

POLYMORPHISM IN *POEPHILA GOULDIAE* GOULD

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1. INTRODUCTION

Polymorphism is not an uncommon phenomenon among birds; most groups include a few species with two or more phases (generally plumage phases), and in some, such as the petrels (Procellariiformes), hawks (Falconiformes), owls (Strigiformes) and herons (Ardeidae), many species are characterized in this way.

Such a condition affords a good opportunity for studying the frequencies of polymorphic characters in wild populations according to their distribution in space and/or time (in birds experiments in captivity are difficult and laborious). Nevertheless, only a small amount of work has so far been done in this direction. Huxley (1942), Mayr (1943), and in a much smaller way Southern (1943), have given somewhat general treatments of the subject, and more detailed studies exist for the guillemot, *Uria aalge* Pont. (Southern & Reeve, 1941), the reef heron, *Demigretta sacra* Gm. (Mayr & Amadon, 1941), the Arctic and pomatorhine skuas, *Stercorarius parasiticus* L. and *S. pomarinus* (Temm.) (Southern, 1943, 1944), and the giant fulmar, *Macronectes giganteus* Gm. (Serventy, 1943).

All these cases so far analysed have shown a more or less definite pattern in the distribution of phase ratios, perhaps to be correlated with environmental factors. So, if each constitutes a true balance of polymorphism (see Ford, 1941) and is not just a stage in a process of replacement, the control will probably be of an ecological nature.

The case of *Poephila gouldiae* is particularly interesting, because it appears to be the first recorded among birds in which the control of the polymorphic balance may be genetic.

2. DESCRIPTION

Poephila gouldiae Gould is a small Australian grass-finch of the family Ploceidae, distributed over the tropical and subtropical zones of that continent. It exists in two common phases, one in which the facial mask is completely black like the rest of the head and another in which this mask is red. Sexual plumage dimorphism affects only the brightness of the colours, so that the phases appear in both sexes. In the females, however, there is considerable variation in the pureness of the red, some extreme specimens having only a few red feathers. Proportions of the brightest birds are not given in the literature, but Legendre (1936) speaks as though there were two clear-cut types—a pure (morphologically speaking) red-headed type, and a type in which the red is mixed with black feathers.

Young birds do not develop the bright plumage until they are about 8 months old, and neither sex nor phase is distinguishable until they are about 5 months old.

A third and much rarer phase has a yellow mask.

3. RATIO OF PHASES IN NATURE

Since much interest is displayed in these birds by aviculturalists, we find occasional biological notes about them in the field by professional bird catchers as well as by naturalists.

In North Queensland, Heumann (1909) states that 75 % of birds seen by him were black-headed, while in north-west Australia, at the other end of the range, Hill (1911) at Kimberley noted the same ratio in large flocks moving northwards. This is further substantiated by Hall (1902), who describes four birds from a collection at the Fitzroy River in the north-west of Australia, of which one only was red-headed. Such a record is of course quite worthless on its own, but it is interesting that it coincides with other estimates. Lastly, there is a reference to a pamphlet published by a firm of bird fanciers (Anon. 1906-7), which quotes Australian trappers as saying that 80 % of Gouldian finches are black-headed (no locality given).

There is evident agreement from various and widely separated parts of the range that black-headed birds are three or four times as numerous as red-headed ones.

The yellow-headed phase is said to occur in the proportion of about 1 to 200-300 of the other two types by one author (Legendre, 1936); 1 to 5000 by Cayley (1932). Either ratio probably gives it the status of a true polymorph, but very little else is known about it except that it apparently occurs all over the range (Cayley, 1932).

The constancy of this phenotypic ratio is interesting, when compared with the condition in most other polymorphic species of birds. Usually the phases are distributed on a cline, one becoming more numerous at the expense of the other in a certain direction or directions. Such a cline in polymorph ratio is often correlated with environmental factors.

In the case of the Gouldian finch, however, the ratio is constant in all parts of the range for which information is available, and the polymorphic balance may therefore be maintained by some genetic mechanism, as is known to occur in some Lepidoptera.

It becomes of interest to determine what is the genetic control of the red- and black-headed phases.

4. THE GENETICAL EVIDENCE

Fortunately, the Gouldian finch is widely kept as an aviary species, so that many crosses between red- and black-headed phases have been made. Unfortunately, these have nearly all been carried out by aviculturalists and proper records are rare, scattered and incomplete. The matter is of such interest, however, that a determined search has been made in all likely recesses of the literature. The results may be briefly surveyed as follows.

A. *Aldersparre's experiments*: These constitute the only crosses carried out by a competent zoologist. His description of the experiments (Aldersparre, 1918) and his conclusions are clear, though based on very small figures (full details of the crosses are given in Table 1); the red-headed factor is a single sex-linked dominant, and there is some evidence to suggest that the red-headed birds may mostly be heterozygotes.

B. *Stresemann's interpretation*. In a full article included in his series of 'Mutationsstudien', Stresemann (1924), arguing from Aldersparre's data, concludes that the factor

for red head is lethal when homozygous. Further, he apparently discards the hypothesis of sex-linkage, since he contends that there must be a sex-linked modifying factor, which needs to be present in double dose for the factor for red head to be given complete expression. This is the way in which he explains the less clearly defined red head in the females (the heterogametic sex).

Table 1. Summary of available data on head-colour inheritance in Gouldian finches

Type of cross	Authority	Parents		Young								
				Red			Black					
				RR ♂	Rr ♂	RO ♀	rr ♂	rO ♀				
1a Black female × red male	Aldersparre (2 separate crosses lumped) Macklin (1928)	Either both rO × Rr, or one rO × RR	* {	Exp.	—	2.25	2.25	2.25	2.25			
				Obs.	—	3	5	1	0			
				Exp.	—	3.375	3.375	1.125	1.125			
				Obs.	—	3	5	1	0			
				Exp.	—	3	3	3	3			
				Obs.	—	3	4	2	3			
				1b	Aldham (per Teague)	rO × RR	Exp.	—	3	3	—	—
							Obs.	—	3	3	—	—
							Exp.	—	3	3	—	—
							Obs.	—	6	0	—	—
2 Red female × black male	Aldersparre (1918) Aldham (per Teague) Butler (1905-6) Teague	RO × rr Do. Do. Do.	Exp.	—	1	—	—	1				
			Obs.	—	1	—	—	1				
			Exp.	—	1.5	—	—	1.5				
			Obs.	—	0	—	—	3				
			Exp.	—	1	—	—	1				
			Obs.	—	1	—	—	1				
			Exp.	—	2.5	—	—	2.5				
			Obs.	—	2	—	—	3				
			Exp.	—	4	—	—	4				
			Obs.	—	4	—	—	4				
3 Black female × black male	Kay, G. T. (in lit.) Teague	rO × rr Do.	—	About 6 broods all black-headed								
			—	About 50 broods all black-headed								
4a Red female × red male	Aldersparre (1918) Teague	RO × Rr Do.	Exp.	2.5		1.25	—	1.25				
			Obs.	3		1	—	1				
			Exp.	1.5		0.75	—	0.75				
			Obs.	1		0	—	2				
			Exp.	4.5		2.25	—	2.25				
			Obs.	4		1	—	4				
			Exp.	8		4	—	4				
			Obs.	6		4	—	6				
			Exp.	1		0.5	—	0.5				
			Obs.	1		0	—	1				
4b	Teague	RO × RR	Exp.	5	—	5	—	—				
			Obs.	5	—	5	—	—				
			Exp.	3.5	—	3.5	—	—				
			Obs.	3	—	4	—	—				
			Exp.	5.5	—	5.5	—	—				
			Obs.	5	—	6	—	—				

* These are two interpretations of the same breeding experiment.

This second contention of Stresemann seems almost certainly wrong. Aldersparre's data can be interpreted much more simply on the hypothesis that the factor pair concerned is sited on the X-chromosomes. The variation in the female plumage, however, which Stresemann attempts to explain in this way, is curious and needs further investigation.

Apart from this Stresemann's suggestion would mean that no females could have pure red heads, which is untrue.

His first contention that the factor for red head is lethal when homozygous is not satisfactory either. Though it is known that a polymorphic balance may be maintained by selection in favour of the heterozygote, complete lethality of the homozygote need not be invoked, for decreased viability would quickly show its effect in the gene ratios.

It is worth while to examine Aldersparre's crosses more carefully on this point, because his birds were recently imported from Australia and there would have been no chance of his increasing the homozygote viability by breeding, as may have occurred in some of the aviculturalists' stocks.

In cross 1*a* (see Table 1) he unfortunately lumped the product of two crosses; it is not even made clear whether the two were broods from the same parents. Both interpretations are given and on the whole the observed ratio in the young agrees better with expectation, if the young are from crosses with different male birds (Rr and RR), but the figures are too small to be conclusive. In cross 4*a* (first three examples), supposing that birds of RR constitution failed to hatch, the revised expectations would be as follows.

	Rr	RO	rO	RR (died)
Expected	1.3	1.3	1.3	
Observed	3	1	1	
Expected	1	1	1	
Observed	1	0	2	
Expected	3	3	3	
Observed	4	1	4	

The agreement between observed and expected is not quite so good as on the alternative hypothesis that the RR class was represented in the young. However, again more figures are needed. Certainly one may say that Stresemann's imputation of lethality to the factor for red head in double dose is not justified, as far as it is based on these figures.

C. *Other crosses from the literature.* All other records tabulated in Table 1 agree with the hypothesis that the factor for red head is a sex-linked dominant. Cross 4*b* shows without doubt that birds of the constitution RR do exist, though this stock had been bred in the aviary for some years with the avowed purpose of establishing a pure red line, and therefore this can hardly be used as evidence for conditions in the wild.

D. *Crosses carried out by Mr P. W. Teague.* Since the foregoing evidence is rather slender, the writer approached Mr P. W. Teague, a well-known breeder of Gouldian finches, who was most willing to co-operate. In the last two years he has reared a number of broods mostly from the critical cross of red-headed female (RO) × black-headed male (rr), and the results have completely confirmed the hypothesis. The writer wishes here to express his great indebtedness to Mr Teague, who carried out these experiments in the face of great difficulties in obtaining proper food for the birds, and, in spite of the fact that, as a breeder, his main interest lay in breeding a pure red-headed line.

Mr Teague's current crosses in pursuit of the last object are also given in Table 1, and these show again that cocks of the constitution RR can be bred, but he tells me (and I have seen some of the birds concerned myself) that a certain proportion of these red-headed cocks are subject to a form of 'vertigo', characterized by head twisting and inability to judge distances. This seems to confirm the suspicion that homozygotic red-headed birds may be less viable than heterozygotes.

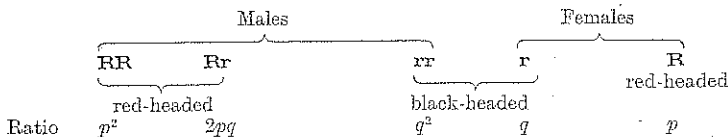
E. *Gynandromorphs.* Though the evidence contained in Table 1, particularly under matings 2 and 4, seems strong enough to establish the nature of the genetic control of

polymorphism in the Gouldian finch, there are collateral lines of evidence to be taken into account. A number of gynandromorphs have been reported in the literature, one of which, described by Harvey (1926), is of especial interest. This was a bird, one side of which was a red-headed male, the other side black-headed female. This strongly suggests that the original zygote was a male heterozygote, in which the dropping out of an X-chromosome at the first cleavage exposed a single gene for black head and also changed the sex from male to female. This certainly fits the hypothesis of red being a sex-linked dominant, because it seems unlikely that these two changes both of colour and sex could have occurred together unless the factor were sex-linked. It seems improbable in birds with their large numbers of chromosomes that an autosomal change would affect the sex, even if sex determination were not controlled entirely by the X-chromosome mechanism.

In two other instances of gynandromorphism reported by Crew & Munro (1938), it is suggested that the result is due to non-disjunction of an autosome (in these cases both sides were black-headed). The authors base this interpretation upon the facts that one specimen, when dissected, proved to have a normal ovary on the female side and no testicular tissue, and that the male side was 3-4 % larger than the female side. They argue that trisomy alone would account for the disparity in size. Since, however, measurements of twenty-four skins show mean lengths for males of 4.5 in. and for females of 4.3 in. (Page, undated), a difference of over 4 %, it is quite possible that gene elimination will account for these gynandromorphs as well as for the first case.

5. GENE RATIOS IN NATURE

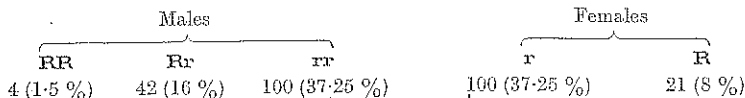
Assuming that the factor for red head is a sex-linked dominant, certain conclusions about the distribution of the various genotypes in the wild may be drawn. The following will be represented in the population:



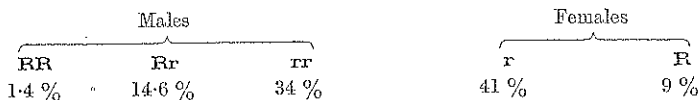
Since in a wild state black-headed birds are about three times as common as red-headed ones, we know that

$$p^2 + 2pq + p = \frac{q^2 + q}{3} \text{ (on the assumption of random mating).}$$

If $q=1$, then $p=0.208$, giving the following ratios:



It must not be assumed that the sex ratio in natural conditions is equal, yet with rough figures such as these, the divergence is probably not real. The adjusted ratios will be



Since the rough estimates of phenotypic ratio in the wild vary between 3 : 1 and 4 : 1, it is as well to give the calculated frequency of genotypes in the latter case also:

Males			Females	
RR	Rr	rr	r	R
2.6 (1 %)	32 (12.8 %)	100 (40.4 %)	100 (40.4 %)	16 (5.4 %)

and adjusting the sex ratio to equality again

0.9 %	11.8 %	37.3 %	44 %	6 %
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Thus in either case a sample of a wild population should have about as many black-headed males as females: on the other hand, red-headed males should be about twice as numerous as red-headed females.

These frequencies could easily be checked by counts in the field, and no doubt it will be possible to get this done satisfactorily after the war. For the moment, however, it is interesting and perhaps significant that an estimate made by Australian trappers (Anon. 1906-7) gives the following results: '80 % of the catch are usually black-headed, 15 % red-headed males and 5 % red-headed females.'

Remembering that these reported frequencies are only estimates and not based on counts, they are in reasonable accord with the calculated ones given above, and there is certainly nothing to contradict the hypothesis of the gene for red head being a sex-linked dominant.

It can also be seen from these ratios that homozygote red-headed birds, even if fully viable, will only occur naturally in the proportion of about 1 % of the population. This would fully account for the difficulty that Stresemann found in the absence of homozygotes from Aldersparre's birds.

6. SUMMARY AND CONCLUSIONS

From the evidence given above the following conclusions are submitted:

- (i) The colour of the face mask in *Poephila gouldiae* is controlled by a single sex-linked gene, the factor for red being dominant to that for black.
- (ii) Homozygous red-headed birds have not been proved conclusively to exist in wild populations, but there is some evidence, slight as yet, that they may do so.
- (iii) Birds of this constitution bred in aviaries do sometimes show pathological symptoms, and so their viability may be less than that of heterozygotes.
- (iv) The proportion of the two phases in wild populations is approximately constant (3-4 black-headed to 1 red-headed) throughout the range. Black-headed cocks should be only slightly less numerous than black-headed hens, but red-headed cocks are twice as numerous as hens of the same colour.
- (v) These ratios agree fairly closely with those to be expected in a random-mating population with the observed gene ratios.
- (vi) It looks therefore as if a balance of polymorphism existed in *Poephila gouldiae*, controlled by a genetic mechanism not unlike that recorded in some Lepidoptera (though here the control is in the autosomes).

The writer is greatly indebted to Dr E. B. Ford and to Mr H. G. Callan for their helpful criticism and advice, and to Mr P. W. Teague for carrying out the crosses already mentioned in the text.

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