# INVESTIGATION OF THE MECHANISM MAINTAINING POLYMORPHISM IN THE NEW ZEALAND FANTAIL, RHIPIDURA FULIGINOSA (SPARRMAN)

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## ABSTRACT

Counts of the black and pied morphs (or forms) of the New Zealand Fantail *(Rhipidura fuliginosa)* in East Otago in 1969 gave a total of 824 pied (88.22%) and 110 black (11.78%). These proportions do not differ significantly from those established by other workers for the South Island.

However, morph frequency was found to vary in relation to the type of vegetation, the feeding station, and possibly also to altitude. Of the three vegetation types sampled, native hardwood forest had the highest frequency of the black morph (21%) and kanuka-manuka the lowest (5%). Introduced conifer forest had an intermediate value (14%). More pied birds were observed feeding in the canopy than in the ground to shrub layer, while the black morph showed the opposite trend. Only a restricted altitude range was sampled, but the data indicate that the black morph may be more common at higher than at lower altitudes.

Breeding data reported up to September 1970, are analysed and shown to fit the hypothesis (Caughley 1969) that the difference between pied and black is controlled by a single genetic locus with pied birds homozygous for a recessive allele. Allele frequencies are estimated as $p_1$ (black) 0.06 and $p_2$ (pied) 0.94 and morph frequencies overall agree well with those expected on the basis of Hardy-Weinberg equilibrium. There is no evidence, therefore, to implicate heterosis as a mechanism for maintaining the polymorphism. Differential habitat utilization may be such a mechanism but is unlikely to be the only one. Much work remains to be done in analysing the fantail polymorphism.

## INTRODUCTION

Polymorphism as defined by Ford (1965) frequently takes the form of albinism or melanism in birds. The Fantail, *Rhipidura fuliginosa,* with its black and pied forms, is an example of the melanistic type. The range of the fantail includes Australia, Tasmania, New Zealand, the New Hebrides, New Caledonia, Norfolk, Lord Howe, Banks, and the Solomon Islands (Fleming 1949; Leach 1968) but only in New Zealand is it polymorphic. The species is believed to have arrived in New Zealand from Australia before the Late Pleistocene (Fleming 1961) and has presumably become polymorphic since then. As with most polymorphic species in birds, the fantail morphs were originally described as distinct species, and were still accepted as such by Oliver (1955). However, numerous reports of interbreeding of the two ' species ' led to early suggestions (Philpott 1919; Stresemann 1923) that they should be merged, and Fleming (1949) did so.

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The black morph is rare in the North Island, but relatively common in the South Island. Early references to the frequencies of the two morphs are rather vague. Buller (1882) and Stresemann (1923) reported that the black morph was more common than the pied of the South Island, but no data were given. From 1943 to 1963, Mrs. I. Tily (pers. manuscripts) made counts in the Dunedin district, but as most of these were carried out in the same restricted area, a small sample is likely to have been counted repeatedly. Because no information is available on movement of fantails it would be unsafe to assume that her figures were representative of a large area although Oliver (1955) did so.

Pior to Caughley (1969), attempts to define a genetic model for the dimorphism were misled by the large percentage of pied birds which suggested to early workers unfamiliar with the principles of population genetics that the pied condition must be dominant (e.g. Oliver 1926, 1955). But models based on this assumption did not fit the breeding data.

As with most studies on polymorphic birds species, no attempt has been made to explain the mechanism maintaining the polymorphism, other than to assume that the morph frequencies must reflect Mendelian ratios. Of the three classes of polymorphism listed by Ford (1965), namely ' Neutral,' ' Transient,' and ' Balanced,' I have assumed that the fantail polymorphism fits the last mentioned, as there is nothing to suggest that morph frequencies are anything but stable. Stead (1932) reported that they had been stable for 30 years. Of the maintenance mechanisms for polymorphism listed by Williamson (1958), three can be meaningfully discussed.

1. *Heterosis.* Here the heterozygote is at a selective advantage compared to the two homozygotes and Ford (1965) suggested that this is the most common basis for polymorphism. Caughley (1969) postulated this as the maintainence mechanism in the fantail, but gave no evidence. If heterozygotes are at an advantage it would not be possible to obtain correct estimates of allele and genotype frequencies by assuming the Hardy-Weinberg formula as Caughley did.

2. *Preferential mating* with a member of the other morph(s). This has been demonstrated for the Arctic skua, *Stercorarius parasiticus,* (Berry & Davis, 1970). Mating appears to be random in the fantail and so this maintenance mechanism may not operate.

3. *Selective values varying in space or time,* or different ecological preferences of the different morphs. This is based on an extension of Gause's Principle, and assumes that for polymorphism or any other kind of sympatric diversity of form to exist, these different forms must have slightly different ecological preferences. Two types are illustrated: (a) *Different Temporal Selective Advantage* of the different morphs. This has been demonstrated in the Butterfly *Colias eurytheme* (Ford, 1965) where the orange morph of the female is at a selective advantage in summer while the white morph is at a corresponding

selective advantage in winter. The brevity of my study precluded investigation of this mechanism, but it should not be overlooked in future work.

(b) *Different Spatial Selective Advantage* or different habitat utilization by the two morphs. This has been demonstrated in the dipper *Cinclus cinclus* (Mayr & Stresemann, 1950), where the white-breasted morph is more frequent in lowland forest and the brown-breasted morph is more frequent in the open treeless steppes. Intermediate frequencies occur in intervening areas.

The aim of this study was to investigate whether the last mentioned maintenance mechanism might be operating, by seeking correlations between morph frequencies and factors such as vegetation type, feeding station and altitude. A genetic model for the dimorphism is postulated, and allele frequencies are calculated from observed population ratios and mating data, and then used to investigate the possible presence of heterosis.

## METHODS

Periodic visits between 29 December 1968 and 26 August 1969 were made to forest, bush, scrub, and open areas within a thirty mile radius of Dunedin. Reserves and gardens within the city were also observed and the numbers of each fantail morph recorded. In general, new ground was covered on each visit, but in the few cases where the same area was recounted in a subsequent survey, there was an interval of at least two months between counts. Recounting was normally avoided and no area was counted more than twice. Gibbs' (1961) procedure was adopted on each visit: I walked slowly through the bush in a set direction, counting the numbers of birds seen. Gibbs' method was slightly modified because of having to distinguish which morph was heard. So when a bird could be heard but not seen, the search was continued away from the track till the bird could be observed. However, a small number of birds could not be located, and accordingly were not recorded. Extreme care was taken to avoid recounting the same bird during any one visit.

## DESCRIPTION OF OBSERVATION AREAS

Most of the habitats visited could be grouped into three major types:

(1) *Native Hardwood Forest:* Initially this was divided into three categories, but because of insufficient numbers and basic similarities, these were subsequently grouped together. The first of the three was termed '*Transition Bush,*' that is, forest that had regenerated after burning or milling of the emergent podocarps. The canopy consists of *Griselinia littoralis, Fuchsia excorticata, Melicytus ramiflorus, Pseudopanax arboreum, P. colensoi, P. crassifolium, Carpodetus serratus, Aristotelia serrata* and *Pittosporum eugenioides.* The shrub layer includes many of the above mentioned species, but also *Pseudowintera*

*colorata, Coprosma* spp., *Dicksonia squarrosa* and *Cyathea* spp. The ground layer is mainly *Blechnum* spp., *Phymatodes diversifolium, Asplenium* spp. and *Microlaena avenacea.*

The second type, *Broadleaf Podocarp Forest,* is essentially similar except that the emergent podocarps *Dacrydium cupressinum, Podocarpus ferrugineus, P. totara* and *P. hallii* were present.

The third type, *Broadleaf Podocarp Beech Forest,* is similar except for the addition of *Nothofagus* spp. and sparser ground and shrub layers.

(2) *Kanuka-Manuka Association:* Kanuka, *Leptospermum ericoides,* and Manuka, *L. scoparium,* were present in all the previous bush types but formed only an inconspicuous part of shrub and canopy layers. In mature association they formed the great majority of the canopy. Shrub and ground layers had a similar composition to native hardwood forest except that pungas and *Asplenium* spp. were absent, while *Phymatodes diversifolium* was common. All layers were very open.

(3) *Introduced Conifer Forest:* This consisted mainly of *Pinus* spp. but also included some *Pseudotsuga* spp., *Picea* spp., and *Cedrus* spp. Shrub and ground layers were absent but all roads and streams were fringed with small numbers of kanuka, manuka and other species common in the shrub layer of native hardwood forest.

## MORPH FREQUENCIES

Of the 934 fantails scored by me, 824 were pied (88.22%) and 110 black (11.78%). Other counts for the Otago district are summarised in Appendix 1 and total 795 pied (86.98%) and 119 black (13.02%), while substantial counts for other South Island areas (Appendix 1) give a total of 981 pied (88.38%) and 129 black (11.62%). None of these frequencies differs significantly ($X^2 = 0.948$) from the others, and it appears that morph frequencies are relatively stable in the South Island. For the North Island there are only two substantial counts: for all the North Island, Caughley (1969) reported 419 pied and no black birds and in Wellington-Manawatu R. E. Brockie (pers. comm.) recorded 313 pied and 1 black. From incidental observations, I have recorded two black fantails and about 300 pied in the Manawatu and Coromandel. The contrast between the North and South Islands is, then, very striking.

## MORPH DISTRIBUTION IN RELATION TO VEGETATION TYPES

In scoring birds according to the habitat in which they were seen, counts were normally made well away from the boundaries between vegetation types. Table 1 gives the counts for the three major vegetation types encountered.

Heterogeneity $X^2$ tests showed that the different areas for the native hardwood and conifer forest types were homogeneous in their morph frequencies (the considerable range in the hardwood forest samples is only to be expected from the small size of many

TABLE 1

MACROHABITAT DISTRIBUTION OF PIED & BLACK MORPHS

| LOCALE | No.PIED | No.BLACK | TOTAL | Percentage | |
|---|---|---|---|---|---|
| | | | | Pied | Black |
| NATIVE HARDWOOD FOREST | | | | | |
| Leith Valley | 53 | 10 | 63 | 84.1 | 15.9 |
| Waipori | 26 | 5 | 31 | 83.8 | 16.2 |
| Waitati Valley | 18 | 8 | 26 | 69.2 | 30.8 |
| Powder Creek | 10 | 4 | 14 | 71.4 | 28.6 |
| Mount Cargill | 10 | 3 | 13 | 76.9 | 23.1 |
| Taieri Mouth | 7 | 1 | 8 | 87.5 | 12.5 |
| Saddle Hill | 6 | 4 | 10 | 60.0 | 40.0 |
| Total | 130 | 35 | 165 | 78.8 | 21.2 |
| KANUKA-MANUKA | | | | | |
| Powder Creek | 150 | 4 | 154 | 97.4 | 2.6 |
| 3-Mile Hill - Waiora | 50 | 2 | 52 | 96.2 | 3.8 |
| Waitati Valley | 46 | 2 | 48 | 95.8 | 4.2 |
| Leith Valley | 33 | 2 | 35 | 94.3 | 5.7 |
| Pelichet Bay | 33 | 7 | 40 | 82.5 | 17.5 |
| Tirohanga | 19 | 3 | 22 | 86.4 | 13.6 |
| Outram Glen | 18 | - | 18 | 100 | 0 |
| Taieri Mouth | 14 | 1 | 15 | 93.3 | 6.7 |
| Fairfield | 12 | - | 12 | 100 | 0 |
| Otago Peninsula | 10 | - | 10 | 100 | 0 |
| Brighton | 7 | - | 7 | - | - |
| Waironga | 3 | - | 3 | - | - |
| Saddle Hill | 2 | - | 2 | - | - |
| Waipori | 1 | - | 1 | - | - |
| Total | 398 | 21 | 419 | 95.0 | 5.0 |
| CONIFER FOREST | | | | | |
| 3-Mile Hill | 111 | 18 | 129 | 86.0 | 14.0 |
| Berwick | 82 | 15 | 97 | 84.5 | 15.5 |
| Leith Valley | 16 | 2 | 18 | 88.9 | 11.1 |
| Powder Creek | 4 | 1 | 5 | 80.0 | 20.0 |
| Total | 213 | 36 | 249 | 85.6 | 14.4 |
| CITY AREAS | | | | | |
| Total | 59 | 12 | 71 | | |
| OTHER AREAS | | | | | |
| Total | 24 | 6 | 30 | | |
| OVERALL TOTAL | 824 | 110 | 934 | 88.22 | 11.78 |

of them). However, the kanuka-manuka areas were not homogeneous ($X^2 = 21.56$, d.f. 12, $P_{5\%} = 21.03$). The sample from Pelichet Bay was shown to differ significantly ($X^2 = 14.49$, d.f. 1, $P_{5\%} = 3.84$) from all the other kanuka-manuka areas, these forming a homogeneous subgroup. The anomalously high frequency for the black morph in the Pelichet Bay sample appears to be a sampling error: the counts were made in February at the end of the breeding season when 1 black adult paired with a pied bird had a family of 3 black young, boosting the frequency of black. Because this territory marked the end and start of consecutive records, double counting is a likely source of bias. Subsequent visits in the following breeding season in search of breeding pairs revealed only 1 black bird, mated to a pied one, in a territory similar to the one in which the black birds had been observed earlier in the year.

Even when the Pelichet Bay counts are included, the frequency of the black morph in the kanuka-manuka association (5%) is significantly lower than in either the conifer forest (14.4%) or the native hardwood forest (1.2%), ($X^2$ = 17.85 and 79.29 respectively, d.f. 1, $P_{5\%}$ = 3.84). But a difference between the latter two vegetation types could not be demonstrated ($X^2$ = 3.19). Figure 1 illustrates the variation in morph frequencies with vegetation type.

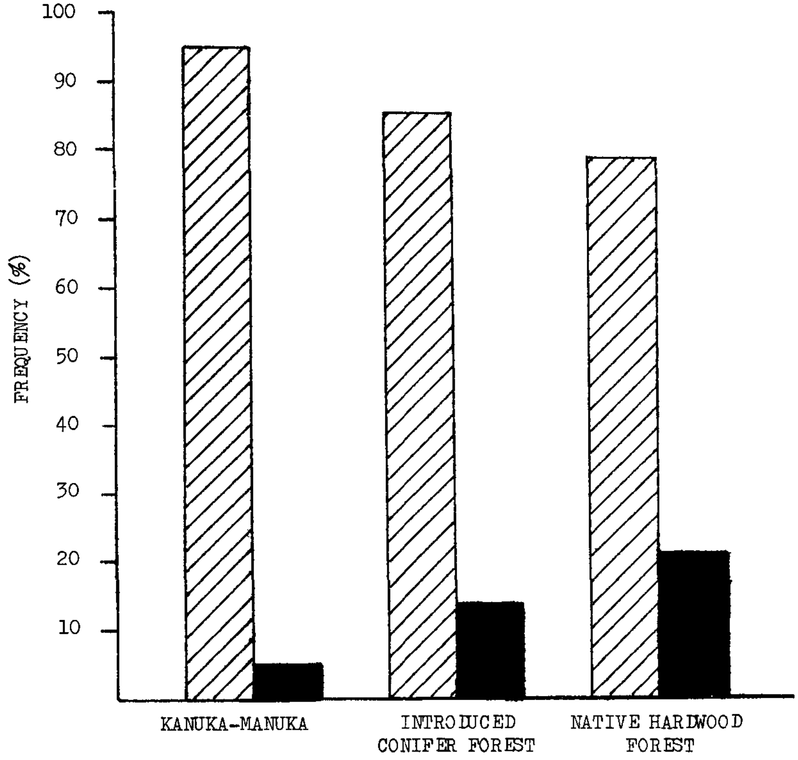

FIGURE 1 — Histogram of frequencies of black and pied morphs in the three major vegetation types. Pied frequencies are cross-hatched and black are blocked in.

The only other count from a known type of habitat is R. H. Taylor's (pers. comm.) for a mixed beech forest in the St. Arnaud district, Nelson. He found 322 pied and 50 black (13.4%) — a value similar to mine for conifer forest, which resembles beech forest in the open nature of shrub and ground layers.

## MORPH DISTRIBUTION IN RELATION TO FEEDING STATION

Four main feeding stations in the bush are recognised: (1) ground to shrub; (2) shrub to lower canopy. This includes understorey trees and is mainly an aerial station, in contrast to (1). As no shrubs were present in conifer forest, the lower limit was arbitrarily set at four feet, but it is a real station none the less. (3) canopy and above; (4) association feeding in which fantails feed on insects disturbed by other birds (almost exclusively other passerines). Table 2 gives the counts of black and pied birds in relation to feeding station for the forest types (also the Dunedin city and 'extra' tallies). The data indicate that pied birds are more likely to be found feeding in the canopy than in the ground to shrub layer, while black birds are commonest in the latter layer and rare in the canopy. (Fig. 2). According to McLean (1912), fantails feed high up on sunny days and near the ground on dull days. But when my data were subdivided according to whether days were sunny or dull, no correlation of feeding station with weather was apparent, so the data were pooled

TABLE 2 FEEDING STATION DISTRIBUTION

of

PIED AND BLACK MORPHS

| FEEDING STATION | NATIVE | | CONIFER | | LEPTOSPERMUM | | CITY | | EXTRA | | TOTAL | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | P. | B. | P. | B. | P. | B. | P. | B. | P. | B. | P. | B. |
| Ground to Shrub | 10 | 13 | 55 | 13 | 56 | 9 | 15 | 3 | | | 136 | 38 |
| Shrub to Lower Canopy | 38 | 10 | 68 | 12 | 71 | 5 | 12 | 2 | 3 | - | 192 | 29 |
| Canopy | 27 | 4 | 66 | 8 | 104 | - | 22 | 3 | 15 | 1 | 234 | 16 |
| Association Feeding | 18 | 1 | 6 | - | 47 | 2 | 51 | 1 | 1 | - | 77 | 4 |
| Edge of Bush | 10 | 6 | 3 | - | 40 | 2 | - | - | - | - | 53 | 8 |
| Over Water | 10 | 1 | 5 | - | 27 | - | - | - | - | - | 42 | 1 |
| Other | 2 | - | - | - | 5 | - | 7 | 3 | 3 | 5 | | |
| Not Feeding | 15 | - | 11 | 3 | 48 | 3 | - | - | - | - | | |

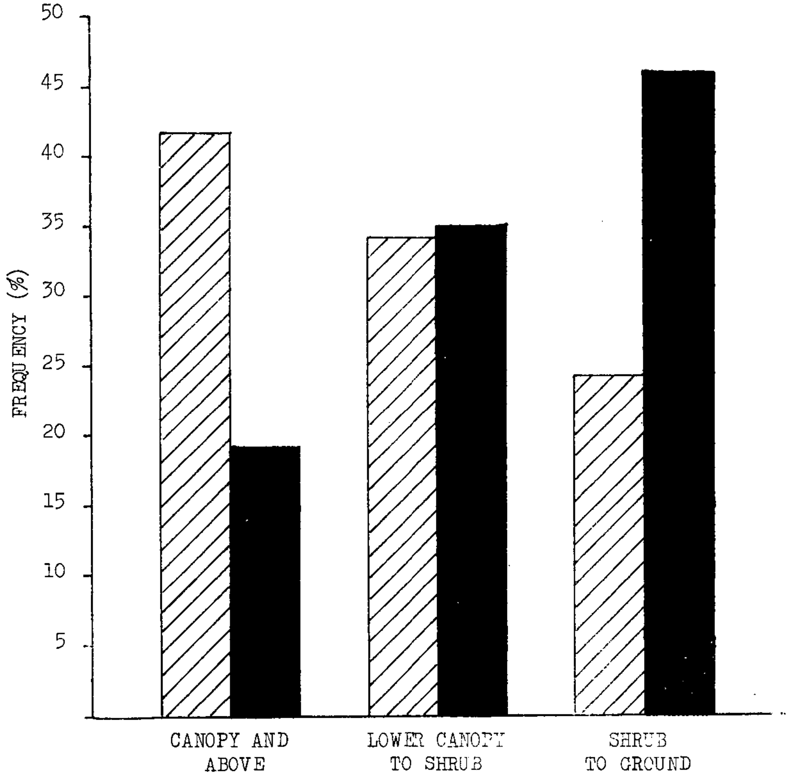

FIGURE 2 — Histogram of the relative frequencies of black and pied morphs in the three major forest feeding stations (% derived from number of morph in each station over total numbers of that morph in all three stations). Pied birds are cross hatched and black birds are blacked in.

## MORPH DISTRIBUTION IN RELATION TO ALTITUDE

Altitude was recorded to the nearest 100 feet (30.5 m) above sea level, and the data grouped into 500′ (152 m) intervals for analysis (Table 3). Most of the areas scored are below 500′, hence the preponderence of birds in the 0 - 500′ group. Only the hardwood forest vegetation type include reasonable numbers in all three altitudinal ranges. Here there is an indication that black birds may be proportionately more common at 1,000′ (304.8 m) and above than lower down, but statistical significance is not attained. On pooling the data for all vegetation types (Fig. 3), a trend similar to that in hardwood forest alone is evident, and the difference in morph frequency between 500′ (152 m) to 1,000′ (304.8 m) and 1,000′ (304.8 m) and above is now statistically significant ($X^2 = 7.64$).

TABLE 3 ALTITUDINAL DISTRIBUTION OF PIED AND BLACK MORPHS

| Habitat | 0 - 500' | | 500' - 1,000' | | 1,000' & above | |
|---|---|---|---|---|---|---|
| | Pied | Black | Pied | Black | Pied | Black |
| Native Hardwood | 51 | 13 | 59 | 14 | 20 | 8 |
| Introduced Conifer | 164 | 31 | 40 | 3 | 9 | 2 |
| Kanuka Manuka | 350 | 19 | 26 | 2 | 2 | - |
| City | 61 | 12 | - | - | - | - |
| Extra | 21 | 1 | - | - | 3 | 5 |
| Total | 647 | 76 | 125 | 19 | 34 | 15 |

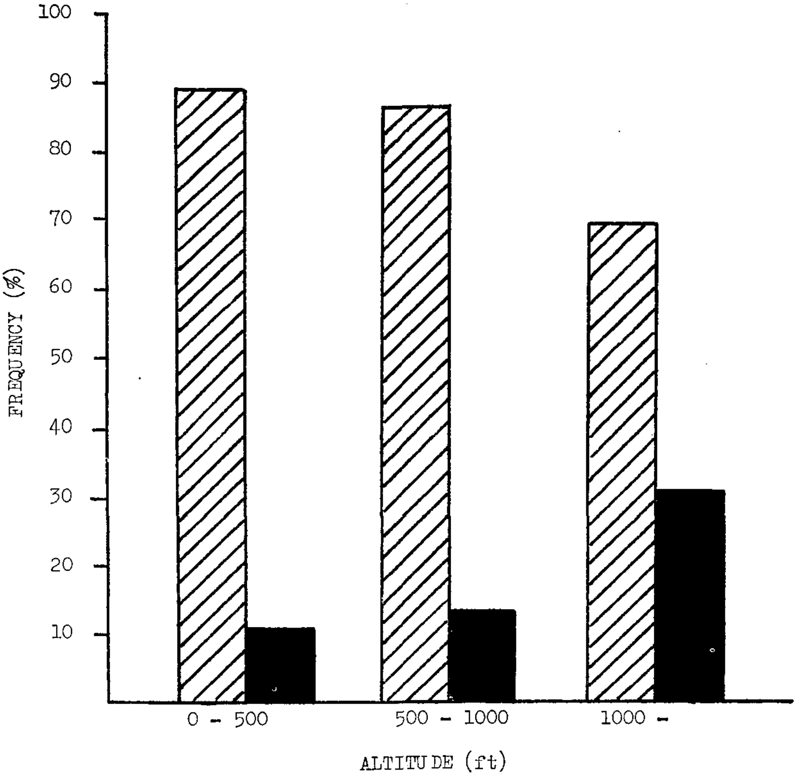

FIGURE 3 — Histogram of the distribution of black and pied morphs with altitude (morph frequencies calculated as a percentage of both morphs within each altitude range). Pied birds are cross-hatched and black birds are blacked in.

## MECHANISMS THAT MAY BE INVOLVED IN MAINTAINING THE POLYMORPHISM

Of the various mechanisms possible, my field observations indicate that differential habitat utilization may be involved in maintaining the fantail polymorphism.

The striking and long recognised difference between North and South Islands in incidence of the black morph suggests that physiological adaptation to climate may also be involved. It is not profitable to speculate on which climatic factor or factors are important in the absence of more comprehensive data for different parts of the South Island. However, distribution of other New Zealand forest birds with darker forms suggest that temperature and precipitation may be involved.

(1) The tomtit *Petroica macrocephala* has a darker South Island form and a melanic one on Snares Islands.

(2) A melanic robin, *P. traversi,* is found only on the Chatham Islands.

(3) Two forms of the weka *Gallirallus australis* exist in the South Island. The lighter buff form is found in low rainfall districts of the eastern South Island. The second form, found in the western South Island and in Fiordland, an area with high rainfall, is dimorphic with a melanic phase (Annotated Checklist, OSNZ 1970).

A great deal more work is required to establish whether and how habitat selection is involved in maintaining the fantail polymorphism. Other factors, such as selective mortality and immigration, also need to be considered.

## GENETIC MODEL

Oliver (1926, 1955) suggested two models on the assumption that pied was dominant (because it was the commoner morph), but neither accounted for the breeding data. Caughley (1969), using Oliver's figures, put forward an acceptable model (with black dominant and pied recessive) which accounted for all but one of the observed crosses. Matings additional to those reported by Oliver are, however, available and the breeding data assembled in Table 4 include all recorded up to September 1970. Thirty-two progenies from black x pied matings give a total of 54 pied and 49 black chicks. This agrees well with a 1:1 ratio ($X^2 = 0.24$). Twenty-six of these progenies were mixed, 3 each contained 4 pied chicks, 2 contained 3 black ones, and 3 one black chick each.

Seven of the eight progenies from black x black matings included black and pied morphs. The eighth family contained one black chick only.

Fifty-seven of the 58 matings between two pied parents recorded when the progeny were at least 11 days old (this being the earliest age (J. Hamel, pers. comm.) at which chicks can be positively classified as black or pied) gave only pied offspring. The 58th mating is a report of Stead's of a brood with one black and two pied offspring. However, like many observed matings, it is assumed that the pair

TABLE 4 RECORDED MATINGS

| Authority | Parents | Young | |
|---|---|---|---|
| | | Pied | Black |
| # A. Philpott (1919) | Black x Pied | 1 | 1 |
| " | " " | 2 | 1 |
| " | " " | 2 | 1 |
| " | " " | 2 | 1 |
| " | " " | 1 | 2 |
| " | " " | 3 | 1 |
| " | " " | 3 | 1 |
| " | " " | 2 | 2 |
| " | " " | 2 | 2 |
| " | " " | 3 | 2 |
| # L.A. Shand (Oliver 1955) | " " | 4 | - |
| # W.R.B. Oliver (1955) | " " | - | 3 |
| # C. Parr (Oliver 1926) | 3 broods | 3 | 9 |
| # per Oliver (1955) | 2 broods | 2 | 5 |
| G. Hamel (pers. comm.) | Black ♂ x Pied ♀ | 4 | - |
| " | " " | 1 | 3 |
| " | Black ♀ x Pied ♂ | 3 | 1 |
| " | " " | 1 | 1 |
| * B.D. Bell | Black ♂ x Pied ♀ | 1 | 1 |
| I.W. St Paul (Notornis 8:212) | Black x Pied | - | 3 |
| A. Blackburn (Notornis 6:209) | " " | 3 | 1 |
| * D.V. Merton | " " | 3 | 1 |
| * J.E. Hilton | " " | - | 1 |
| " | " " | - | 1 |
| * J. Taylor | " " | 2 | - |
| " | " " | - | 1 |
| I. Tilly (Evening Star 7/2/53) | " " | 4 | - |
| C.A. Fleming (Notornis 2:172) | " " | 1 | 2 |
| ( " 1:134) | " " | 1 | 2 |
| P. Moncrieff (1931) | Black x Black | 1 | 2 |
| " (Emu. 34:165) | " " | 1 | 1 |
| G. Hamel (pers. comm.) | " " | - | 1 |
| I. Tilly (Evening Star 7/2/53) | " " | both | |
| per W.R.B. Oliver (1955) | 4 broods | " | |
| E.F. Stead (Oliver 1955) | Pied x Pied | 2 | 1 |
| Numerous others | " " | | |
| | 57 broods | 162 | - |

# Included in Oliver's (1955) ratio of 30 pied : 31 black
* Ornithological Society of New Zealand Nest Record Cards

concerned were not followed right through from nest building to the fledging of the young. Evidence presented below shows that birds observed around a nest after the eggs have been laid are not necessarily the pair that produced the eggs. If one bird deserts its territory, its place may be taken by another bird which may not necessarily be the same morph, and is presumably from a reserve breeding population. Stead's anomalous family may have involved an adopted parent, and therefore is not considered in the genetic model.

Philpott (1919) reported a black/pied mating where the nest was started on 8 November. The first egg was laid on the 11th and one on each of the next three consecutive days. The young left the nest on 12 December, but the pied parent had disappeared previously. A black bird which Philpott assumed to be a member of a previous brood began to assist feeding the young. This black pair then built another nest on 7 January suggesting that the incoming black bird was not an immature one as Philpott thought, but a member of a reserve breeding population.

Mrs. Jill Hamel (pers. comm.) reports a similar case where the pied male, distinguishable by a broken tail feather, of a black/pied pair abandoned the fifth nest soon after the young hatched. Not long after, another pied male (with a complete tail) started to form a territory in part of the black female's territory and eventually began feeding the fledglings and mated with the black female.

A third report from Hilton (Ornithological Society of N.Z. Nest Records) involved a mixed pair building a nest on 6 September. Three days later two pied birds were observed at the nest, but by 20 September the black bird had returned and was sitting on the nest.

The simplest model for explaining the breeding data is that put forward independently by Caughley (1969) and myself (1969), according to which a single locus with two alleles operates the switch mechanism in determining the black/pied difference, and that the pied birds are homozygous for the recessive alleles. All the breeding data fits this except for Stead's one anomalous family discussed above.

If it is assumed that the black parent in pied/black matings with all black progenies is homozygous for the dominant allele, a maximum estimate for the frequency of homozygotes may be obtained (families of only one black offspring were not considered to involve a homozygote). Two of the 32 matings would involve homozygous blacks on this basis, or 0.0625. From the population frequencies, black (BB + Bb) = 0.1178 and pied (bb) = 0.8822 (Table 1). So 0.1178 x 0.0625 = 0.0074 is a maximum estimate of the frequency of black homozygotes, with 0.1178 — 0.0074 = 0.1104 the frequency of heterozygotes. This yields estimated allele frequencies of $p_1$ (B) = 0.0626 and p (b) = 0.9374. If these are substituted into the Hardy-Weinberg formula, the calculated phenotype frequencies are very close to those observed.

| Phenotype | Genotype | Frequency | | |
|---|---|---|---|---|
| | | H/W | Expected | Observed |
| Black | BB<br>Bb | $p_1^2$<br>$2p_1p_2$ | 0.0039)<br>) 0.1213<br>0.1174) | 0.1178 |
| Pied | bb | $p_2^2$ | 0.8787 | 0.8822 |

Thus there is no evidence that heterozygote advantage (heterosis) plays a prominent part in maintaining the polymorphism, contrary to the supposition of Caughley (1969). However, it is clear that further breeding data is required to evaluate the possible role of heterosis.

## APPENDIX 1 COUNTS OF PIED AND BLACK MORPH from other sources

(1) EAST OTAGO

| Authority | Date | Pied | Black |
|---|---|---|---|
| # Allen, J.H. | 1961-62 | 23 | 3 |
| " | 62-63 | 42 | 6 |
| " | 63-64 | 41 | 6 |
| # Poppelwell, W.T. | - | 48 | 6 |
| | - | 50 | 1 |
| " | 60-62 | 65 | 12 |
| " | 64-65 | 27 | - |
| " | 65-66 | 35 | 6 |
| " | 66 | 14 | 2 |
| " | 66-67 | 28 | 5 |
| " | 67-68 | 50 | 3 |
| " | 68 | 30 | 1 |
| # Hamel, G. | 66 | 15 | 4 |
| * " | 66 | 34 | 12 |
| # " | 65 | 3 | 1 |
| # " | 68 | 30 | 1 |
| Dunedin Naturalists' Field Club (Notornis 3:24) | 48 | 15 | 5 |
| " ( " 4:55) | 50 | 31 | 6 |
| " ( " 4:193) | 51 | 27 | 7 |
| " ( " 6:104) | 54 | 9 | 1 |
| Richdale, L.E. (Native Perching Birds) | no date | 154 | 25 |
| McKenzie, H.R. (Notornis 6:209) | 55 | 10 | 4 |
| * Westerskov, K.E. | 69 | 14 | 2 |
| | | 795 | 119 |

(2) Other South Island Areas

| | | | |
|---|---|---|---|
| Caughley (1969) | Canterbury & Westland | 298 | 44 |
| * Jackson | Westland | 361 | 35 |
| * Taylor, R. | Nelson | 322 | 50 |
| | | 981 | 129 |

# Ornithological Society of New Zealand Records

* pers. comm.

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