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Hidden Treasure: Genetic Diversity in Plants and Animals

by

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## INTRODUCTION

Before I begin, may I thank members of the Farrer Memorial Trust very warmly for honouring me with the 1974 Farrer Medal. That the award should have been to me was a tremendous surprise, and therefore all the more appreciated. That it should have been to an animal geneticist demonstrates the wisdom of the Trust members, since an award in this field gives an opportunity for linking Farrer's work on wheat with research on animal breeding. The principles behind his search for improved wheat varieties still inspire not only to-day's wheat breeders, but all those working for genetic improvement of either plants or animals.

William James Farrer was born in England in 1845, and died in Australia in 1906. Those dates are significant, because between them occurred two events of great social and scientific importance - publication of the theories of Darwin and Mendel. As a young man, Farrer was influenced by Darwin, whose 'Origin of Species' appeared in 1859, just 5 years before Farrer began his mathematical studies at Cambridge. Mendel's laws of inheritance, after being published in the mid-19th century, were forgotten until re-discovered early in the 20th. Farrer wrote in a letter in 1905 that he was "now in the throes of mastering Mendel's laws, the practical application of which, however, I have been following for about a dozen years".

An enormous structure of modern genetic theory has been built on Mendel's laws, and those of us accustomed to thinking this research of vital importance should consider with humility that it was not only Farrer who followed the practical application of those laws long before they were formulated. Our far-off ancestors were following them when they chose the most docile animals for domestication, and later developed a wide range of breeds within each species by selecting individuals with the characteristics they wanted - more wool on their sheep, more milk or meat from their cattle. Or when they selected wild plants with the largest seed-heads, and grew grain near their huts.

Progress was made because variation on which selection could operate was not only visible but also partly inherited, and it continued for millennia

before Darwin developed his theory of evolution by observing this same variation in living things. He did not postulate a satisfactory mechanism to explain the reasons for genetic variation; this only became clear when Mendel's laws were re-discovered and developed. The theory based on these laws can now assist us in accelerating the rate of genetic change in plants and animals, but in the process of acceleration it is clearly our responsibility to ensure that we do not lose too much of earlier accomplishments. In setting our sights on genetic improvement towards current material goals, it must be remembered that those goals are not themselves immutable.

Farrer, then, followed in the footsteps of many others. But he benefited from living at a time when new concepts of tremendous importance were under discussion. If we can paraphrase the famous words of Neil Armstrong, first man on the moon, Farrer was able to turn earlier small steps into a giant leap.

Farrer's own words can be cited as evidence of the influence on him of Darwin's stress on the value of variation. In a talk to ANZAAS in 1898 he said: "Whenever well-directed attention is given to the improvement of a domesticated plant in any quality in which it is variable, that quality can be increased and developed to an indefinite extent". Not all variation, of course, is inherited; some is caused by environmental differences, but it is the genetic portion which can be used for permanent changes. Use of variation, or diversity, to improve production was one of the main principles behind Farrer's work. There were others, to be discussed later - let us first define genetic diversity.

Genetic differences can be considered at three levels - between species, between breeds or varieties within species, and between individuals within breeds or varieties. What is meant by an "individual" animal or plant is easily defined. The definition of a "species" is not always clear-cut, but in general it is accepted that individuals belong to different species if they will not inter-breed to produce viable and fertile offspring. The definition of "breed" or "variety" is even more difficult, but again a general description would be a group of individuals which will inter-breed

with other groups and produce fertile offspring, but which is differentiated from them by genetically-controlled characteristics. Plant breeders do not use the word "breed" at all, preferring "variety", (and, for greater clarity, "cultivar"), while animal breeders may use either "variety" or "type" or "strain" to describe sub-groups within a breed. Customs vary in different countries; in the U.S.S.R. there are several Merino "breeds" of sheep which in Australia would be called Merino "strains". For present purposes, I have adopted the definition of breed (or variety for plants) given above, namely, a group capable of inter-breeding with others of the species, but differing from them in certain genetically-controlled characteristics.

Farrer worked with between-variety and between-individual differences, but let us look at genetic diversity at all three levels.

#### BETWEEN-SPECIES VARIATION

The number of species of plants and animals is vast. Some have been domesticated, in that they are bred and cared for by man, others have not. Whether domesticated or wild, many contribute to man's needs, which may be classified as material, cultural or spiritual. Material needs include food, clothing, buildings or other shelter, household, medical or industrial goods and (in the case of animals), draught power (traction or transport). Cultural needs include recreation, education and scientific research. The last lies on the border between material and cultural needs, since it is used not only to improve productivity, but also to gain a greater understanding of biology in general, and of man, his environment and his history. Spiritual needs cover a control of man's arrogance and a sense of responsibility towards other living things.

It would be impossible to discuss here all species of plants and animals, wild or domesticated. As illustration, Table 1 lists the species of domestic animals, and some breeds within them, while Table 2 gives the areas of the world in which they are now found (Turner 1971a).

Domesticated animals belong to only a handful of the total, of 4,237 mammalian species listed by Morris (1965). Many of the still-wild species contribute to man's cultural needs through recreation (e.g. African game parks, zoological gardens), while others serve material needs (fur-bearers trapped for skins, antelope harvested for meat).

Increased population pressure and food requirements have decreased the areas available to wild animals and plants, and threatened many species with extinction. The human conscience has been stirred, and a widespread demand for conservation has arisen, some emotional, some based on sound reasoning. Serious attempts have been made not only to conserve many remaining wild species in their own habitats, but also, in the case of animals, to assess the best methods of using land, by balancing the contributions which can be made by wild or domestic animals. The investigations are particularly pertinent to difficult environments, with low rainfall and/or high temperatures and a harsh terrain, where livestock have not previously been used, or have not thrived. Wild animals may use the land alone, or in association with livestock; optimal use may involve leaving the animals entirely in their wild state (perhaps harvesting them at intervals), "farming" them by improving the habitat and possibly restraining their movement, or domesticating them entirely.

Because of Africa's great abundance of wildlife, the question of greater use has received most attention there. Practical arguments in favour of greater use of wild animal species, rather than reliance entirely on introduced livestock, include their better adaptation to prevailing conditions, better utilization of available plant material, better disease resistance, lower water requirement, less fat in the carcass, and in some cases a lower input of capital in terms of property improvements (de Vos, 1973). To these should be added, perhaps cynically, the point that species which are serving man's needs are more likely to be conserved, though in least need of special measures.

Many problems remain to be solved in using wildlife (Skinner 1967, Skinner et al., 1971). Not all species lend themselves to domestication.

Among those from Africa, the common eland (a large antelope) seems most adaptable; in 1961 I saw a herd at Ascania Nova, in the Ukraine, which was brought in from the steppe by a man on horseback, like a mob of cattle. This herd has been under selection for milk production since 1963 (Skinner 1967). Various other antelope (springbok, blesbok, impala, and kudu) are farmed in South Africa (de Vos 1973, Skinner 1973). Skinner considers that research should also be directed to productivity studies for zebra, red deer, mountain reedbuck, giraffe and warthog.

Coming nearer home, during the rural slump of the late 1960's and early 1970's efforts were begun in New Zealand to domesticate deer (red and fallow) in order to diversify meat production (Morcan 1973, Bird 1974), and in Australia there have been serious attempts recently to re-domesticate the feral water-buffalo in the Northern Territory. Neither animal is a native, both having been introduced and adapted well as wild animals. The deer have not previously been domesticated anywhere, but the buffalo was introduced to Australia as a domestic animal. Both species have already been harvested for meat from the wild; the income from buffalo meat in the Northern Territory in 1971 was \$Aus 1.25 million (Tulloch 1973).

Again in Australia, one enterprising pastoralist in northern N.S.W., has established a kangaroo farm; the animals will be kept within fences and periodically harvested. Studies have also been made in this country (Leigh 1974) of the comparative grazing habits of kangaroos, feral goats and livestock. These goats are also periodically harvested for meat in many parts of Australia, and have an export market; their husbandry is currently under observation by the N.S.W. Department of Agriculture. The recent finding (Smith, Clarke and Turner, 1973) that some feral goats are carrying the luxury fibre cashmere may also lead to a new look at animals previously regarded as vermin to be exterminated.

With plants as with animals, only a fraction of the world's available species are used for man's material needs. Considering food alone, about 15 species make the main contribution (Mangelsdorf 1966): five cereals (rice, wheat, corn, sorghum, barley); two sugar-plants (cane, beet);

three root crops (potato, sweet potato, cassava); three legumes (common bean, soybean, peanut); two so-called tree crops (coconut, banana). It has been estimated (Mangelsdorf loc. cit.) that 30 percent of all human energy comes from one species, rice. For this reason, considerable research has been directed to understanding of the rice-plant and the next most important food grain, wheat. There are strong arguments for increasing research not only on species currently exploited for food, but on the potential value of others not yet used.

Between-species differences are important in relation to primary decisions on land use. This applies to both plants and animals, but a glance at Table 2 will illustrate the point for animals. Some species, such as llama and alpaca in the high Andes, have very specialized habitats, and have not flourished elsewhere. Others, such as cattle and sheep, are widespread. Even so, there are areas better suited to one species than another; cattle are grown further north in Australia than sheep, for example.

This question of adaptation to a particular area becomes of even greater importance in considering differences between breeds or varieties within a species. I intend to illustrate this mainly with one plant and one animal species - wheat, which was Farrer's main interest, and sheep, which is my own.

#### WITHIN-SPECIES VARIATION - PLANTS

##### Farrer and Wheat

We plunge straight into Farrer's work when we start discussing varietal differences within a species. What exactly did he accomplish, and how? And what developments in wheat breeding have followed, using his line of approach?

Farrer's basic training at Cambridge was in mathematics, and he had intended to follow this with medicine (Russell 1949). For health reasons he abandoned his medical course in its first year (1870) and came

to Australia. He worked first on stations in the Canberra area, and as early as 1873 wrote a pamphlet urging a scientific approach in agricultural training. In 1875 he became a licensed surveyor, and was engaged by the Lands Department on surveys in the Dubbo area. Here he saw wheat fields devastated by rust, and had his initial thoughts about trying to improve the wheat plant; in his address to ANZAAS in 1898 he said that he first became interested in improving wheat in 1882. He believed in prevention of rust by seeking a resistant variety, rather than cure by chemical treatment, and suggested that farmers search for individual plants free from rust in an affected crop, using seed only from these. In this he was following the precepts of modern medicine, which ranks prevention above cure.

Farrer thus came to wheat breeding through interest; he had no formal training in agriculture or plant breeding. Let this be a warning to those institutional employers who insist nowadays that job-applicants must carry in their hands a piece of paper indicating their correct formal study! Farrer had no such piece of paper; neither had Darwin himself, who also planned originally to do medicine, but entered Cambridge with the clergy as his goal, then set off on the "Beagle" soon after graduation. Wallace, who developed a theory of evolution so similar to Darwin's that their work was presented jointly to the Royal Society in 1858, was, like Farrer, a surveyor - and also an architect. And what relevant piece of paper had the monk, Gregor Mendel? Passionate interest is even more important than formalized training in a specified direction, and cannot fail to lead to acquisition of the necessary basic knowledge.

Farrer's passionate interest led him to start his own experiments in 1885. He began with selection towards rust-resistance, growing his plants on a property near Canberra. (This being International Women's Year, I feel it incumbent upon me to mention that the property was available to him through his wife, a local grazier's daughter).

In 1886 Farrer resigned from the Lands Department to devote himself entirely to his wheat breeding. He was not content to use only wheat varieties available in N.S.W.; by 1905 his plantings had included varieties not only

from other parts of Australia, but also from Algeria, Arabia, Argentina, Asia Minor, Britain, Chile, China, Egypt, Fiji, France, Hungary, India, Mexico, Roumania, Russia, Siberia, Spain, Sweden, Turkestan Turkey and U.S.A. By this time he had larger and more varied areas available for planting, as in 1898 he joined the N.S.W. Department of Agriculture as Wheat Experimentalist.

Initially Farrer selected within each variety, but by 1889 he was using cross-breeding combined with selection. Characteristics from a number of varieties would be brought together to form a new one, and Farrer reaped the benefit of the wide range of genetic material he assembled. In using cross-breeding combined with selection, plant breeders have four advantages over animal breeders - single-gene control of many characteristics, self-fertilization in many plants (including wheat), a short generation interval and a large number of progeny from each parent, occupying a small space. Mendelian laws of inheritance state that characteristics are controlled by genes assembled in pairs, one of each pair coming from each parent. In some cases a single pair is the main determinant of a characteristic, while in others many pairs are involved. Re-combination of characteristics is much simpler with single-gene control, and known cases occur more often in plants than animals. Self-fertilization makes achievement of homozygosity more rapid, particularly when single genes are involved. One, and sometimes two, wheat crops can be grown per year, but from the birth of a ewe to the first lambing of her daughter is usually at least 4 years. And one wheat plant produces many more seeds than one ewe. All these advantages accelerate the rate of genetic improvement.

Although Farrer began by looking for rust resistance, he soon became interested in general improvement of the wheat plant - not only for his own region, but for different parts of Australia, as he realized clearly that different environmental conditions required different plant characteristics for maximum productivity. Further, he was prepared to define productivity in terms of wheat quality as well as quantity; he collaborated with F. B. Guthrie, cereal chemist of the N.S.W. Department of

Agriculture, in experiments to define baking quality, and had samples of different wheats processed right through to bread. In the same way the pioneer English farmer, William Bakewell, greatly improved British sheep breeds, about a century before Farrer, because he too insisted on looking for meat characteristics when selecting his animals. There is a parallel also in recent Australian work to determine the relative importance in processing of various wool characteristics (Australian Wool Board 1973), and to encourage breeders to concentrate on them (Turner 1973).

Farrer's greatest achievement lay in producing drought-resistant wheats, through which the wheat-growing areas of Australia were widely extended. In 1897, N.S.W. had 1 million acres (405 thousand hectares) under wheat; by 1915 the area had expanded to over 4 million acres (1.6 million hectares). His wheats were earlier maturing, of higher yield and better baking quality than the varieties previously grown in Australia. And, although he failed in his earliest objective of producing a completely rust-resistant variety, he paved the way for later breeders to tackle the problem of breeding for disease-resistance. Now, nearly 70 years after he finished his work, Farrer's varieties have all been replaced in Australia, but his most successful, Federation, lasted here on significant acreages for some 30 years, and was still being grown in the Pacific North West of U.S.A. until the late 1940's (Pugsley 1975).

We can perhaps reduce Farrer's guiding principles to two main ones - clear definition of objectives, and use of genetic diversity to attain them. He was able to accumulate a wide range of working material because of constant communication with colleagues all over the world - communication which we now take for granted, but which was rarer in his day.

#### Wheat - After Farrer

What has happened in the wheat breeding field since Farrer? I propose to jump from Australia in 1906, when he died, to Mexico in 1944, where what is now known as the "green revolution" began.

In 1944, four American agricultural scientists, led by Dr. George Farrar, (a plant pathologist) arrived in Mexico City in response to an appeal by the Mexican Government to the Rockefeller Foundation. The Foundation financed a Centre whose objective was to improve cereal production in Mexico; it was run jointly by the Foundation and the Mexican Government until 1963, when it was taken over entirely by the latter. On withdrawing from the purely Mexican project, the Rockefeller Foundation joined with the Ford Foundation to establish, still in Mexico, the International Corn and Wheat Improvement Centre (CIEMYT in the Spanish initials).

The name most closely associated with the work of the Mexican centre, and later of CIMMYT, is that of the American, Dr. Norman Borlaug, who was awarded the Nobel Peace Prize in 1970 for contributions towards solving the world's hunger problems. (Another Nobel award in the same year is probably more widely known - the Literature Prize to Alexander Solzhenitsyn).

Borlaug and his associates used the same principles which had guided Farrer, with the added advantage of a knowledge of theory based on Mendel's laws. Their objective was to develop wheat varieties for Mexico, and later to distribute them throughout the wheat areas of the world. Their technique was to accumulate genetic material from many parts of the world; CIEMYT inherited initially 60,000 wheat varieties from the Mexican programme, plus 6,000 from a world wheat collection.

From this genetic diversity wheat varieties have been developed which, like Farrer's, are early maturing and adapted to a wide range of conditions, largely because they are insensitive to changes in day length. They are also high-yielding, provided they receive correct amounts of fertilizer and water. Their capacity to use fertilizer efficiently arises from their dwarf stature: tall plants tend to fall over (lodge) when the grain-heads become heavy, but the short-stemmed varieties remain upright.

Under dry conditions and without adequate fertilizer, however, the new wheats may sometimes not produce as well as traditional varieties. They are largely disease-resistant, but to keep them so requires constant breeding work, because pests such as rust are capable of rapid genetic change

themselves, and a wheat resistant to a rust common when and where it was developed may find itself attacked within a few years, or in another region, by a different variety of the pest. This ability of the rust to change demonstrates a need for genetic diversity, not only between regions but also from farm to farm. It has even been suggested that there should be diversity within one stand, but this has not yet been practised.

In 1970 hopes for the new wheats ran high; many publications appeared (e.g. Brown 1970) heralding them as able to end the world's food shortages, if properly handled. But problems have appeared, many of which, called "second-generation problems", are social, and do not concern us here. The main hurdle, from the geneticist's viewpoint, is the energy crisis. The new wheats reach their genetic potential in yield only if they have appropriate supplies of fertilizer and water, and are protected against pests. Supply of fertilizer, water and pesticides requires power - power for the operations which produce or extract, then distribute, fertilizer, power to pump and distribute water, power to produce and spray pesticides. And power has become limited because of the energy crisis, forcing wheat breeders to look again at their varieties.

In some countries, seed from the new wheats was initially imported and sown over large areas, examples being (Brown loc. cit.):

1966	India	18,000 tons
1967	Pakistan	42,000 tons
1968	Turkey	22,000 tons

In others, including Australia, the Mexican wheats have been used as parents to derive locally adapted varieties, rather than for grain production themselves. In Australia the dwarf wheats yielded well, but their quality characteristics were unsuitable for the Australian wheat industry, which is largely based on "hard" wheat for bread-making. Only in 1974 were acceptable commercial varieties released in Australia which were based partly on Mexican dwarf wheats. Pugsley (1974) pointed out that this was 32 years after an International Conference on Rust in Wheat, held at Adelaide in

1892, had received a report on dwarf wheats (originally from Japan), and their possible use to prevent lodging.

#### Threatened Losses and Conservation - Wheat

Available genetic diversity contributed to success both for Farrer and the Mexican programme. But the thousands of varieties involved are eventually reduced to a few successful ones, which are sown over large areas. This has also been the case with other plants, notably rice, which has a story similar to that for wheat. The Rockefeller and Ford Foundations collaborated in 1962 with the Philippines Government to establish the International Rice Research Institute (IRRI) in the Philippines. Here 10,000 varieties were initially assembled, and again a few successful dwarf varieties were developed, once more dependent for success on correct applications of water fertilizer and pesticides, and so subject to power limitation as in the case of wheat.

The reduction of thousands of varieties to a successful few, together with the widespread use of these throughout the world and consequent displacement of traditional types, has concerned some breeders, who foresee a need to maintain stores of genetic diversity. Already, for example, it is necessary to look for varieties less dependent on exact application of water and fertilizer than the present CIMMYT and IRRI cereals. Breeding may suffer a serious loss of flexibility if traditional varieties, or even primitive varieties and wild types, are allowed to disappear.

The Russian plant geneticist N.I. Vavilov (1887-1943) first made a comprehensive study of the origin of cultivated plants, and suggested that "centres of diversity" existed in various parts of the world, containing concentrations of great variation in different species. He travelled widely, amassed an immense collection of cultivated plants, and was interested in the concept of using genes from a range of origins. Others have followed him in urging the establishment of collections to conserve plant genetic resources.

An Australian very active in this field is Sir Otto Frankel, now a Senior Research Fellow in CSIRO's Division of Plant Industry, who is a member of FAO's\* Expert Panel on Plant Exploration and Introduction, and has written widely on the need for conservation (e.g., Frankel and Bennett, 1970, Frankel, 1973, Frankel and Hawkes 1975). A working partnership between FAO and IBP\*\* was inaugurated in 1965, and resulted in an integration of effort. Two hand-books have been published (Frankel and Bennett loc. cit., FAO 1973), and another is in press (Frankel and Hawkes loc. cit.). Some Genetic Resources Centres now exist in the acknowledged centres of diversity, and others have to be created. In addition, various collections exist in other parts of the world. These cover a number of food plants, but not all, and tend to be mainly a storage of plant-breeders' products, though with some primitive varieties.

For wheat, Australia has a national collection at Tamworth, the curator of which is Mr. K. J. Symes, of the N.S.W. Department of Agriculture. The collection now has 17,500 varieties, from all wheat-growing areas of the world. The section on primitive species is not yet strong, but is to be built up. Farrer is not forgotten - most of his varieties are there, listed under a special code (Symes 1972, Single personal communication).

In Vavilov's collection, plants were re-grown every few years. Storage techniques are now sufficiently advanced to enable seeds of some species, including wheat, to be kept for long periods without re-growing, while computer systems have simplified information retrieval. Constant use is made of the Australian Wheat Collection; seeds are made available to breeders for developing new varieties, and plantings are made in different environments to obtain information on adaptation, though the harvests from these are not stored (Symes loc. cit.).

So much for genetic diversity in wheat, both between varieties and between individuals. What can we say about these levels of diversity in animals, particularly sheep?

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\* FAO - Food and Agriculture Organization of the United Nations.

\*\* IBP - International Biological Programme.

WITHIN-SPECIES VARIATION - ANIMALS

Sheep

Plant breeders divide their varieties into wild, primitive and developed, the last being further sub-divided into varieties of yesterday and those of to-day. Classification of sheep breeds is more difficult, partly because sheep are mobile and their owners in some parts of the world are nomadic; breed differences are not always clear-cut. Classification into wild and domestic types is simple, but the primitive/developed categories may overlap.

Wild sheep belonging to some 6 breeds still occur in different parts of the world. Their numbers are small, and they inhabit relatively inaccessible regions: Ovis ammon, high mountains from the Himalaya to Mongolia; O. musimon (mouflon), nearly extinct in its native Corsica and Sardinia but transferred successfully to European reserves; O. vignei (urial), Central Asia; O. orientalis, the Middle East, O. canadensis (bighorn), the Rockies; O. dalli, Alaska and N.W. Canada (Mason 1969).

Wild sheep grow a coat of stiff, coarse fibres ("hair"), similar to that of many goats, with only a small, shorter undercoat of what we would recognize as wool. They exist now mainly in nature reserves or parks, and although many experimental crosses have been made with domestic sheep, O. aries (see Gray 1972), no great material use has been made of them, except in U.S.S.R. For example, genes from wild sheep were introduced to domestic sheep in an attempt to improve adaptation to altitude in the mountains of Kazakhstan. A large arkhar (O. ammon) ram was shot there and his semen used on domestic ewes. The animal himself can be seen, stuffed, in a Moscow Exhibition.

The Russians are enthusiastic about returning to wild breeds for infusing extra vigour into domestic relatives, and in particular have studied skin development in wild sheep (Panfilova 1965). At Ascania Nova, in the Ukraine, there is a large zoological park containing various wild and domestic birds and animals, where many such crosses have been tried, including mouflon with domestic sheep, and zebra with horse.

Sheep were probably among the earliest animals domesticated, and their material uses are many and varied (Table 1). In Australia we are accustomed to think of the main locally-grown product as wool, and apparel wool at that; in other countries the wool may be grown not only for clothing, blankets and other fabrics, but for carpets, tents - and even harness; for example, in the special donkey market of Damascus one can buy belly-bands for donkeys made from Awassi wool. Other products in Australia are meat, skins, and, on just one farm, milk for cheese; around the Mediterranean and other parts of Europe, milk, for drinking or processing, is the main sheep product, while in the U.S.S.R., Iran and South Africa the woolled lambskin is the main source of income from the Karakul breed (Persian lamb or astrakhan). In Africa and India, woolless breeds provide meat and leather; in the narrow passes of the high Himalaya sheep are used for transport, while Lebanese farmers in the Beqa'a Valley will pay nomadic tribesmen to leave their sheep on the stubble of recently-harvested fields to manure the ground.

With this variety of uses, it is no wonder that large numbers of breeds have developed. The most useful classification is on coat type, which ranges from hair, with very little wool (similar to that of wild sheep) through to the fine, soft fibres of the Merino. The coat is dependent on the follicles in the skin from which the fibres grow.

These follicles are of two types, primary and secondary. The former are initiated and mature before birth; each has a complete set of accessory structures - sudoriferous (suint or sweat) and sebaceous (wax) glands and erector pili muscle. Secondary follicles are initiated before birth, later than the primaries, but some of them mature before, some after birth. Accessory structures for secondaries include only a sebaceous gland, and sometimes not even that.

Follicles have been studied both in horizontal and vertical skin sections. The measurement which gives greatest discrimination between breeds, made on horizontal sections at the sebaceous gland level, is the count of secondary and primary follicles per unit skin area, and in particular the ratio of number of secondaries to number of primaries. The differences in

average diameter between fibres from primary and secondary follicles also varies considerably between breeds.

All fibres are of the same substance, keratin, but fall into three main categories, wool, hair and kemp. Wool and hair (sometimes called "heterotype") fibres grow continuously, the difference between them being that hair has a "medulla" (tube of air down the centre, which can be continuous or interrupted), while wool is solid. Kemp is a medullated fibre which has been shed from its follicle, or else has an extremely large medulla. Fibre shedding is another characteristic which varies between breeds, ranging from a regular cyclical operation for wild and hair sheep to normally continuous growth for the fine wool Merino.

Sheep are classified on coat type as "hair" sheep or "woolled" sheep, with a further subdivision of fleeces from woolled sheep into "carpet wool" and "apparel wool", the main difference between the two being that carpet wool has a higher average fibre diameter and higher proportion of medullated fibres. This distinction applies on world markets; when fleeces are consumed locally, as with many village or nomad flocks, any available wool is used for whatever purpose is required.

Sheep growing mainly hair are usually not shorn, and the fibre is not regarded as a product. Carpet wool, with its high fibre diameter and high percentage of medullated fibres, is used commercially for carpets, rugs and felts, being often blended with coarse, low-priced apparel wool containing a lower percentage of medullated fibres (e.g., fleeces from the New Zealand Romney). The proportions of the two wool types used in the blend vary in different countries, and the exact role of medullation is not clearly understood; its main function is probably to lower costs by increasing the area of carpet obtained from a given weight of raw wool.

Apparel wool covers a wide range, from coarse wool with some medullation to fine wools with none; kemp is undesirable, as it is in all commercially used wool because it takes up dye differently from other fibres. Apparel wool is used for clothing, blankets and general textiles, depending on fibre diameter. Price depends on diameter, finer wools being higher-priced.

Examples of hair breeds with little or no wool are the Sudan Desert (Sudan), the Somali (Somalia) and the Nellore (India). The breeds are used for meat and skins, which make fine leather. The secondary/primary follicle ratio of hair breeds is around 1, and they have a low follicle count per unit skin area, with a large difference in diameter between fibres from primary and secondary follicles. Although fibres from the secondary follicles are seen in skin sections, they are often short and inconspicuous in the coat. A high proportion of the fibres from primary follicles are medullated. Data for the Nellore breed are in Table 3.

Insert Table 3 near here

Apparel wool breeds can be considered divided further into "Merinos and the rest", since the Merino is characterized by a secondary/primary follicle ratio sharply different from that of all other breeds. The Merino usually has a ratio of over 15, while for other breeds with no Merino blood it is less than 10. The evolutionary origin of this difference is not known. Associated with the high secondary/primary ratio the Merino has a high total follicle count, a fine fibre diameter, and a low difference in diameter between fibres from primary and secondary follicles.

Apparel wool breeds other than the Merino are classified further into longwool, downwool and crossbred (or coarsewool) types, breeds for the last not always being clearly defined. Because of the sharp differentiation of the Merino from all others, most countries classify all Merinos as "fine wool" breeds, but in Australia, where 76 percent of the 145 million sheep are Merino, there is a further subdivision into fine, medium and strong wool strains.

The percentage of medullated fibres in the fleece of apparel wool breeds ranges from zero in fine wool Merinos, through zero or a very low percentage in medium or strong wool Merinos, to a higher but still low percentage in other apparel wool breeds.

Carpet wools lie between hair and apparel wool breeds in follicle characteristics, and have a high percentage of medullated fibres (Table 3).

Within breeds, follicle characteristics are in general governed by many gene pairs, so that progeny lie half-way between their parents. Heritability is high, and follicle characteristics, fibre diameter or percent medullated fibres can be altered by selection of individuals. The difference between the Merino and other breeds in follicle characteristics, however, is too great for selection to be considered at present as a practical way of bridging the gap.

There are some exceptions to inheritance through many gene pairs; a single gene substitution changes the apparel wool fleece of the N.Z. Romney into carpet wool. A new breed, the Drysdale, has been developed, using this gene, and a healthy carpet industry has been based on it (Ross 1971). Other similar genes are currently being investigated, both in New Zealand and Australia.

Inheritance of follicle characteristics when breeds are crossed is not so clear. Crosses between apparel wool breeds have resulted in intermediate progeny (e.g., the Corriedale, from Merino and English Leicester), but crosses between apparel and either hair or carpet wool breeds have given differing results, the progeny sometimes being intermediate and sometimes showing dominance one way or the other (e.g., Burns, 1967, Rønningen and Gjedrem, 1970).

Although fleece types can be used to classify many sheep breeds, Mason and Maule (1960) found it impossible to use this criterion alone for breeds in eastern and southern Africa. All would be classed as hair or carpet wool breeds, but the fleece type was often too variable for separation. Instead these authors used tail type - thin-tailed, fat-tailed or fat-rumped. Fat-tailed and fat-rumped sheep occur also in other parts of the world, but are seldom seen in apparel wool breeds, unless these have been produced by grading-up from a fat-tailed or fat-rumped type.

The evolutionary value of fat storage in tail or rump is not clearly understood. Many experiments on tail-docking of lambs have been carried out, but usually with the aim of evaluating the effect on the meat carcass; the docked animals have been well fed. No results have been published

showing whether or not animals with docked tails can survive and produce as well as their undocked fellows when grazing or browsing in the field under nutritional stress.

Sheep breeds differ in characteristics other than those which we have been discussing, including, of course, size. One characteristic, which has been receiving considerable attention recently, is reproduction rate. Most sheep breeds lamb once a year, producing one, two or occasionally more lambs per birth. Even the Australian Merino has been known to produce up to 6, without hormone stimulation, but this is rare. There are a few breeds in the world, however, which regularly produce 2 to 3, and sometimes up to 5 or 6, lambs per birth. One is the Finn (from Finland), which has now been imported into many countries for crossing (e.g., Britain, U.S.A., South Africa, N.Z.). It is a small sheep, growing a white apparel wool of about 30 $\mu$  in diameter, and its average litter size is between 2 and 3 (Donald and Reed, 1967). The Romanov (from the U.S.S.R.) is a similar breed but with a pigmented fleece; it has been used for crossing in France.

Another highly prolific breed is the Chios (from Greece and Turkey, but called Sakis in the latter country), which has been crossed experimentally with the Awassi in Lebanon (Fox 1974). It grows a poor carpet wool fleece, has a long, slightly fat, tail, and again averages 2 to 3 lambs per birth.

The Finn and the Romanov normally lamb once a year; the Chios is normally lambed only once, but with good feed is capable of lambing twice a year. There are 4 other known breeds capable of lambing twice a year, with 2, 3 or 4 lambs each time. Two of these, the Hu and the Han, are in China (Epstein 1969): both are fat-tailed and produce carpet wool. Another, the Dalman (or D'Mane), is in Morocco; it is thin-tailed and its "fleece" is variable, some sheep having only hair and others varying amounts of short, coarse wool mixed with hair (Fallon 1974). The fourth prolific breed is the Priangan, in Java (Kilgour 1963). This is again thin-tailed and grows a light fleece of poor carpet wool (pigmented), but can lamb twice a year, with 2 to 3 lambs each time.

Although none of these highly prolific breeds would be especially valuable for characteristics other than fecundity, interest in them is considerable, because a higher reproduction rate is being widely sought everywhere to increase the sheep's productivity. There is no evidence, however, that the task of incorporating their genes into other breeds will be simplified by the presence of a single major gene; all crosses so far have indicated multigene inheritance.

Research is being directed towards determining why some sheep differ from others in fecundity. Comparison is being made not only of breeds (the Finn and British breeds, Land 1974) but also selected groups within one breed (Australian Merino) and between individuals within these groups (Packham and Triffitt, 1966, Bindon et al 1971, Bindon 1973). It is clear that ewes which are more prolific are shedding more eggs, and there are differences in the level of luteinizing hormone in the blood plasma. Rams from highly fecund groups also display a higher libido than those from groups with lower fecundity. This work may lead eventually to genetic manipulation which could tailor the sheep to a required fecundity level. Without genetically different sheep as research material, these investigations could not be made.

#### Threatened Losses and Conservation - Sheep

There is thus great genetic diversity at present among sheep breeds. But animal breeders, like plant breeders, are concerned about potential losses. Reasons for this are clear - genetic improvement is achieved through variation, and without variation there can be no further improvement.

FAO and the Commonwealth Bureau of Animal Breeding at Edinburgh have been interested in the question for many years. FAO in 1966 appointed an Expert Panel on Conservation of Animal Genetic Resources, which has published 4 reports, one on the general problem (FAO 1966), the others on cattle, pigs and poultry. The First World Conference on Genetics Applied to Livestock Production, held in Madrid in 1974, convened a Round Table on conservation, with papers from many animal breeders (Mason 1974, Bowman 1974, Epstein 1974, Majjala 1974, Sanchez Belda 1974, Laurans 1974).

Threats to existing genetic diversity in domestic animals can occur from two directions:

1. Loss of genes within a breed by intense selection, particularly if artificial insemination is used, or by random drift if populations are small,
2. Loss of whole breeds through replacement by others thought to be superior in productivity.

Loss of genes within a breed is, so far, less serious with sheep than with cattle. The widespread use of progeny-tested bulls, and the development of frozen semen banks for storage, have intensified a problem envisaged by Edwards as long ago as 1959. Australia herself has probably suffered from using too few sires in recent imports of frozen cattle semen.

Loss of whole sheep breeds is a much more serious threat at present. As mentioned earlier, average fibre diameter is the most important processing characteristic, fine wool being preferred. During the last few decades there have been widespread programmes aimed at replacing hair, carpet wool or coarse apparel wool breeds with ones producing finer wool. Because of the Merino's outstanding fleece characteristics, various Merino types have been used for crossing.

This work has had varying success, partly because of the range of climatic and environmental conditions under which the replaced breeds are grown. Hair breeds are indigenous in hot, tropical areas, some with high, some with low rainfall, situated in Africa and India. Carpet wool and coarse apparel wool breeds belong to the same areas and to similar ones in the Middle East and Asia, but also to cooler regions in Europe and Asia. (The Americas, like Australia, had no indigenous domestic sheep; the "wool" of the Incas came from alpaca and vicuña).

The Merino is certainly a very adaptable breed, being grown in all sheep areas of Australia, but its productivity varies. In the northern parts of Australia, clean wool weights for medium wool Merinos average only 1.4 to 2.3 kg, compared with 2.3 to 2.7 kg in the pastoral areas of N.S.W., while the corresponding lamb-marking percentages (lambs marked for every hundred ewes mated) are 20 to 50 and 60 to 80 (Brown and Williams 1970).

The Merino, or its derivatives, have been successfully used for up-grading in the cooler regions of the world - for example, in the U.S.S.R., Turkey, the Himalayan foothills, the highlands of Kenya, and Inner Mongolia. In the hot Indian plains, neither the Merino nor its half-bred, the Corriedale, has been very successful.

Instigators of plans for breed changes are interested not only in seeking finer wool, but in improving sheep productivity. The average clean wool weight per head for all adult sheep in Australia is 2.3 to 2.8 kg, compared with 1.0 to 2.0 kg for carpet wool breeds in various parts of the world. Frequently this difference has been taken at its face value, and the assumption made that the Merino (or any other introduced breed) will automatically improve production, with no comparison of an introduced breed, and its crosses, against the indigenous breed to be replaced. Performance of a breed in its homeland is no indication of how it will fare when transplanted elsewhere, and an indigenous breed may possess valuable genes for survival in its own environment. At a Sheep and Forage Workshop conducted by the Ford Foundation Arid Lands Agricultural Development Programme at Beirut (Ford Foundation 1974), the Sheep Breeding Panel passed a unanimous resolution, adopted later by the whole Workshop, that no widespread crossing of an introduced breed should be made until that breed and its crosses had been tested against indigenous breeds in the latter's environment. Delegates at the Workshop came from the Middle East and North Africa, regions with a large number of breeds, many with low productivity.

Testing productivity, however, caters only for material needs in a particular place at a particular time. Requirements may change, the environment may change, or other parts of the world may need a sheep breed not particularly valued in its homeland. The shepherds of Inner Mongolia, for example, have kept some of their carpet wool sheep uncrossed with fine wools because the fleeces of their indigenous sheep are more suitable for lining their heavy overcoats. There is already a shortage of carpet wool in the world because of crossing programmes, and this should stay the hand of cross-breeders, or stimulate production elsewhere. The hair and carpet breeds

of tropical regions are likely to be sought by countries without indigenous sheep, to start a new industry or replace an unsatisfactory introduced breed. South Africa has developed a new woolless breed (Dorper) for dry regions with spiny vegetation, by crossing two introduced breeds, Somali (called in South Africa Blackhead Persian) and Dorset. The use of carpet or hair breeds in tropical Australia has already been suggested (Turner 1971b), while hair breeds, which require neither shearing nor blowfly control, were advocated by many during the slump in wool prices early this decade.

Varying material needs may thus save some of the existing sheep breeds from disappearing, but not all. Arguments rage, of course, about the need for conservation. Those opposed to it fall into two main camps - the extremists who argue that sheep (and other livestock) will not be needed at all in the future, and the less extreme who think that a breed is not worth conserving unless retention is automatically dictated by material needs. Those in favour of conservation would agree with my title - that we can see the need for some breeds, but other genetic resources are hidden treasure, whose value may not be obvious at present. Let us examine the three types of argument.

First, consider those who say that livestock cannot be afforded in future because of pressures on land - food can be obtained from plants or micro-organisms, clothing from man-made fibres, and so on. As far as food is concerned, there have indeed been many analyses pointing out that a far greater quantity of vegetable than animal protein can be produced per hectare of arable land, the ratio sometimes being as high as 5-10 to 1, depending on the type of production considered. But the key word is arable land. Certainly if livestock are to be fed on grain to produce meat for human consumption, it would be more efficient to give the grain straight to the human population. But plant protein production requires water and a certain level of soil fertility, as the "second generation" problems of the "green revolution" have amply demonstrated. There are many regions of the world which will support grazing or browsing animals, but will not grow plant protein suitable for human consumption. It is hard to obtain an exact measure of the extent of such regions, but one estimate gives the area as

double that of arable land. Further, livestock can be fed industrial wastes unsuitable for humans, while the other source of protein, micro-organisms, depends in some cases on the petro-chemical industry, already shown to have finite resources.

Those who have argued in favour of concentrating on production of plant protein have been mainly agricultural workers or economists from the developed world, discussing how to feed developing countries which so far have been unable to grow enough food for themselves. But what has happened when those developing countries have set out to improve their own conditions?

Search for oil in Libya and Saudi Arabia has revealed vast underground reserves of water. This is being brought to the surface and used for irrigation. For growing only plant protein? Certainly not. Each country has a very large sheep breeding project to produce sheep meat, planned to involve tens of thousands of breeding ewes. In Libya, the Kufra Project has installed vast irrigation sprays, rotating slowly in circles, and producing rosettes of brilliant green in the Saharan sands. In Saudi Arabia, more conventional channel-type irrigation is being used. Both projects are in their early days, and it is too soon to say when their objectives will be achieved. The point is, now that they have resources and money, these countries have elected to try and increase their meat supplies, and have not chosen to rely on vegetable protein, or even protein from micro-organisms. Iran is also using some of her oil money to increase sheep meat supplies, both by growing more of her own and by building cold stores to handle imported carcasses.

The People's Republic of China can perhaps be cited as a country which has been working hard at its own overall plans to improve living conditions for all its people. Here plans include increased livestock improvement and increased numbers (particularly in relation to sheep), as well as increased grain production. A pragmatic people like the Chinese, with limited areas of usable land, might well have opted for alternative sources of protein, if this were really the final acceptable answer.

Synthetic meats to replace mutton, and man-made fibres to replace wool, have been cited as signifying the doom of sheep in the years to come.

Perhaps they may help to provide some of the extra food and clothing for the increasing world population. There is not time to deal with these developments in detail, and others are more competent than I to do so, but one reference is worth making. Economic forecasts are notoriously difficult and untrustworthy, but FAO does attempt to give some lead about demand and supply of agricultural products. Its forecasts for 1980 indicate that the world demand for wool will remain at the 1970 level, while the demand for sheep meat will exceed supply (FAO 1971 - Table 4). This is only a short-term forecast, but it does indicate that livestock are not likely to disappear suddenly.

Insert Table 4

The second argument against conservation is that effort should not be expended on deliberate conservation; if a breed is worth having, because of high productivity or a wanted product, it will automatically be retained. This point of view is based too much on material needs here and now; it ignores the existence of cultural needs, and of differing material needs in other times and other places, as we discussed earlier. The Finn breed, for example, was facing extinction in its own land before other countries became intensely interested in its prolificacy (Maijala 1970).

If it be agreed that we have a responsibility to maintain genes for future generations, which breeds should be saved, and how?

One problem is the lack of documentation about the particular characteristics of a number of breeds. FAO and the Commonwealth Bureau of Animal Breeding have again been trying to fill this gap, with a number of publications (Mason, 1967 and 1969, Mason and Maule 1960, Epstein 1969). Mason (1974) pointed out what an enormous task it would be for any central agency to collect the necessary data for cataloguing all breeds and then to provide information on demand. Turton (1974) outlined the computer services now being used by the Commonwealth Bureau of Animal Breeding to collate data from abstracts. Mason further stated that FAO is hoping to extend the areas covered by its catalogues to southern Asia, U.S.S.R. and Latin America.

Even before this further information becomes catalogued, however,

Mason felt some categories of livestock could be listed immediately as deserving of special conservation efforts. These are:

1. Indigenous breeds uniquely adapted to their environment, or showing high levels of hybrid vigour in crosses,
2. Highly productive breeds little known outside their own country,
3. Genetically unique breeds,
4. Bizarre or beautiful breeds,
5. Historically important breeds.

Examples of sheep breeds in these categories are: Under (1), the seaweed-eating sheep of some Atlantic islands; under (2), the highly prolific breeds already discussed; under (4), piebald Jacob's sheep; and under (5), the French Rambouillet.

Fortunately some countries have already decided to take action on conservation. The Bulgarian Government is paying various farms round the country to retain flocks of the 20-odd native breeds before all have disappeared under improvement schemes (Hinkovski, 1975), while Bowman (1974) describes steps being taken to place groups of sheep from diminishing breeds in farm-parks in Britain.

This brings us to the question of how breeds are to be conserved. The task for animals is more difficult than for plants. Seeds of many plants can now be stored for long periods, but although semen can be frozen and stored for long periods for some species (e.g. cattle), the technique is not yet perfected for all; for sheep in particular use of frozen semen has not always been successful. Storage of fertilized ova is still a long way off, though it may eventually be feasible. Mason (1974) regards maintenance of groups of animals as the most valuable method of conservation, since the animals are then accessible, either for recreation (visits by the public in parks), research, or use in cross-breeding.

It is to be hoped that more countries, and more people, will come to realize that animals are as much part of our cultural heritage as our ancient documents and buildings. But reasons for conservation are not only

cultural - we may need to turn back the clock a little, as the wheat breeders have had to do, to breed for new needs or tougher conditions. This we cannot do without maintaining genetic variation.

Let me conclude with thoughts on a passage from Shakespeare:

"Sweet are the uses of adversity

.....

And this our life exempt from public haunt  
Finds tongues in trees, books in the running brooks,  
Sermons in stones, and good in everything".

There will not be good in every sheep breed, but we could well find good in a number of them, though it may be hidden now. And I would paraphrase the first line of the quotation to:

"Sweet are the uses of diversity".

Farrer realized it with his wheats - let us follow him, not only for plant and animal breeding, but in applying the same concept to a species not yet discussed, Homo sapiens. I am not suggesting genetic manipulation of human races, but a full and unprejudiced acceptance of the tremendous cultural value to man of his own genetic diversity.

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TABLE 1

Types of domestic animals and their contribution to man's material needs

Animal type	Contribution
Buffalo	Traction, transport, meat, milk, leather, horn
Camels:	
Alpaca	Textile fibre, meat
Camel	Traction, transport, meat, milk, fats, textile and other fibre, leather, fuel, fertilizer (bone and dung)
Llama	Transport, textile fibre, meat
Vicuña	Textile fibre
Cat	Hunting (of rodents)
Cattle	Traction, transport, meat, milk, fats, leather, textile and other fibre, fertilizer (bone and dung) fuel, horn, glue, blood (for food and for serum in biological products)
Dog	Transport, meat, hunting (for food), guarding (man or animals), working (cattle or sheep), guiding (the blind), tracking.
Elephant	Traction, transport, ivory
Equines:	
Ass	Traction, transport, meat, milk, leather, fuel
Horse	Traction, transport, meat, milk, leather, fibre (hair from mane and tail), fuel, fertilizer, blood (for serum)
Mule	Traction, transport, fertilizer
Fur-bearers:	
Chincilla, ermine, fox, marten, mink and sable	Fur
Goat	Meat, milk, textile and other fibre, leather, fertilizer, horn, blood (for serum)
Monkey	Harvesting (coconuts)
Pig	Meat, leather, bristle, fats
Reindeer	Traction, transport, milk, meat, leather, textile and other fibre
Rabbit	Meat, textile fibre, fur, laboratory animal, (biological products)
Rodents:	
Ferret	Hunting (for food)
Guinea-pig	Meat, textile fibre, laboratory animal (for preparation of biological products)
Hamster	Laboratory animal (biological products), fur
House	Laboratory animal (biological products)
Rat	Laboratory animal (biological products)
Sheep	Textile and other fibres, meat, milk, fats, leather, fur, fuel, fertilizer, horn, transport
Yak	Transport, textile fibre, meat, milk, leather

Reprinted from Turner (1971a) by courtesy of "Outlook on Agriculture"

TABLE 2

World distribution of types of domestic animals

Type	Regions where found	
	Indigenous, or introduced at least 500 years ago	Introduced within last 500 years
Buffalo	South-east Europe, North Africa, Middle East, Southern USSR, Pakistan, India, Ceylon, South-east Asia, China, Indonesia, Philippines	Northern Australia (mostly feral, but re-domestication beginning)
Camels:		
Alpaca	Andean countries of South America	
Camel	North Africa, Middle East, Pakistan, India, China	Australia (formerly used for transport, now mainly feral)
Llama	Andean countries of South America	Introduction attempted in Australia, but failed
Vicuña	Andean countries of South America	
Cat	Widespread	Widespread
Cattle	Widespread	Widespread
Dog	Widespread	Widespread
Elephant	India, Burma, Ceylon	
Equines:		
Ass	Ireland, Mediterranean, Europe, Middle East	Central America, Northern Australia (formerly used for transport, now mainly feral)
Horse	Widespread	Widespread
Mule	Widespread	Widespread
Fur-bearers	Northern Europe, USSR	Australia, North America, South Africa, Israel
Goat	Widespread	Widespread
Pig	Widespread	Widespread
Reindeer	Northern Europe, Northern Asia	
Rabbit	Widespread	Widespread
Rodents:		
Ferret	Europe	Australia
Hamster	Europe	North America
Guinea pig	Europe, Peru	Australia
Mouse	Widespread	Widespread
Rat	Widespread	Widespread
Sheep	Widespread	Widespread
Yak	Northern India, Southern China	

TABLE 3

Follicle and fibre characteristics for some sheep types  
(Approximate means of breed means)

Fleece type	Breed or strain type	Total no. follicles per mm <sup>2</sup>	Ratio secondary to primary follicles (No.)	Mean fibre diameter $\mu$	Ratio primary to secondary follicle diameter	Percent medullated fibres	Reference
Hair	Nellore (India)	6	1.7	59.1	5.3	34	2
Carpet wool	Bikaneri (India)	10	1.5	34.4	1.6	60	2,3
	U.K. breeds	10	3.3	39.7	2.8	n.a.*	1
Apparel wool	Merino: (Australia) Fine	70	19.6	17.5	1.1	nil	1
	Medium	62	21.4	20.8	1.2	nil	1
	Strong	57	17.0	24.0	1.3	nil	1
	Down wool (U.K.)	21	5.5	28.7	1.0	n.a.	1
	Long wool (U.K.)	17	5.0	37.5	1.3	n.a.	1

\* no figure available

1. Carter and Clarke (1957); 2. Krishnarao et al (1960)
3. Narayan (1960)

TABLE 4

Meat - World demand and supply  
 (FAO Agricultural Commodity Projections, 1971)

Type of meat	Year	Tons (millions)		
		Demand	Supply	Difference (Supply-demand)
Beef and veal	1970	39.7	40.0	+0.3
	1980	53.4	51.7	-1.7
Mutton and lamb	1970	7.2	7.2	0
	1980	10.0	9.4	-0.6
Pigmeat	1970	35.1	35.1	0
	1980	45.7	45.8	+0.1
Total	1970	82.0	82.3	+0.3
	1980	109.1	106.9	-2.2