There may be differences in migratory behaviour in relation to the size of juvenile subadults. It is not yet clear whether these differences are related to swans of different geographical origin (different breeding populations) or if they depend on differential growth rates. The necks of short-necked juvenile swans grow more in their second or later years than do those with longer necks. Swans in the study area start breeding comparatively late in life, often not until the ages of 6 to 7 years. Breeding, beside other things, is associated with higher weights than is normal for non-breeders.

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POPULATION GENETICS OF *CYGNUS OLOR*

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Introduction

Genetic variants can be detected from small blood samples by electrophoresis. The proteins in a small blood sample can be separated on starch gels buffered to a specific pH by applying an electric field. The proteins move to different positions and can be located and identified by histological stains. Samples from different individuals may show different patterns on electrophoresis, and some of these differences are genetically determined. In *Cygnus olor* two proteins show such genetic polymorphism – the enzymes esterase and lactate dehydrogenase.

Esterase

Cygnus olor plasma shows three phenotypic patterns for esterase characterized by:

- a) three slow bands, termed *SS;*
- b) six bands, termed *SF;*
- c) three fast bands, termed *FF.*

Blood samples from complete families, both parents and all their cygnets, make it possible to test whether the patterns are inherited. Table 1 shows that the esterase patterns are inherited in a simple Mendelian fashion, behaving as co-dominant alleles at an autosomal locus.

The genotypes occur at similar high frequencies throughout Britain (Fig 1). Since

Table 1. Esterase inheritance data.

Phenotypes of parental mating	Number of cygnets with phenotype			Expected ratios			Chi^2	Probability	
	SS	*SF*	*FF*	*SS*	*SF*	*FF*			
SS x SS	90			1	0	0	–	–	
SS x FF		42		0	1	0	–	–	
FF x FF			4	0	0	1	–	–	
SS x SF	56	58		1	1	0	0.035	0.9	$p > 0.8$
SF x FF		11	16	0	1	1	0.926	0.5	$p > 0.3$
SF x SF	9	20	10	1	2	1	0.077	0.98	$p > 0.9$
Total		316					1.038	0.9	$p > 0.8$

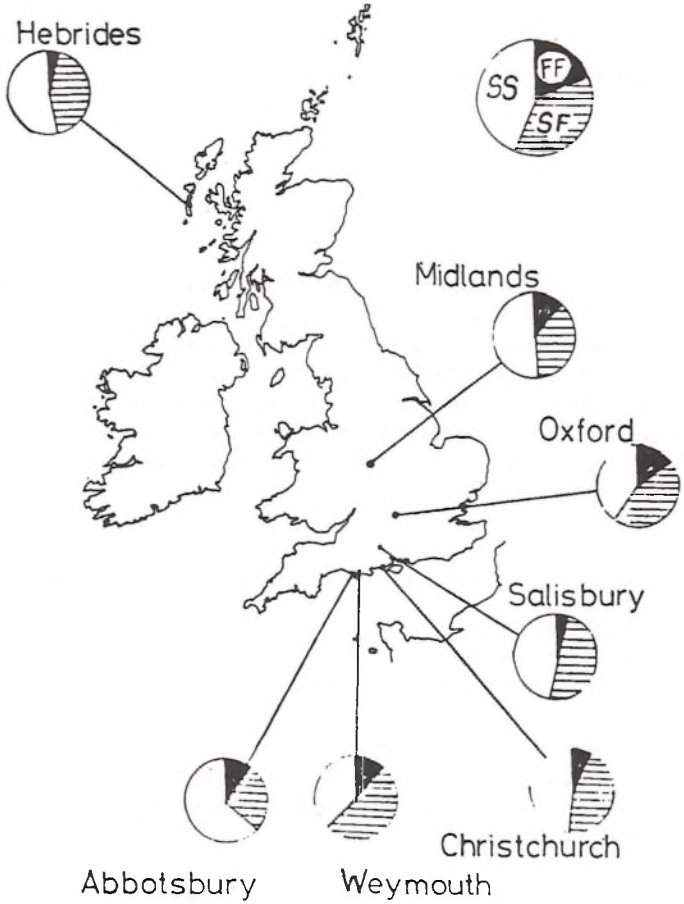

Fig 1. Esterase genotype frequencies in Britain.

genotypic ratios are *SS:SF:FF,* 5:4:1, the question arises of how both the *S* and *F* alleles are maintained in all areas at these high consistent levels.

Most homozygous *S* females lay larger clutches earlier in the season, thus producing more cygnets. Heterozygous females may lay early or late, with large or small clutches. Homozygous *F* females generally lay small clutches late. The whole population does not become homozygous *S,* because the mates of heterozygous males lay larger clutches irrespective of date; there is thus a balance achieved between the genotypes – *S* alleles gain an advantage in *SS* females, while *F* alleles gain an advantage in *SF* males (Figs 2 and 3). It is likely that these differences between genotypes in breeding success may be achieved through habitat preference.

Lactate dehydrogenase

Individuals show two phenotypic patterns for this enzyme, termed *AA* and *Aa.* Complete family data show that these patterns are also inherited as co-dominant alleles at autosomal loci (see Table 2).

Table 2. Abbotsbury breeding data 1978. Number of cygnets per mating type.

Genotypes of parental mating	Genotypes of cygnets *AA*	*Aa*	Expected ratios
AA x AA	45	0	1:0:0
AA x Aa	22	16	1:1:0

Note: The ratio of cygnet genotypes was not significantly different from the expected ratios.

The *Aa* heterozygote is localized and rare. It generally occurs at less than 1% frequency; however, in the colonies at Abbotsbury and Weymouth it is above 15% frequency and is particularly frequent in the resident breeding segments of these two populations (Fig 4). Yet even at the site where it is most frequent, a natural *Aa x Aa* mating has not been observed.

Within the Abbotsbury population, *Aa* individuals are more likely to breed, to fledge cygnets and to have larger broods at fledging (see Table 3 and Bacon 1979).

These factors give *Aa* individuals a relative fitness of about 2.4 compared with *AA* individuals. A selected advantage of this magnitude is required to keep the *a* allele at the observed high frequency in the face of diluting forces from a high frequency of *AA* immigrant breeders at the colony.

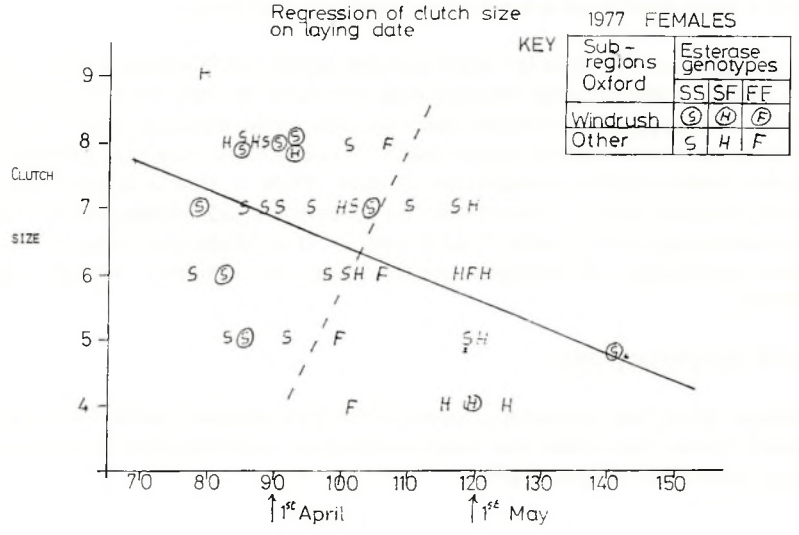

Fig 2. Relative breeding success of females by genotype.

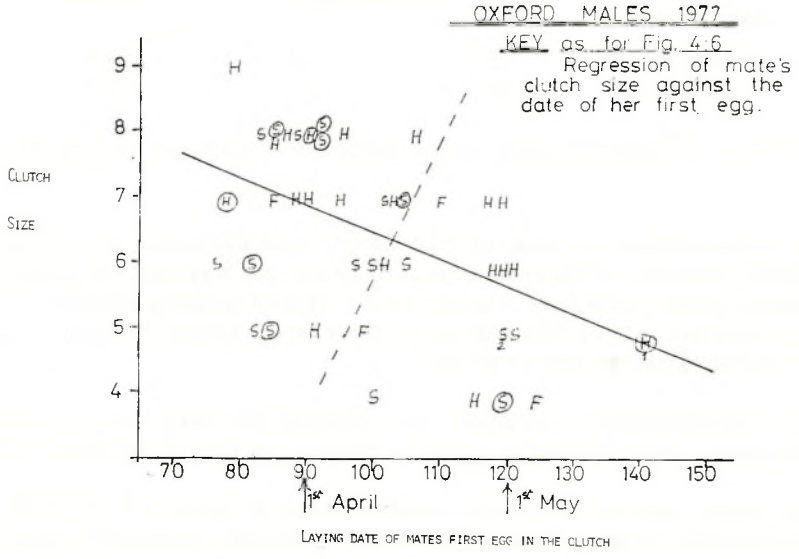

Fig 3. Relative breeding success of males by genotype.

Table 3. Relative fitnesses at Abbotsbury for three attributes by lactate dehydrogenase (LDH) genotype.

Fitness due to factor	LDH genotype		Relative fitness
	AA	*Aa*	of *Aa*
Probability of nesting	0.14	0.19	1.35
Probability of fledging	0.52	0.82	1.58
Mean brood size*	5.00	5.56	1.13
Total advantage			2.40

* For broods greater than 0, therefore independent of the probability of fledging.

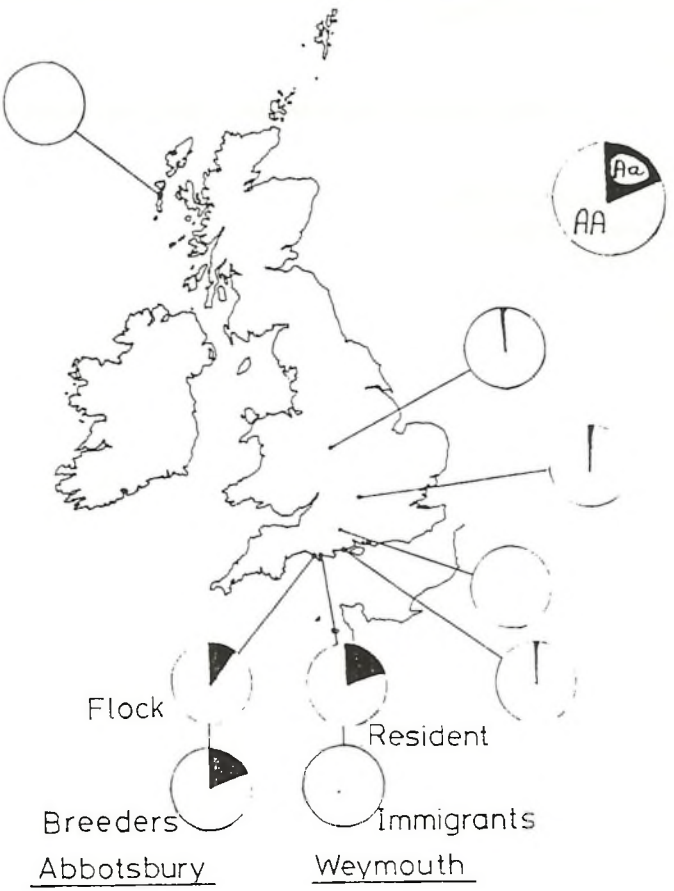

Fig 4. Lactate dehydrogenase genotype frequencies in Britain.

Summary

Electrophoretic methods were used to separate biochemical variants which were used as genetic markers. Protein samples were obtained from small blood samples and separated in horizontal starch gels. Complete family data for two polymorphic enzymes were entirely consistent with their patterns being determined by Mendelian inheritance of two co-dominant alleles at autosomal loci; these loci were not linked. Some 2500 blood samples from *Cygnus olor* were collected, representing eight study sites.

At a lactate dehydrogenase locus the *a* allele was generally rare, with less than 1% *Aa* heterozygotes; however, at two colonial sites the heterozygote frequency was significantly higher.

The esterase polymorphism displayed genotypic frequencies of 5:4:1 at all sites except one colony where they were 6:3:1. *SS* females laid significantly earlier in the season than other genotypes and the mates of *SF* males produced larger than average clutches at all seasons. The data further support the suggestion that the productivity differences between esterase genotypes are influences by habitat factors.

References

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