

SHORT COMMUNICATIONS

AN EXPLANATION FOR THE ASYMMETRICAL 'HYBRID' ZONE BETWEEN WHITE-BACKED AND BLACK-BACKED MAGPIES

Two colour forms of the Australian Magpie inhabit eastern Australia. A white-backed form is found mostly in the south-east, including Tasmania, and a black-backed form is found in central and northern Australia. The two forms overlap and interbreed in northern Victoria and southern New South Wales. Morphological, biochemical and behavioural work has revealed no evidence of species differences between White-backed and Black-backed Magpies (Hughes 1980). Thus, the zone of overlap should possibly be referred to as an intermediate zone, rather than a 'hybrid' zone (Burton & Martin 1976).

Burton & Martin (1976) showed that the 'hybrid' zone between White-backed and Black-backed Magpies in northern Victoria is strongly asymmetrical; the zone of White-backed Magpies and intermediates is much narrower than the zone of black-backed birds and intermediates. Two explanations were suggested. First, the 'hybrid' zone may be moving southward, and the narrow white-backed and intermediate zone is being over-run by a black-backed invasion from the north. Secondly, the zone may be stationary and the asymmetry may reflect stronger selection against intermediates in the south than in the north of the zone.

I would like to offer an alternative explanation of the asymmetry, based on some recent evidence from field observations of magpie family groups where black-backed parents were recorded with white-backed and nearly white-backed offspring, but white-backed parents were never recorded with black-backed offspring. Hughes & Mather (1980) suggested that back colour in magpies is coded for by a small number of genes, with genes for black backs dominant to genes for white backs. If this is the case then I shall show that an asymmetry would be expected in the zone where selection pressures change from favouring white-backed birds to favouring black-backed birds.

Consider the simple case where two loci, on separate chromosomes, code for back colour. At both loci, genes for black backs (b_1 and b_2) are dominant to genes for white backs (w_1 and w_2), so that at each locus black genes, in either homozygous or heterozygous condition, produce the black phenotype. If the effect is cumulative, then for a totally black back, both loci must have at least one allele for black. An intermediate will have at least one black gene at one locus and whites at the other locus and a white-backed bird will have two white alleles at each locus.

If black and white alleles are in equal frequencies then the following phenotype frequencies would be expected:

$$\frac{9}{16} \text{ black: } \frac{6}{16} \text{ intermediate: } \frac{1}{16} \text{ white.}$$

If the frequencies of black and white alleles are not equal, then the expected frequencies of each genotype can be calculated from the individual allele frequencies. For example, if the frequency of both black alleles is $\frac{1}{4}$ and the frequency of both white alleles is $\frac{3}{4}$, then the expected frequency of the genotype

$$\frac{b_1}{b_1} \frac{b_2}{b_2} \text{ is}$$

equal to $(\frac{1}{4}) \times (\frac{1}{4}) \times (\frac{1}{4}) \times (\frac{1}{4}) = \frac{1}{256}$ and the expected frequency of the genotype

$$\frac{w_1}{w_1} \frac{w_2}{w_2} = (\frac{3}{4}) \times (\frac{3}{4}) \times (\frac{3}{4}) \times (\frac{3}{4}) = \frac{81}{256}$$

In this way, expected phenotype frequencies can be calculated for varying gene frequencies and curves can be drawn up for variation in phenotype frequency across the 'hybrid' zone (Fig. 1). It is assumed that selection will act equally on duplicate alleles producing the same phenotype; thus that at each point the frequency of b_1 = frequency of b_2 and the frequency of w_1 = frequency of w_2 .

Figure 1 shows the change in expected phenotypic ratios across an intermediate zone changing regularly from all white alleles on the left hand side to all black alleles on the right hand side. Figure 2 shows results from the transect through the 'hybrid' zone along which the rate of change in phenotype frequencies was most constant (Burton & Martin 1976). This curve is similar to the predicted one in Figure 1. However, the curves cannot be compared statistically because the x-axis in the observed and expected graphs are not comparable. In the predicted curve the x-axis is the proportion of black alleles in the population; in the observed curve it is the distance along the transect. However, observations can be compared with predictions from the model at specific points along each transect. At each sample site, the proportion of black-backed birds was used to calculate the expected number of white-backed and intermediate birds. A χ^2 test was used to determine whether observed values deviated significantly from expected

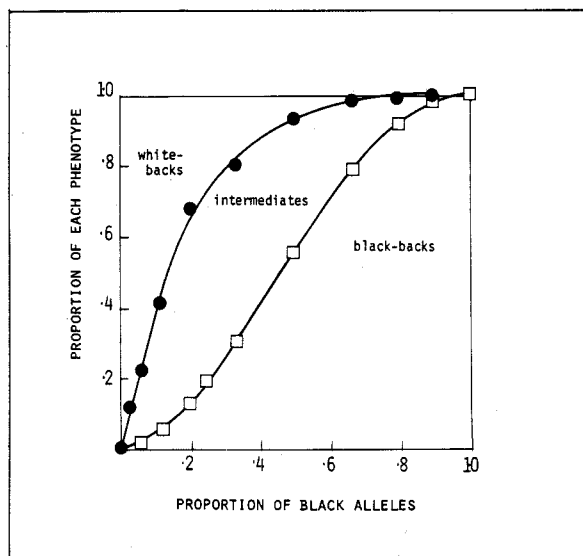


Figure 1. Compositions of populations from the 2 locus model, for varying proportions of black alleles.

- = predicted frequency of black-backs
● = predicted frequency of black-backs plus intermediates

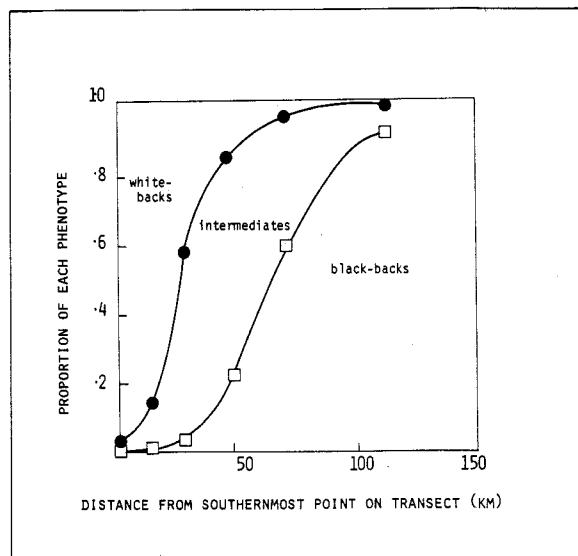


Figure 2. Composition of magpie populations along a transect across the 'hybrid' zone in Victoria (Burton & Martin 1976).

- = frequency of black-backs
● = frequency of black-backs plus intermediates

TABLE 1

Results of χ^2 tests comparing observed phenotype frequencies (Burton & Martin, 1976) with those expected from a system of cumulative alleles with duplicate effect. Expected frequencies of two phenotypes at each point along the transect were calculated by using the observed frequency of one phenotype to read off predicted frequencies of the other two phenotypes from the model.

Sites	Transect	χ^2	df	Significance Level
1 - 10	1	6.89	8	n.s.
11 - 19	2	5.44	6	n.s.
20 - 26	3	15.34	2	.01
27 - 32	4	26.44	5	.01
33 - 38	5	29.52	5	.01
39 - 47	6	32.34	7	.01
48 - 53	7	25.97	5	.01
54 - 58	8	10.06	3	.05
59 - 67	9	20.84	7	.01

values; only two of the nine transects did not deviate significantly from predictions ($p < .05$) (Table 1).

Similar curves were calculated for models with three and four loci respectively. The proportion of heterozygotes was much greater than was observed in the population and all transects showed significantly different phenotype frequencies from those expected

from models with three or four loci with cumulative effect, using a χ^2 test as described above ($p < .05$).

Figure 3 shows the predicted curves for white-backed, intermediate and black-backed birds as one moves across the 'hybrid' zone. The predicted 'hybrid' zone is asymmetrical, with black-backed and white-backed curves crossing where the frequency of black

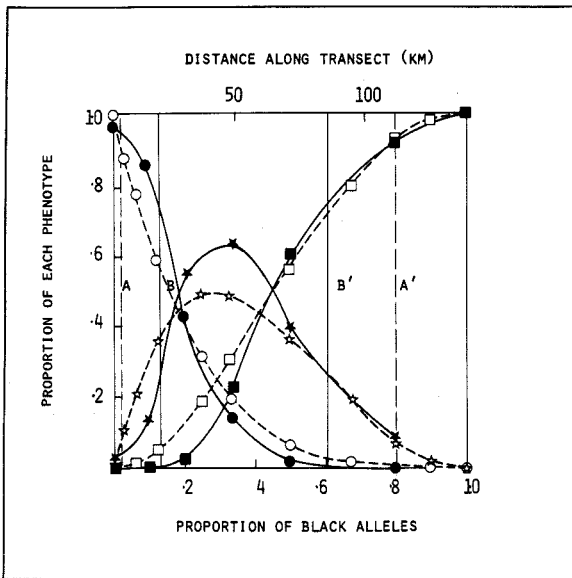


Figure 3. Observed and expected phenotype frequencies across the 'hybrid' zone.

- = predicted frequency of white-backs
- ☆ = predicted frequency of intermediates
- = predicted frequency of black-backs
- = observed frequency of white-backs
- ★ = observed frequency of intermediates
- = observed frequency of black-backs

Area to the left of line A = predicted area of white backs and intermediates

Area to the right of line A' = predicted area of black backs and intermediates

Area to the left of line B = observed area of white backs and intermediates

Area to the right of line B' = observed area to black backs and intermediates

alleles is 0.29. If the zone were symmetrical the curves would cross where the black-allele frequency was 0.50. The observed curves have been superimposed on these axes by equating the place where black alleles are at a frequency of 0.8 on the predicted graph with site 33 on the observed graph, as the two curves are very close here. The deviations of the observed curves from those expected change in direction depending on the allele proportions. To the left, where the proportion of black alleles is small, there are fewer black-backed birds than predicted, and to the right, there are fewer white-backed birds than predicted.

The model assumes that there is no change in selection across the 'hybrid' zone, only that different phenotypes are favoured on either side of the zone. However if selection does change gradually across the 'hybrid' zone, then fewer black-backed birds than predicted by the model would be expected in

the area dominated by white-backed birds and fewer white-backed birds than predicted would be expected in the area dominated by black-backed birds, as is shown in Figure 3.

Figures 2 and 3 show that intermediates extend further into the black-backed zone than would be predicted by the model, even if selection pressures do change across the 'hybrid' zone. If white alleles are recessive to black alleles, then only a very small proportion of them will be expressed in the zone of mostly black alleles. Because natural selection acts only on the phenotype, then the rate of loss of white alleles from the area of black-backed birds and intermediates will be much lower than that of black alleles in the zone of white-backed birds and intermediates, where all the black alleles are expressed.

Assuming gene-flow to be equal in either direction white alleles will extend further into the area of black backs than black alleles into the area of white backs. This argument assumes that at each site the selection coefficient of intermediate phenotypes is between those of white-backed or black-backed phenotypes.

In Figure 3, the white-backed and black-backed curves cross slightly to the right (.31) of the expected point (.29). As this is probably in the region where white alleles are favoured, such a deviation (slightly more white-backs than predicted by the 'no selection' model) would be expected. In this area there are more intermediates than predicted, which may suggest that intermediates are favoured over either parental type in parts of the 'hybrid' zone, possibly where natural selection changes from favouring white alleles to favouring black alleles.

The model presented above, that of duplicate genes with cumulative effect, is only one of a number of possible explanations for the variations of back colour observed in the Australian Magpie. If the two loci had slightly different effects, for example, one produced a slightly broader black band than the other, then the considerable variation observed among intermediates (Burton & Martin 1976) could be explained. Environmental influences may also affect the width of the black band in intermediate birds.

Burton & Martin (1976) interpret the black-backed and white-backed morphs as being the products of previous isolation between the two populations. They suggest that the high frequency of parental phenotypes in the contact zone is evidence of secondary intergradation. However, the high frequency of parental phenotypes (particularly black-backed birds) could equally well be interpreted as representing the results of crosses between intermediates, (producing both parental types and more

intermediates) as shown in the model (Fig. 3).

The asymmetry in the intermediate zone observed by Burton & Martin (1976) would also be predicted. The zone of black-backs and intermediates would be expected to be about eight times wider than the zone of white-backs and intermediates (if selection were not operating across the intermediate zone (Fig. 3). In the transect from stations 33 – 38, the zone of black-backs and intermediates was at least three times as wide as the zone of white backs and intermediates. (The end point of the zone of black-backs and intermediates was not observed by Burton & Martin (1976)).

Burton & Martin's (1976) results agree fairly closely with those predicted from an epistatic system of duplicate genes with cumulative effects (Stansfield 1969). Deviations from expected frequencies are explained in terms of a gradual change in the direction

of selection across the 'hybrid' zone, with no need to invoke either asymmetrical selection or an invasion of black-backs, for which there is little evidence.

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APPARENT BAITING BEHAVIOUR BY A BLACK KITE

On 22 June 1979 Larry Haydon and I were observing birds from the bank of the Lennard River at the camping-ground of Windjana Gorge National Park in the West Kimberley of north-western Western Australia. Our attention was drawn to the extraordinary antics of a Black Kite *Milvus migrans* which allowed us to approach to within a few metres. The bird picked up a scrap of bread from the ground with its talons, carried it into the air and dropped it into the river, which was only about 10m wide.

The Kite then flew to a eucalypt branch overhanging the water. The floating bread attracted several dozen small fish and freshwater crayfish (cherabins *Macrobrachium* sp about 20cm long). While they were feeding on the bread, the Kite dived from its perch and appeared to attempt to catch them by striking into the water with its talons.

This performance was repeated several times over an hour. During the time we watched, the bird was unsuccessful, repeatedly returning to its perch with no prey. On two later occasions, it returned to the ground and collected and dropped more bread. On a still later occasion, it succeeded in capturing a large cherabin, but one that had surfaced away from the bread. The crayfish was carried to the bird's perch and eaten.

Black Kites are well-known as scavengers and feed largely on carrion; also on small mammals, insects and reptiles. I can find no published account of this species 'fishing' in any manner in Australia or elsewhere. The bird we observed fishing appeared clumsy but was successful at least once.

The apparent use of a bait to attract the fish is even more unusual. This bird had evidently not only acquired a taste for live aquatic animals. It had apparently learned of their attraction to bread and exploited this knowledge by deliberately dropping scraps onto the water, thus attracting them to the surface and within striking range. Is it possible that this habit was learned by the bird observing human picnickers throwing bread-scrap into the river?

Boswall (1977, *Avicult. Mag.* 83: 146-159, 220-228; 1978 *Avicult. Mag.* 84: 162-166) has reviewed the few other cases where avian species are known to employ bait. One Green Heron *Butorides virescens* in Florida used pellets of fish food and three others bread scraps to lure fish within range of their bills. Yet another bird of this species, in Kenya, baited fish also with bread left lying about by visitors. A captive Sun Bittern *Eurypyga helias* in Britain baited fish with mealworms. A Pied Kingfisher *Ceryle lugubris* was seen by two observers on different