oystercatchers. New Zealand Journal of Marine and Freshwater Research.

BANCROFT, G. 1927. Breeding birds of Scammons Lagoon, lower California. Condor 29 (1): 29-57, text - figs 1-18.

BERRY, R. J.; DAVIS, P. E. 1970. Polymorphism and behaviour in the Arctic Skua (*Stercorarius parasiticus* (L)). Proceedings of the Royal Society B 175 (1040): 255-267, text - fig 1, tables 1-9, pl. 1.

BRATHWAITE, D. H. 1950. Notes on breeding of Variable Oystercatchers. Notornis 4 (1): 22-24, text - fig 1.

BULLER, W. L. 1873. A history of the birds of New Zealand. 1st ed. Pp. 1-384, text illus. London: Van Voorst.

——— 1888. A history of the birds of New Zealand. 2nd ed. Vol. II. Pp. 251-359, pls 15-50. London: published by the author.

CAUGHLEY, G. 1969. Genetics of melanism in the Fantail *Rhipidura fuliginosa.* Notornis 16 (4): 237-240, tables 1-5.

COOKE, F.; GOOCH, F. G. 1968. The genetics of polymorphism in the goose *Anser caerulescens.* Evolution 22 (2): 289-300, tables 1-11.

CRAIG, J. L. 1972. Investigation of the mechanism maintaining polymorphism in the New Zealand Fantail, *Rhipidura fuliginosa* (Sparrman). Notornis 19 (1): 42-55, text - figs 1-3, tables 1-4, appendix 1.

DUNN, L. C. 1937. Studies on spotting patterns II. Genetic analysis of variegated spotting in the house mouse. Genetics 22 (1): 43-64, text - fig 1, tables 1-5.

FALLA, R. A. 1939. New Zealand oystercatchers. Records of the Canterbury Museum 4 (5): 259-266, tables 1-3, pl. 1.

FALLA, R. A.; SIBSON, R. B.; TURBOTT, E. G. 1966. A field guide to the birds of New Zealand and outlying islands. Pp. 1-254, pls 1-18, text illus. London-Auckland: Collins.

JEHL, J. R.; RUMBOLL, M. A. E.; WINTER, J. P. 1973. Winter bird populations of Golfo San Jose, Argentina. Bulletin of the British Ornithologists' Club 93 (2): 56-63, text - figs 1-3, table 1.

LI, C. C. 1955. Population genetics. Pp. 1-366, text - figs 1-82, tables 1-82. Chicago & London: University of Chicago Press.

MATHER, K. 1949. Biometrical genetics, the study of continuous variation. Pp. 1-162, text - figs 1-16, tables 1-32. London: Methuen & Co. Ltd.

MAYR, E. 1963. Animal species and evolution. Pp. 1-797, text - figs 1-65, tables 1-43. Cambridge, Massachusetts: Harvard University Press.

MUNRO, R. E.; SMITH, L. T.; KUPA, J. J. 1968. The genetic basis of colour differences observed in the Mute Swan *(Cygnus olor).* Auk 85 (3): 504-505, table 1.

O'DONALD, P.; DAVIS, P. E. 1959. The genetics of the colour phases of the Arctic Skua. Heredity 13 (4): 481-486.

OLIVER, W. R. B. 1955. New Zealand birds. 2nd ed., rev. and enlarged. Pp. 1-661, text illus., 12 unnumb. col. pls. Wellington: A. H. & A. W. Reed.

OSNZ. 1970. Annotated checklist of the birds of New Zealand. (The Checklist Committee, F. C. Kinsky, Convenor), Ornithological Society of New Zealand, Inc. Pp. 1-96, maps 1-4. Wellington &c.: A. H. & A. W. Reed.

ROTHSCHILD, W. 1899. [*Haematopus reischeki,* sp.n.]. Bulletin of the British Ornithologists' Club X (LXV): iv-v.

SHAUGHNESSY, P. D. 1970. The genetics of plumage phase dimorphism of the Southern Giant Petrel *Macronectes giganteus.* Heredity 25 (4): 501-506, tables 1-4, pl. 1.

SHORT, L. L. 1969. Taxonomic aspects of avian hybridization. Auk *86 (1): 84*-105, table 1.

SINNOTT, E. W.; DUNN, L. C.; DOBZHANSKY, Th. 1950. Principles of Genetics. 4th ed. Pp. 1-505, text - figs 1-202, tables 1-44. New York: McGraw-Hill.

SOUTHERN, H. N. 1945. Polymorphism in *Poephila gouldiae* Gauld. Journal of Genetics 47 (1): 51-57, table 1.

STRESEMANN, E. 1927. Die schwarzen Austernfischer *(Haematopus).* (Mutationsstudien xxvi). Ornithologische Monatsberichte 35: 71-77.

Dr Allan J. Baker
Royal Ontario Museum
Department of Ornithology
100 Queen's Park
Toronto, Ontario
M5S 2C6
Canada