Introduction

Thirty-five years ago, prolific sheep were only known to a few breeders in isolated areas of the world, where the sheep industry was only secondary. Chance played a big role in the discovery and recognition of prolific sheep. The intensification of sheep production in certain areas of several countries required sheep with high fertility, prolificacy and extended breeding season to offset the higher cost of production associated with such intensive systems. The classical work on improving prolificacy in sheep by selection indicated that the methods used were not fast or effective enough in increasing reproductive efficiency. Crossing with what were then considered as prolific sheep, breeds with average rates of about 200, brought about moderate increases in prolificacy in the crosses, but emphasis was kept on ovulation rate and lambs born rather than on lambs weaned. Therefore, discovering sheep which showed natural super prolificacy was bound to have an immediate and great impact on the sheep industry of most of the major producing countries in the world.

The severe restrictions on importing sheep from Europe delayed the introduction of European prolific sheep into Australia and New Zealand. However, the discovery of prolific Merino strains in Australia, and the identification of the Booroola gene, resulted in a parallel interest in prolificacy in Australia and New Zealand. Prolific breeds native to Asia and Africa were recognized and studied only after the importance of prolificacy became apparent. Also after prolific sheep from temperate regions introduced into tropical and subtropical regions failed to achieve their high performance due to the severe hot and dry climate, different feeding and management practices and emphasis on number of lambs born.
The prolific breeds discovered in the 1960s and 1970s were scarcely investigated and apart from the observed high productivity, little has been known on their other characteristics. Also, these breeds were rarely crossed with other breeds, so their performance in crossbreeding was also unknown. With increased interest in the prolific breeds, studies to investigate their performance were initiated. The effect of these studies was an increase in prolific sheep popularity and their widespread importation into different countries. There, they were studied under different environments and crossed with a variety of local breeds. At present, there is a wealth of information on what prolific breeds can achieve experimentally and commercially. In addition, many new breeds more suitable for the local conditions were developed utilizing genes from the prolific sheep as a source of prolificacy and genes from the local breeds as a source of adaptability. However, emphasis was usually given to producing animals with one quarter high-fertility blood and one-time gains, rather than establishing a long-term objective and developing genotypes accordingly.

The discovery that prolificacy can also be caused by major genes has had a strong impact, since prolificacy could be maintained after backcrossing to offset undesirable traits inherited from the prolific sheep. The discovery of several breeds with major genes for prolificacy indicated that the process of prolificacy, though complex, can be changed drastically with minor interventions from man through planned manipulation of these major genes. However, the introduction of single powerful genes into a complex system depending on a multiplicity of genes can be disruptive.

Highly prolific breeds can be as successful under extensive grazing conditions as under intensive production systems (Erkanbrack and Knight, 1995). In fact, the effect of selection for survival to weaning under extensive conditions was almost as important as selection for prolificacy itself in increasing the number of lambs weaned or marketed per ewe or per acre, which is reproductive efficiency.

The importance of small ruminants in general, and high-fertility breeds in particular, is greatly increased as the world is failing to keep food production up with population growth. This decline in per capita food production, under way for about 10 years now, has not yet resulted in food shortages in developed countries but may do so with the next severe widespread drought. This decline in per capita food production seems due to low farm prices, generally below the cost of production, which is resulting in loss of family farmers and also in abandonment of considerable farm land each year. On the other hand, retail prices for food consumed are increasing, resulting in some suppression of food consumption. These negative trends can only result in human disaster if not reversed.

Most field crops have already reached their practical genetic limits in efficiency as also has poultry meat. Swine are increasing in efficiency but will soon reach their practical genetic limit. Both poultry and swine as
well as feedlot beef depend on feeding grains. Accordingly, if the downward trend in feed grain production continues, chicken and pork and possibly beef will most probably also decline. Small ruminants offer the best possibility to bring farm families back, as they can continue to increase in reproductive efficiency for the next 50 to 100 years. Small ruminants have another advantage in that production can be started with only a few females and almost any kind of land, which means a very low initial investment. This advantage does not hold for almost any other form of food production. Thus, family farmers have an opportunity to return to food production largely with small ruminants. The already high reproduction efficiency of many small ruminants, especially the high-fertility breeds, makes this alternative highly attractive. However, there are many more research opportunities to further increase the efficiency of small ruminants to produce food and fibre. In every case, emphasis should be kept on efficiency and profitability. The purpose of this chapter is to describe these future research opportunities roughly in order of their priority.

Future Research Opportunities

*Introduction — Selection for reproductive efficiency is no longer slow*

The new selection technology developed by Erkanbrack and Knight (1995) shows that selection for reproductive efficiency in sheep can not only be highly effective under extensive range conditions but also can be as much as several times as effective as selection on a calculated index. Briefly, this technology involves use of weaning litter weight or number as the selection index which is much more effective than use of an index calculated from various production traits. Then, ram lambs are selected on their mother's average lifetime production and the change from ram lamb father to son is made each year. This rapid selection can result in gain in reproductive efficiency of as much as 5% per year. Gains in net returns can be much higher: if net returns are 20% of overall production, the gain in net returns may be as much as 25% per year. Little increase in feed is required as adults may be reduced as numbers of young are increased.

The new rapid selection technology can be applied more effectively and completely on research stations than on farms (Erkanbrack and Knight, 1995). This permits moving the genetic level of reproductive efficiency of high-fertility breeds upward more rapidly in research flocks than in the industry. Thus, sale of breeding stock, especially ram lambs, to breeders and producers can increase efficiency and net returns at a more rapid rate (Terrill, 1989). The US Sheep Industry increased something like 10% in reproductive efficiency in the 1980s largely from rapid selection, while there has been little or no impact of biotechnology on the industry yet.
We need to concentrate on maximizing rate of progress in spite of the low heritability of prolificacy and to give more attention to selection for survival to weaning.

**Select for feed efficiency**

Primary selection should be directed to reproductive efficiency and secondary selection to feed efficiency. The improvement of feed efficiency along with reproductive efficiency is important because increased feed efficiency not only increases net returns but it also is closely related to rate of gain of the lambs and with high lean content of the carcass (Erkanbrack and Knight, 1988). Selection for feed efficiency is expensive and meticulous and can best be done on an experimental farm. Its close relationship to net returns and to meat quality justifies research attention.

**Improve meat from prolific breeds and crosses**

Studies generally indicated that carcasses from prolific sheep are inferior to those from meat-type breeds, and crosses inherit the undesirable traits from their prolific parents. Examples of these are: poor conformation, greater fat deposition in body cavity and reduced fat cover on the carcass, higher proportions of the anterior parts of the carcass, and poor dressing percentages of north European prolific breeds. Meat from these breeds is also sometimes characterized by undesirable strong flavour. Prolific sheep from the tropics and subtropics are also poor in carcass conformation and have slow growth rate. Research is urgently needed to improve carcass and meat quality. The *callipyge* gene may have some effect on improving meatiness and reducing fat in prolific sheep (Jackson *et al.*, 1994; Snowder *et al.*, 1994), but is probably already receiving adequate research attention.

Needed selection should emphasize improvement of lamb meat flavour. High priority should be given to prevention of strong or undesirable flavours, as such might turn consumers away from lamb consumption. The chemical basis for desirable and undesirable flavours should be determined, but priority should be given to selection for desirable flavours or against undesirable flavours, as soon as possible. In addition, selection pressure should be for minimum fat content, both external and internal, and for higher proportions of desirable lean cuts such as the loin and leg. Also, the effect of feeding diets such as canola on reducing saturated fat in the carcass, deserves attention.

**Import more high-fertility breeds**

The multiplicity of ecosystem areas in North America and other regions in the world, indicates that many breeds can be accommodated and that total ewe numbers will probably increase in time by millions. Population growth is increasing in the world while food production is generally declining. Thus, a rapid increase of reproductive efficiency should accompany increases in ewe numbers. Sheep have the capacity to increase
in both efficiency and numbers somewhat independently.

High-fertility breed comparisons should be made in different ecosystems to provide farmers with guidelines for their choice of breed. High-fertility breeds can best be compared when under rapid selection as the rate of increase in efficiency, under the same selection pressure, may vary with breeds as well as with ecosystems. Likewise, comparisons on research farms may be more reliable than those farmers are able to make.

One prolific breed which deserves special attention and consideration is the Cambridge breed developed in the United Kingdom (Owen, Subchapter 3.10). Its development began with the screening of foundation ewes from a variety of breeds. Then, effective selection practices, beginning with Cambridge at 1 year of age, were used to develop not only a high prolificacy but quite acceptable milk and wool production. Their prolificacy and survival to 50 days indicate that they would be capable of almost doubling ewe numbers every year and they would be likely to be highly profitable in most temperate ecosystems.

**Production of transgenic sheep**

Although the use of transgenetic sheep to increase reproductive efficiency may not be useful for small ruminants because of the complexity of the traits and their probable dependence on multiple genes, transgenes may be very useful and effective in aiding selection improvement of small ruminants (Terrill, 1988).

Transgenes have been introduced into the sheep genome and have proved to be expressible and heritable (Rexroad et al., 1989; Ward et al., 1993). Improvement of high-fertility breeds may be facilitated by use of transgenes, by nuclear transfer to increase the number of offspring of highly productive ewes and thus to increase selection differentials and to decrease generation intervals on the female side.

The presence of major genes for high fertility in sheep offers an opportunity to demonstrate the comparative use of selection alone for reproductive efficiency and selection with transgenic introductions of the major genes for high fertility.

**Technology to produce identical siblings**

Technology should be improved to split embryos to provide identical siblings for destructive testing to facilitate selection for traits such as carcass merit or resistance to internal parasites and disease (Willadsen and Polge, 1981; Utsumi et al., 1988). Also embryos can be cloned by nuclear transplantation (Seidel, 1989). The 16 nuclei in a 16-cell embryo could be transplanted into 16 one-cell embryos in which the original genes had been destroyed. Ewes with high productivity can produce the original embryos while ewes with low success can be used to develop the multiple identical offspring. A few identical offspring might be obtained so that one or more could be used in breeding and the others could be used for testing which requires killing the individual. Until the chemistry of meat
flavour is better understood, taste panels requiring cuts of meat would be essential.

Adapt high-fertility breeds to the ‘STAR’ system of lambing

Producers lambing once a year at presumably the optimum time of the year can gradually shift to lambing every 7 months or about five times in 3 years under the STAR system. The Cornell University, Mt Pleasant flock, under the STAR system with Finnsheep-Dorset cross ewes is producing about three times the United States average or about three lambs per ewe per year (Hogue, 1995). Ewe lambs are bred at about 7 months and lamb at 1 year in the same month of their own birth. Lambing is done in a large shed and the lambs remain under cover to market time. Ewes that lamb in the system successfully are kept in the system, and those that fail are either sold or dropped back to once a year lambing. Of course, feeding and management must be adjusted to both these systems. This transition through selection for adaptation to the system can be done more effectively on a research station than on farms.

Develop multi-nipple trait in sheep

The multi-nipple trait has been shown to be highly heritable and well suited to multiple lamb rearing (Kovrennev, 1966; Majala and Kyle, 1988). Development of four- or six-teated ewes of superior milk production should be accomplished by selection before the average litter size in high-fertility sheep breeds reaches those levels. The weaning of litters of four to six lambs by the ewe mothers would greatly increase sheep reproductive efficiency. The success in developing the Wealdin Four-quarter sheep in the United Kingdom (Hope 1993, Subchapter 3.13) can be used as an example. Transgenic efforts might be helpful in this regard.

Improving wool production and quality of high-fertility breeds

In general, fur and pelt quality of lambs from prolific Romanov and Finnsheep is superior, but wool production and fleece characteristics of these breeds is inferior to those of other less prolific breeds. Little attention to this aspect of production has been given in the past and it needs much more attention in the future. The efforts to eliminate fleece colour of Romanov sheep in developing a strain of White Romanov by crossing with Romnelet at Agriculture and Agri-Food Canada station at Lethbridge, Alberta, is a positive effort in the right direction. Strains of fine-wool, medium wool, and carpet wool Romanovs could be developed in the same way using Rambouillet, Columbia, Navajo-Churro, or similar white breeds, respectively, as sources of white wool genes.

Likewise a variety of coloured strains, from white to black, of high-fertility breeds with high-quality carpet wool, well suited to hand processing, should be developed. Retired people are living longer and the hand processing of wool provides an attractive and satisfying avocation.
Improve adaptability of prolific sheep in hot and dry conditions

The few studies conducted on temperate prolific sheep imported into subtropical conditions indicated unfavourable adaptability of these breeds to the hot and dry conditions. Most of these studies were also conducted under unfavourable feeding and management conditions, which might have had confounding effects on the outcome of the studies. More research is needed under controlled environment to assess the adaptability of these temperate breeds to subtropical conditions. Study of the adaptability of prolific breeds from the subtropics to temperate areas is also needed.

Develop new triple-purpose high-fertility breeds

It is possible with present available knowledge on the characteristics and performance of the different prolific breeds to combine genotypes and develop new breeds with superior meat, wool, and milk production. By developing such new breeds under different nutritional and climatic conditions, the newly developed breeds can fit within different ecosystems.

Increase genetic variability

Research is needed to determine optimum number of ewes in a closed breeding group to retain adequate genetic variability. Also needed is investigation of ways of increasing genetic variability in high-fertility breeds, possibly through transgenic research to prolong the limits to reproductive efficiency.

Improve forages for small ruminants

Research efforts should be directed to improve forages, especially alfalfa, for small ruminants to increase year-round forage quality and carrying capacity for both grazing and hay production in each important ecosystem area. Attention should also be given to fast-growing trees and shrubs, not only to decrease erosion on slopes and gulleys, but also to provide useful feed for sheep and goats.

Apply preceding proposals to the Boer goat

The Boer goat probably already has superior meat conformation and somewhat high-fertility as compared with other sheep and goat breeds. Further improvement by application of the preceding proposals is highly desirable.

Other research with lower priority

Much is to be learned yet on nutrition and managing growth, reproductive physiology and behaviour of high-fertility sheep, but consider-
able research is under way on these aspects and priority must now be
given to those aspects already listed which will probably have greatest
impact on reproductive efficiency and net returns.

Very little information is available on the performance of prolific
genotypes under systems ranging from plain-air to total confinement.
More research is needed in this area, combined with complete economic
evaluation, including simulation studies, to identify the optimum system
for raising prolific sheep.

Progress in genome mapping is being reported continuously (Broad
and Hill, 1994), yet the sheep genetic map lags behind those of all the
other livestock and poultry. More advanced genetic mapping would
help locate the major genes and find suitable gene markers. More
research in molecular genetics is needed to find useful major genes, and
means to identify valuable alleles and use them. With this developed,
a continuous need will exist for developing genetic markers to identify
carrier animals.

Despite the efforts in Australia and New Zealand to investigate the
reproductive physiology of Booroola, and the European efforts to
investigate the Finn sheep and Romanov, present knowledge is still
scanty. For example, research is needed to explain the streak ovary
condition in the Romney sheep with the $\text{FecX}$ gene in New Zealand
(see Subchapter 3.11).

A major problem with prolific sheep is the high lamb mortality
and slow growth rate of prolific lambs. Many of these problems are
associated with the behaviour of the ewe and the newborn lambs at
parturition and during nursing. Information on the process of parturi-
tion and the interaction between the ewe and its newborn lamb should
help us to understand the causes of loss and means to prevent their
occurrence.

Prospects for the Future

With the continuous evolution of prolific sheep, discovery and develop-
ment of new breeds, conservation of endangered and rare prolific breeds,
it is not unlikely that, within the next few decades, prolific sheep will
be raised and used in all advanced sheep-producing countries and those
with developing sheep industries. The continuous research efforts will
help find solutions to the present problems of prolific sheep. Finally, the
countries which adopt a policy of a moratorium on exporting their
prolific genotypes will realize that it is to the advantage of everyone to
reverse these policies and adopt open ones.

The increasing demand for food and the continued human population
growth will probably lead to marked increases in small ruminant
populations. The continual development and improvement of high-
fertility breeds of sheep and goats will help make these increases
adequate for the human species.
A century from now we shall probably find prolific sheep everywhere, adapted to the different climatic and management situations, to provide the increasing population with much needed meat, milk, wool and fertilizers.

References


production of monozygotic identical goat twins from split embryos. *Memoirs of the College of Agriculture, Kyoto University* 131, 1–6.
