INTRODUCTION

Three types of crossbreeding, for new breed synthesis, grading up, and repeated crossing between continuing purebred populations, have been identified and well illustrated for sheep in reviews by Rae (1952 and 1956). Bowman (1966 and 1967) updated the surveys of experimental data, and more results are published every year as workers in each country report on trials designed to investigate the benefits from crossing among their native breeds and between these and imported animals. It seems likely, however, that the greatest advances in the past decade have taken place in our understanding of the overall mechanisms of crossbreeding systems, rather than in the development of actual new breeds or crosses, or the extension or simplification of existing systems.

This understanding should enable future systems to be designed to give even greater efficiency, both for countries like the United Kingdom with a tradition of crossbreeding, and for those where purebreeding has remained the dominant commercial practice. It is for this reason that the present review concentrates mainly on these more theoretical advances.

CURRENT CROSSBREEDING IN BRITAIN

The sheep industry in Britain illustrates most of the possible crossing systems and these have already been written about by many authors. The extent of crossbreeding and some details of the different crosses are summarized in a recent report to the Meat and Livestock Commission (MLC, 1972). The widespread 3-breed cross involves the use of first-cross (F₁) ewes mated, on lowland farms, to Down
rams to produce the slaughter generation. The first-cross ewe is frequently by a 
Longwool ram (e.g. Border Leicester) out of a small hill breed of ewe (e.g. Che­ 
viot). In some areas the hill ewe herself (e.g. Welsh Mountain) is crossed directly 
with a Down ram to produce 2-breed-cross fat lambs. Some examples of 2-breed 
rotational crossing schemes can also be found. Thus lowland flocks may use 
Suffolk and Clun rams alternately, selling fat lambs after keeping back their own 
replacement ewe lambs; similarly many hill flocks switch fairly regularly between 
Scottish Blackface and Swaledale rams. One or two new synthetic breeds have 
been formed in recent years by crossing two or more breeds and then interbreed­ 
ing, notably the Colbred (BARBER and YOUNG, 1965), but these do not appear to 
have had much success.

Theory of crossbreeding systems

The usually accepted measure of heterosis is the deviation of the performance 
of the first-cross animal from that of the mid-parent mean. So long as attention 
was mainly focussed on the occurrence of heterosis at the level of the individual 
trait (body weight, fleece weight, litter size) it was difficult to explain the very 
widespread utilization of crossing systems in commercial practice. There have in 
fact been relatively few convincing demonstrations of the existence of such hete­ 
orosis (DONALD, READ and RUSSEL, 1963), and the comparatively high heritability 
of several traits makes it unlikely that crossbreds will in fact show advantages 
over the parental mean for these single traits (adult body weight, carcass and 
wool traits).

SMITH (1964) focussed attention on the usefulness of looking at a breeding and 
selection system in terms of a combination of the reproductive performance of 
the parents, and the productive efficiency and quality of their (crossbred) offspring. 
His approach was extensively developed by MOAV (1966) who used the term 
«profit heterosis», and classified a variety of quite different mechanisms, all of 
which can produce heterosis in overall profitability. He showed how crossbreed­ 
ing systems would prove beneficial by exploiting sex linkage and maternal effects; 
the non-linear relationship between a trait and profits; and the unequal con­ 
tributions of sire and dam to profit; in addition to the much narrower class of 
non-additive gene action effects.

The dependence of overall profit on these various aspects of maternal and 
offspring performance was explored for sheep by LARGE (1970) and, more generally, 
crossing programmes emphasized the vital importance of a purely biological 
parameter not included in MOAV's synthesis: the excess fertility in the species over 
that needed merely to maintain a constant population size. A crossing system 
operating within a single environment must depend for its success upon the 
balance between the profit heterosis shown and the expenses incurred in maintain­ 
ing purebred populations of somewhat inferior breeds (the parental breeds). Only 
if the level of heterosis is high enough, or the necessary proportion of the total 
population which needs to be purebred is low enough (HILL, 1971), will a cross­ 
breeding system be attractive when viewed over the entire population.

As ROBERTSON points out, the low reproductive rate of the female sheep would 
rule out the development of specialized lines, or even the exploitation of existing
lines, to support a sheep crossing system within a single uniform environment. The fact that organized crossing using such lines is so widespread in Britain only makes sense when seen from an overall national standpoint. Sheep grazings vary from cheap mountain pasture which can support little else but the small specialized hill breeds, through the still poor marginal and upland farms, to fertile lowland temporary pastures, or root and forage crops grown in rotation on largely arable farms.

It therefore seems that if various crossbreeding systems are to be compared with each other, and with purebreeding systems, for use in a specified environment, then the models should not only include the information used by Moav, but should also have data on the performance, availability and price of animals existing in other related areas. Whether in fact, when dealing with such a complex, dynamic and interacting system, it will be possible to deduce firm conclusions from a model approach is not clear, but it must surely be worth the attempt. This is just one example of the increasingly recognised importance of integrating genetic, biological and economic details to produce animal breeding systems which are useful in the real world.

The sheep industry in Britain demonstrates the use of specialized lines (breeds) to an advanced degree, with several of the most influential breeds, e.g. Suffolk and Border Leicester, having their influence entirely through their role as male lines. These breeds were originally developed to exploit particular geographic and farming regions. Thus the large white-faced Leicester sheep were evolved to produce purebred mutton from the fertile pastures and root-fields of the Scottish borders. The Down breeds were bred to exploit the folded roots and green crops essential to maintain fertility of the arable farms on the lighter soils in Southern and Eastern England. These original functions have now entirely disappeared and the breeds have been developed to complement the virtually unchanging hill breeds, so that their 2- and 3-breed-cross progeny can exploit the lowland grasslands for fat lamb production. In Large's (1970) analysis of the biological efficiency of meat production in sheep he shows clearly how the greatest efficiency is obtained from a small breed of ewe, producing a large litter and crossed with a large breed of ram, leading to a high growth rate and slaughter weight in the lamb.

In most other European countries the sheep industries appear to have remained at the stage where the various local types are still largely bred pure within fairly traditional systems (Skarman, 1963). Much of this still goes on in Britain and it is considered that one of the most urgent tasks is to provide satisfactory information on the relative performance of different breeds. A recent survey carried out by the Meat and Livestock Commission (MLC, 1972) disclosed that 50 pure breeds and over 300 specific types of crossbred ewe were kept in British flocks. It is obvious that many of these breeds and crosses can have no real advantages over several others for any specified environment, and much useful simplification could be carried out in the future. Dickerson (1969) has set out the theory of the design of experiments to discriminate between breeds and crossing systems. Clearly the initial comparisons must be between those groups which already exist in significant numbers, or which appear useful on the basis of data currently available. Equally clearly such a large number of breeds has not been maintained without the existence of some degree of real or presumed genotype-
environment interaction, particularly when the «environment» is widened to include the overall economic situation, including prejudices amongst local buyers of fat, store and draft animals. Sheep production still takes place to a large extent through the exploitation of semi-natural environments and these still vary very much more than do the environments where we now keep pigs or poultry. Sheep do not often, except in the true hill areas, provide a major proportion of farm income, and their profitability in the last 2 decades has not been particularly good. All of these factors militate against the rapid rationalisation of breed selection or crossbreeding systems, even when accurate information becomes available on which to offer advice.

SUMMARY

Crossbreeding may have three different forms: new breed synthesis, grading up, and repeated crossing between continuing purebred populations. Perhaps because sheep production has not been particularly profitable in recent years we have not seen many new breeds developed, and traditional patterns of pure and crossbreeding have continued. There has been a considerable increase in our understanding of the theory of crossbreeding since the concept of overall production or profit has been integrated into genetic theory. A crossing system may exploit «profit heterosis» arising from a number of different mechanisms. Nevertheless, because of the low reproductive rate of almost all existing female sheep, such systems are only of commercial interest where surplus females are available from one environment for exploitation in another. Thus the well developed stratification pattern in Britain takes the relatively unproductive but well-adapted hill ewes, and by the use of specialized sire lines produces first cross ewes and 3-breed-cross lambs for meat production in more favourable lowland environments. We may expect to see existing breeds and crosses evaluated more carefully in the future in order to see where designed crossbreeding systems can prove more useful, but such work will not be simple.

RESUME

Le croisement peut prendre trois formes différentes: une synthèse produisant une nouvelle race, une amélioration de qualité, et le croisement répété entre des animaux de race pure qui continuent de se reproduire. C'est peut-être parce que la production de moutons n'a pas été particulièrement avantageuse pendant les dernières années que nous n'avons pas vu le développement de beaucoup de nouvelles races, et l'on a vu la continuation de manière traditionnelles d'élevage en race pure et croisée. Nous comprenons considérablement mieux la théorie de croisement depuis que l'idée générale de production totale ou bénéfice a été intégrée dans la théorie génétique. Un système de croisement peut exploiter «la hétérose rentable» qui se produit d'un nombre de mécanismes différents. Néanmoins, à cause du taux bas de reproduction de presque toutes les brebis actuelles, de tels systèmes sont d'un intérêt commercial seulement quand on peut obtenir les femelles de surplus d'un environnement pour les exploiter dans un autre. De
cette façon le système bien développé de stratification en Grande Bretagne prend les brebis de montagne relativement improductives mais bien adaptées, et, en utilisant des lignes masculines spécialisées, produit des brebis de premier croisement et des agneaux croisés de trois races pour la production de viande dans un environnement de terre basse qui est plus favorable. On peut s'attendre dans l'avenir à une évaluation plus profonde des races et des croisements existants par voir de quelle façon les systèmes de croisement projetés peut se rendre utile, mais un tel travail ne sera pas facile.

RESUMEN

El cruzamiento puede tomar tres fórmulas distintas: una síntesis produciendo una nueva raza, mejoramiento de clase y el cruce repetido entre animales de raza pura que siguen reproduciéndose. Tal vez porque la producción de ovejas durante los últimos años no ha sido especialmente lucrativa no hemos visto el desarrollo de muchas nuevas razas, y hemos seguido con la cría pura y cruzada de la manera tradicional. Ha crecido apreciablemente nuestra comprensión de la teoría del cruzamiento desde que el concepto de producción en su totalidad o beneficio ha sido integrado en la teoría genética. Un sistema de cruzamiento puede aprovecharse de «la heterosis económica» que resulta de varios mecanismos distintos. Sin embargo, a consecuencia de la baja razón de reproducción de casi todas las ovejas actuales, tales sistemas son sólo de un interés comercial, donde se puede sacar hembras sobrantes de un ambiente con la intención de explotarlas en otro. Así es que el sistema bien desarrollado de estratificación en Gran Bretaña toma la oveja de montaña, relativamente improductiva, pero bien adaptada, y al emplear líneas paternas especializadas produce ovejas de primer cruce y corderos de cruce de tres razas por la producción de carne en el ambiente más propicio de tierra baja. Podemos esperar por el porvenir una evaluación más profunda de las razas y cruces actuales para ver dónde pueden utilizarse de la mejor manera los sistemas de cruzamiento planificados, pero tal trabajo no será fácil.

REFERENCES


