on variant forms of hordeins, including the genetic analysis which showed that these proteins are coded for by two loci, hordein 1 and hordein 2 positioned approximately eight units apart on the short arm of chromosome 5 in barley. Some of the initial work on the *in vitro* synthesis of hordeins is also described. This aspect may have merited some expansion, as different cereal research groups have been successful in cloning plasmids with inserted DNA sequences that code for storage proteins.

Attempts to improve protein quality by mutation are described in several articles. Mutants derived so far appear to have some yield disadvantage, e.g. reduced seed size in addition to any improvement in quality. They also divide into types that may improve in yield characteristics by the introduction of modifier genes, and other mutants in which the yield disadvantage appears to be a pleiotropic effect of the quality improvement, e.g. the Risø mutants, which have a high grain lysine content but a strong tendency to produce shrivelled grains. Doll suggests that increases in lysine content should be sought by combining variants for the relatively lysine-rich soluble proteins, thus attempting to avoid any reduction in the storage protein fraction. Whichever breeding method is successful, it has become clear that improvement in protein quality is not a simple breeding objective.

In the chapters on legume seed proteins it is pointed out that comparisons made of storage proteins in legumes are complicated by the difficulties inherent in extracting the proteins efficiently. It is also evident that a more methodical system for naming the protein fractions currently known as legumin, vicilin, phaseolin, etc. would help in making the appropriate comparisons. A few summarizing diagrams of these protein fractions separated on SDS–PAGE might have been helpful here, especially in tracing evolutionary relationships. The book also includes sections on the minor cereals and legumes and finishes with an interesting chapter on the nutritive value of seed proteins.

The different areas of research drawn together in this text provide the reader with sound background information on the seed proteins and also indicate promising lines of future work, e.g. gene cloning, which should pave the way for further research.

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The Arctic Skua, A Study of the Ecology and Evolution of a Seabird. By PETER O'DONALD. Cambridge University Press, Cambridge, England CB2 1RP (1983). 324 pages, £25.00. ISBN 0 521 23581 2.

The central tenet of the neo-Darwinian synthesis is that evolution proceeds by a bias in contribution of numbers of offspring to future generations, by parents of the present generation. Those individuals which contribute proportionately larger numbers of descendants are deemed the most 'fit'; if variation in fitness is associated with the presence or absence of a particular gene, then natural selection operates on that gene. For this theory of evolution to be predictive, one needs to assign selection coefficients to the genes segregating in the population of interest. This is clearly a mammoth task, both conceptually and practically, for not only does the fitness of an individual depend on its entire assemblage of genes, rather than single loci, but fitness also varies among individuals not solely because of differences among them in genotype, but also because of the different environments they inhabit. ('Environment' in this context is the geneticist's shorthand for those factors which comprise the entire field of ecology!) Empirical measurements of fitness associated with alternate alleles at even a single locus are thus exceedingly difficult to obtain, and are for the most part confined to special laboratory populations, usually of *Drosophila*. This monograph is Peter O'Donald's attempt to tackle this problem in a natural population, and summarizes nine years of research on the genetics and ecology of the Arctic Skua (*Stercorarius parasiticus*) on the Shetland Islands of Fair Isle and Foula.

Skuas are ideal subjects for such an undertaking. The species as a whole is polymorphic for three distinct plumage phenotypes: pale, intermediate melanic, and dark melanic. The polymorphism is stable temporally, and clinal over the species range, varying from a high frequency of melanics at the southern end of the range to 100 % pale at the northern end. Arctic Skuas have a discrete annual breeding season, and often return to their natal colony in subsequent years to breed, which allows identification of all members of a colony and their progeny. All the ingredients are therefore available to obtain complete life-history data for the animals of each of the three phenotypes, so that estimates of relative selection coefficients obtained for these phenotypes should enable prediction of the future genetic constitution of the population with respect to the colour polymorphism.

O'Donald deduces that over much of the life cycle the three colour phenotypes do not differ in fitness: they have similar clutch sizes, incubation periods, periods to fledging, and probabilities of survival. However, there are marked differences in the fertility components of fitness, as the different phenotypes vary in age at maturity and reproductive rate. Pale birds breed for the first time when they are 4 years of age, on average 6 months younger than melanic (dark and intermediate) individuals. However, pale birds are correspondingly less successful in their first year of breeding, and have a lower reproductive rate than melanics, although the reproductive success of all phenotypes is similar in later years. The lowered reproductive rate of pale birds more than compensates for the gain in earlier maturity, accruing an overall advantage to the melanic phenotypes. O'Donald explains the mechanism of sexual selection in terms of variation in breeding date of males forming new pairs in any one breeding season. Non-melanic males take, on the average, 4 days longer to find a mate when first breeding than melanics; later breeding reduces fledging success, and consequently fitness. It is postulated that the sexual advantage of melanic males operates through female preference for dark individuals. When all components of selection are considered jointly, the dark melanic phenotype is favoured overall, therefore natural selection should ultimately remove the pale phenotype from this population. Since the frequency of the phenotypes is stable temporally, it is hypothesized that this is a consequence of migration along a cline in which there is a gradient of selection favouring the pale phenotype in the north, and the melanic phenotype in the south.

The story is convincing, but only superficially. Detailed examination of the data reveals the extent of the difficulties involved in measuring selection directly from the field. For example, it was not possible to show unambiguously that the genetic basis of the colour polymorphism was a single locus with two semi-dominant alleles, as the classification of phenotype of young birds altered with time, and the sample of adult chicks from known matings was small. Even though this remains the most likely hypothesis, it is not strictly possible to make predictions of the future genetic constitution of the population when the underlying mechanism of inheritance is unknown; it is therefore hardly surprising to find that observed 'genotype' frequencies deviate from Hardy–Weinberg expectation. Calculation of selection coefficients from the demographic data is likewise confounded by real life. It is simple in principle to obtain relative fitnesses of genotypes in the population by following a cohort of newly fledged chicks of all genotypes, and recording survival and reproduction at intervals, so that their contribution to the next generation may be assessed. In practice, the number of chicks in any one cohort is too small for this, and survival rates must be obtained indirectly from the age distribution. The latter method is only reasonable if mortality is constant across generations, if population size is constant, and if there is no migration. Since the immigration rate is known to be greater than 40 % per generation, the population increased exponentially in the period 1948–62, and birds cannot be caught in the period after fledging until they return to breed at 4 years old, this accords the calculation of selection coefficients the status of an informed guess.

This monograph will be of interest to research workers and students in ecological genetics, if only to emphasize some of the pitfalls to be avoided in future studies. The author's somewhat idiosyncratic style of writing may well prevent the book from having wider appeal. The book is frequently used as a vehicle for vehement and tangential attacks on the work of colleagues who advance contradictory hypotheses, and the method of presentation of the results is often infuriating, with insufficient distinction among hypothesis, fact, and conclusion. Explanations are often pitched at a level which does not aid subsequent understanding of the subject under discussion; for example, I do not think a lecture on the advisability of choosing the correct degress of freedom for estimating variance is particularly central to the understanding of the concept of heritability. O'Donald's attitude to statistics is somewhat cavalier; he chastises other authors for neglecting to do the appropriate statistical tests, yet his own heritabilities of breeding dates are conspicuously without standard errors. At the other extreme, while a regression of breeding data on territory size of $-0{\cdot}0002623$ may undeniably be statistically significant, given sufficient observations, the biological significance of a regression of this magnitude is dubious.

Nevertheless, for the reader with a background in population genetics, *The Arctic Skua* provides much useful information on the ecology, genetics, and behaviour of this fascinating seabird, and conveys a feeling for the daunting complexity of the study of natural selection.

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