

## New Zealand Society of Animal Production online archive

This paper is from the New Zealand Society for Animal Production online archive. NZSAP holds a regular annual conference in June or July each year for the presentation of technical and applied topics in animal production. NZSAP plays an important role as a forum fostering research in all areas of animal production including production systems, nutrition, meat science, animal welfare, wool science, animal breeding and genetics.

An invitation is extended to all those involved in the field of animal production to apply for membership of the New Zealand Society of Animal Production at our website [www.nzsap.org.nz](http://www.nzsap.org.nz)

[View All Proceedings](#)

[Next Conference](#)

[Join NZSAP](#)

The New Zealand Society of Animal Production in publishing the conference proceedings is engaged in disseminating information, not rendering professional advice or services. The views expressed herein do not necessarily represent the views of the New Zealand Society of Animal Production and the New Zealand Society of Animal Production expressly disclaims any form of liability with respect to anything done or omitted to be done in reliance upon the contents of these proceedings.

This work is licensed under a [Creative Commons Attribution-NonCommercial-NoDerivatives 4.0 International License](http://creativecommons.org/licenses/by-nc-nd/4.0/).



You are free to:

**Share**— copy and redistribute the material in any medium or format

Under the following terms:

**Attribution** — You must give [appropriate credit](#), provide a link to the license, and [indicate if changes were made](#). You may do so in any reasonable manner, but not in any way that suggests the licensor endorses you or your use.

**NonCommercial** — You may not use the material for [commercial purposes](#).

**NoDerivatives** — If you [remix, transform, or build upon](#) the material, you may not distribute the modified material.

<http://creativecommons.org.nz/licences/licences-explained/>

## Is there an association between dam live weight and litter structure in a flock of grazing Perendale sheep?

R.M.W. SUMNER\*, H.V. HENDERSON and A.M. SHEPPARD

AgResearch Ruakura, Private Bag 3123, Hamilton 3240, New Zealand

\*Corresponding author: roland.sumner@xtra.co.nz

### ABSTRACT

Observational data from a grazing Perendale flock collected between 1985 and 2002 were analysed to investigate whether there was any association between variation in pasture availability over the summer, as reflected in live weight at joining and/or liveweight change between weaning and the subsequent joining, in association with litters of different sizes and sex structure, and the sex ratio of lambs born during the following spring, under pastoral farming conditions. The flock was managed at Whatawhata Research Centre until 1997 and thereafter at Winchmore Research Station. Data for a total of 3,516 lambs were analysed. Between year variation and variation associated with all the assessed factors, was consistent with chance variation. The proportion of males born was not significantly different from 0.50. Ewe age was significant at Winchmore when adjusted for lambing year, and litter size in both the previous and current lambings and liveweight change of the dam between weaning and joining, with more males born to mature ewes. Three percent more male than female lambs died between birth and weaning at both locations. It is unlikely sheep farmers can consistently influence the sex ratio of their lamb crop through changes in their flock management procedures.

**Keywords:** Perendale sheep; sex ratio; dam live weight; dam liveweight change; litter structure.

### INTRODUCTION

Male and female animals differ in their relevance within different farming systems. In New Zealand sheep are farmed to produce meat and wool. Meat production utilises young rams and ewes and cull adult ewes, while approximately two thirds of the wool production is harvested from breeding ewes. In addition replacement rams and ewes are required to enter the breeding flock.

According to the laws of Mendelian inheritance there is an equal chance of either a male or a female lamb resulting from fertilization of a single sheep ovum. While an equal number of sperm carrying either an X or a Y chromosome may be produced at meiosis in the testis, researchers have described a number of ways in which there could be maternal influence on the sex of the offspring, both before and after conception (Grant & Chamley, 2010) and a differential advantage to male embryos at implantation (Mittwoch, 1996). Sheep have not been used in these studies. Potentially there may also be a difference in *in utero* mortality between male and female embryos in sheep as observed in cattle (Skjervold & James, 1979), resulting in the sex ratio at birth in a group of individuals differing from 1:1. This may potentially be followed by a differential neo-natal and post-natal mortality between the two sexes independent of a birth weight effect. The presence of such effects is however, hard to quantify in farmed livestock due to the interaction of a diverse range of environmental factors.

Variation in the sex ratio within a population is postulated as a key tenet of evolutionary theory.

Trivers and Willard (1973) proposed that where one sex has more variable reproductive success, dams in good condition would be advantaged by producing more of that sex, which in the case of sheep is the male, whereas dams in a poor condition would be advantaged by producing more of the reproductively stable sex, which in the case of sheep is the female. Similarly it is argued that it would be beneficial if a higher proportion of females born to young and old animals, and a lower proportion of females born to breeders in their middle years when they are likely to be the most productive (Clutton-Brock & Iason, 1986). With extensive theoretical considerations and empirical tests having been undertaken during the intervening years, the results have been inconsistent between and within species (Hewinson & Gaillard, 1999). While the Trivers-Willard hypothesis has been reported to occur in a free grazing flock of Rocky Mountain bighorn sheep (Hogg *et al.*, 1992), the effect may be of little practical significance within flocks of farmed sheep (Skjervold, 1979).

Extrapolation of the Trivers-Willard hypothesis to the effect of differing litter size would suggest that single births should have a higher sex ratio, defined as the proportion of males, than multiple births. In reality an effect of declining sex ratio with increasing litter size has been reported within the Norwegian sheep recording system (Skjervold, 1979) and in a flock of Suffolk sheep in Ireland (Kent, 1995).

The importance of the *in utero* environment and its impact on the future life course of the fetus is embodied in the developmental origins of the health

and disease hypothesis postulated by Barker (2007). The hypothesis proposes that aspects of an individual's phenotype may be influenced by signals from the mother, in anticipation of the environment to be experienced post-natally. Such predictive adaptive plasticity would be expected to generate progeny better suited to their environment and thus improve the likelihood of future mating success. The periconceptual period appears to be a major developmental window for this fetal programming of phenotype. Notably, both nutritional and non-nutritional signals acting during the periconception period can have an impact on the sex ratio within a group of progeny (Rosenfeld & Roberts, 2004). Measures of maternal body condition taken prior to conception provide stronger evidence of a relationship with sex ratio than measurements of condition taken after conception (Rosenfeld & Roberts, 2004). In a recent trial, Green *et al.* (2008) reported a skewing of the sex ratio towards males following feeding ewes a diet enriched with rumen-protected polyunsaturated fatty acids for four weeks before joining. The observed shifts in sex ratio described above may thus reflect *in utero* programming. The impact of this on production remains to be evaluated.

With objective data on the effect of maternal nutrition in the preconception period in farmed livestock being limited, it is important with respect to meeting supply contract requirements, to gain an understanding of the role of ewe nutrition prejoining on the sex ratio of the resulting progeny. Is there an association between variation in pasture availability over the summer, as reflected in live weight at joining and/or liveweight change between weaning and the subsequent joining in association with litters of different sizes and sex structure, and the sex ratio

of lambs born during the following spring, under pastoral farming conditions in New Zealand?

It has not been economically feasible in recent years to establish a trial with at least two nutritional treatments, running over several seasons to investigate this question. As an alternative a database containing a set of observational data collected over 18 years from a single flock of grazing sheep was analysed to ascertain if there were any indications of a sex bias associated with lambing year, ewe age, litter size in either the present or the previous lambing and the distribution of sexes in twins.

## MATERIALS AND METHODS

### Sheep

Ewe live weight and lambing data collected between 1985 and 2002 from a flock of approximately 200 individually identified Perendale breeding ewes were used in this study. The ewes were initially maintained at the Whatawhata Research Centre, near Hamilton, on North Island hill country and relocated to the Winchmore Research Station, near Ashburton, on South Island finishing breeding country in 1997. The flock, which was maintained to study the inheritance of wool bulk (Sumner *et al.*, 2007), consisted of two selection lines that were managed as a single flock, except over mating and lambing. No rams were introduced from outside the flock after 1988. Ewes were culled from the flock at weaning when five years of age or at joining if their condition was such that the shepherd deemed they would not survive the forthcoming winter and associated pregnancy. In some years healthy five year-old ewes were retained for another year to increase the number of dams in breeding groups where the numbers of dams were limiting.

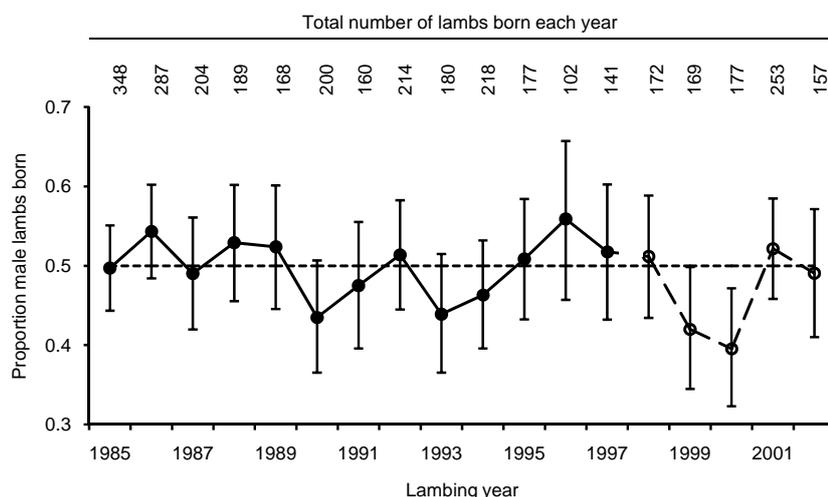
Ewes were single-sire joined for two cycles beginning in mid to late March after oestrus synchronization in most years. Ewes within each selection line were re-randomised to mating groups annually, avoiding half-sib or dam-offspring matings, and lambed in groups based on the genotype of the dam.

### Measurements

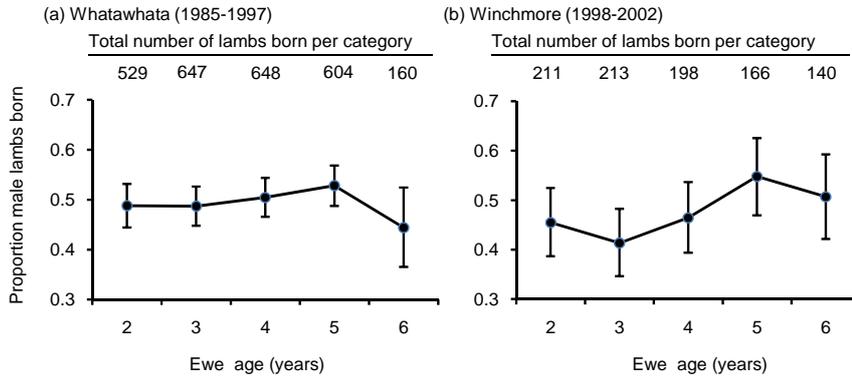
#### *Dam live weight*

Ewes were weighed each year at weaning in December and pre-joining in late February / early March, and the liveweight change over this period calculated; a period when no ewes were shorn. No liveweight change data were

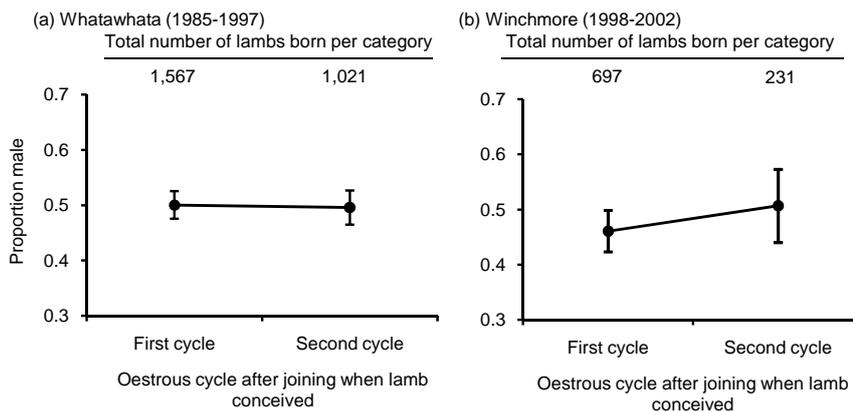
**FIGURE 1:** Proportion of males born to all ewes in each year with their 95% confidence interval. The total number of lambs born each year is shown above the graph. ● and solid line = Lambs born at Whatawhata; ○ and dashed line = Lambs born at Winchmore.



**FIGURE 2:** Proportion of males born to all ewes of each age at Whatawhata and at Winchmore with their 95% confidence interval. The total number of lambs born in each ewe age group of ewes is shown above the graph.



**FIGURE 3:** Proportion of males born that were conceived during the first and second oestrous cycles of the ewes while joined with the rams at Whatawhata and at Winchmore with their 95% confidence interval. The total number of lambs born in each oestrous cycle group is shown above the graph.



available for the rising two-year-old dams as this age group of ewes was not weighed as yearlings the previous December when they did not have lambs at foot.

**Progeny data**

All lambs, born alive and dead, were individually identified, and the identity of their dam recorded within 24 hours of birth.

**Statistical analysis**

The proportion of male lambs was analysed using a generalised linear mixed model with logit link in GenStat (Payne *et al.*, 2009) and “ewe” as a random effect on account of individual ewes being potentially retained in the flock for more than one year. Lambing year, ewe age and number of lambs born (single, multiple) in current lambing with prejoining live weight or, for adult ewes, liveweight change between weaning and joining and number of

lambs reared following the previous lambing, were included in the model. P values for dropping individual effects from the full main-effects model are reported.

A 95% confidence interval for a proportion of male lambs, shown on the graphs, was calculated using the method of Clopper and Pearson (1934). Where this confidence interval does not include 0.5 the proportion is significantly different ( $P < 0.05$ ) from 0.5. The P value for testing a 1:2:1 ratio within the lambs born as twins for the number of sets of twins with ewe-ewe, ewe-ram and ram-ram sex groupings was calculated from a chi-squared goodness of fit test.

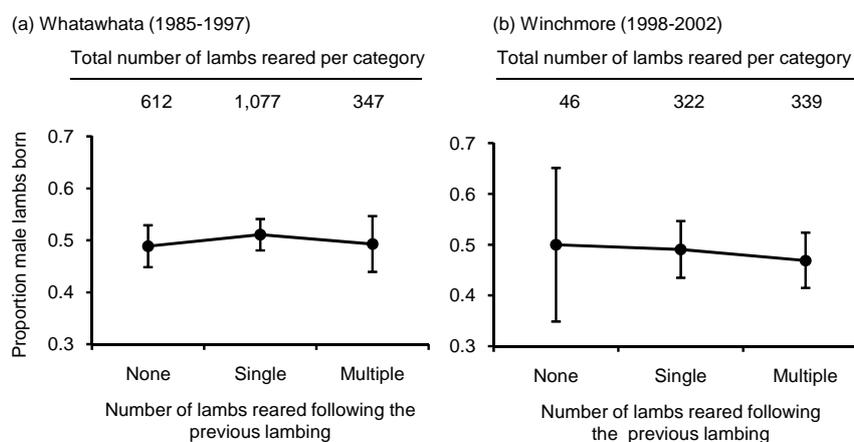
**RESULTS**

There were a total of 3,516 lambs born to 1,025 ewes of all ages in the years 1985 to 2002 (Figure 1). The number of lambs born in each year ranged from 102 to 348. The overall proportion of males, 0.49, did not differ significantly from 0.50 ( $P = 0.32$ ). The proportion of males born between years was consistent with chance variation ( $P = 0.11$ ) with an observed range of 0.40 to 0.56, although the two lowest years at

Winchmore were significantly lower than 0.50. The overall proportion of males born at Whatawhata, 0.50 ( $P = 0.9$ ), and Winchmore, 0.47 ( $P = 0.09$ ), were not significantly different from 0.50. As reported by Sumner *et al.* (2010) the mean birth weight of males and females was  $3.9 \pm 0.8$  (standard deviation) kg and  $3.7 \pm 0.7$  kg respectively from juvenile ewes and the mean birth weight of males and females were  $4.2 \pm 0.8$  kg and  $4.0 \pm 0.8$  kg respectively from adult ewes.

The proportion of males born in each age group of dams at each location is shown in Figure 2. The variation in the proportion of males born from over the age groups had an observed range of 0.49 to 0.53 ( $P = 0.39$ ) between three year-old and five year-old ewes at Whatawhata and between 0.41 and 0.55 ( $P = 0.20$ ) for the same age groups of ewes at Winchmore, although the proportion of males for

**FIGURE 4:** Proportion of males born to three year-old and older ewes for differing numbers of lambs reared in the previous lambing of the same dam at Whatawhata and at Winchmore with their 95% confidence interval. The total number of lambs reared in each previous litter size group is shown above the graph.



three year-old ewes (0.41) was significantly different from 0.5.

The proportion of males born at each location that were conceived during the first and second oestrous cycles of the ewes while they were joined with the rams, are shown in Figure 3. The proportion of males born following conception to each oestrous cycle were not significantly different at Whatawhata ( $P = 0.85$ ) or at Winchmore ( $P = 0.26$ ) and did not differ significantly from 0.50.

The proportion of males within the lambs born as singles and as twins at Whatawhata were 0.49 and 0.50 respectively ( $P = 0.7$ ), while the corresponding proportions of lambs born at Winchmore were 0.47 and 0.46 respectively ( $P = 0.9$ ). The numbers of sets of ewe-ewe, ewe-ram and ram-ram twins were 152, 306 and 155 ( $P = 0.98$ , for goodness of fit with 1:2:1 ratio) at Whatawhata and 97, 152 and 72 ( $P = 0.09$ ) at Winchmore. Thus both the proportion of males within lambs born as a single and the distribution of

males within sets of twins, were consistent with chance variation.

With serial data collected from the same ewe we assess if there was any relationship between the size of the litter reared during the previous lambing, on the proportion of males born in the subsequent lambing. The proportion of males born to adult ewes rearing litters of different sizes at the previous lambing, shown in Figure 4, ranges from 0.51 to 0.49 ( $P = 0.57$ ) at Whatawhata and 0.50 and 0.47 ( $P = 0.30$ ) at Winchmore, was consistent with chance variation and did not differ significantly from 0.50.

The proportion of males present at weaning was 0.49 at Whatawhata and 0.46 at Winchmore ( $P = 0.16$ ). Sixteen percent of females and 19% of the males born, both live and dead, at Whatawhata ( $P = 0.18$ ) and 2% of the females and 5% of the males born at Winchmore ( $P = 0.02$ ) did not survive to weaning indicating a 3% greater mortality in males up to weaning at both locations ( $P = 0.03$ ).

The effect of including prejoining live weight (overall mean  $53.4 \pm 7.0$  kg ranging from 48.6 to 57.3 between years) as a covariate to evaluate the effect of lambing year, ewe age and number of lambs born (single, multiple) in current lambing is summarized in Table 1. There was a significant effect between lambing years at Winchmore but not at Whatawhata.

The effect of including live weight change of the adult ewes between weaning and joining (overall mean  $-0.5 \pm 3.9$  kg ranging from -6.2 to 3.4 between years) as a covariate to evaluate the effect of lambing year, ewe age and previous number of lambs reared following the previous lambing and number of lambs born (single, multiple) in current lambing is summarized in Table 2. There was a significant lambing year and ewe age effect at Winchmore and consequently for the combined data set.

**TABLE 1:** P values for dropping individual effects from a main effects model of lambing year, ewe age and number of lambs born (single, multiple) in current lambing with prejoining live weight included as a covariate in a generalised linear mixed model with "ewe" as a random effect for the proportion of male lambs born in all the recorded lambings at each location. Bold text indicates significance at  $P < 0.05$ .

Effect	Location		Both sites combined
	Whatawhata	Winchmore	
Lambing year	0.48	<b>0.05</b>	0.14
Ewe age	0.39	0.20	0.20
Number of lambs born in current lambing	0.86	0.47	0.89
Prejoining live weight	0.85	0.62	0.77

## DISCUSSION

The database used for the analyses reported here was collected as part of a genetic study on the inheritance of wool bulk. The specific analyses reported here were undertaken as an addendum to the genetic evaluation. When the initial genetic evaluation was planned no consideration was given to the possibility of overlaying

**TABLE 2:** P values for dropping individual effects from a main effects model of lambing year, ewe age, number of lambs reared following the previous lambing and number of lambs born in current lambing (single, multiple) with liveweight change between weaning and joining included as a covariate in a Generalised Linear Mixed Model with “ewe” as a random effect for the proportion of male lambs born to the recorded lambings of adult ewes (three-year-old and older) at each location. Bold text indicates significance at  $P < 0.05$ .

Effect	Location		Both sites combined
	Whatawhata	Winchmore	
Lambing year	0.42	<b>0.03</b>	<b>0.02</b>
Ewe age	0.20	<b>0.03</b>	<b>0.04</b>
Number of lambs reared following previous lambing	0.57	0.30	0.30
Number of lambs born in current lambing	0.87	0.56	0.71
Live weight change weaning to joining	0.26	0.74	0.42

any differential management procedures to potentially influence the sex ratio of the progeny. Hence, while these analyses have used data from an extensive database collected over 18 years, the lack of any repeated within year treatments has severely limited the potential to detect any significant trends in any of the assessed responses on the sex ratio of the progeny due to a potential confounding with between year effects. Nevertheless this situation mirrors that faced by sheep farmers each year. It is all very well to detect a significant response in skewing the sex ratio in a controlled situation established to maximize variation in a controlled manner, such as was demonstrated by Green *et al.* (2008), but what happens on a commercial farm faced with between year variation in climate and variable pasture availability (Figure 1)? Under such conditions flock managers strive to reduce between-year variation in the performance of their stock. The practical question is can farmers influence the sex ratio of the lambs born each year through changes in aspects of the management of their ewe flock?

The overall sex ratio in this study was 0.49 with a 95% confidence interval of  $\pm 0.02$ . This was within the range reported by Skjervold (1979) of  $0.489 \pm 0.001$  for a much larger population of several Norwegian breeds which were significantly different. One breed was the Cheviot which is the base breed from which the Perendale was evolved by crossbreeding with the Romney.

The analyses reported in this paper show that there were no significant differences in the proportion of males born between years although there were two low years at Winchmore, between ewes of different ages, between lambs conceived in

the first or second cycle after ewes were joined with the ram, with lambs born as singles or within lambs born as twins or lambs grouped according to the litter size reared by the dam at the previous lambing. All the observed trends were consistent with chance variation. As such the proportion of males born in each of the evaluated categories did not differ significantly from 0.50. While the observed trends in this study were not significantly different, they mirrored those reported by Kent (1995) for a single flock and Skjervold (1979) for a much larger group encompassing many flocks. These combined sets of data indicate that the sex ratio in sheep is influenced by a range of environmental factors.

The data analysed in this study suggested the association between either live weight at joining (Table 1) or liveweight change between weaning and joining (Table 2) with the observed sex ratio in the subsequent lambing crop to be weak. The

weak association between these measurements and the sex ratio may, in a managed flock, be an indirect reflection of the basic aim of competent farmer managers to reduce the effect of seasonal variations in feed supplies. Results across a series of trials suggest a tendency in ungulates subjected to nutritional stress around mating and pregnancy for there to be a higher proportion of males born subsequently (Clutton-Brock & Iason, 1986). Such a trend was evident at Winchmore in two years when the ewes experienced a negative weight gain over the summer when more males were born the following spring. The reverse occurred in two other years. This response is opposite of the effect argued by Trivers and Willard (1973) whereby parents in superior conditions who are able to expend more energy and other resources should produce more sons whereas parents in inferior conditions should produce more daughters

Peri-natal and post-natal mortality is a major form of reproductive inefficiency. The proportion of lambs that were born and did not survive to weaning in this study equates with an average of 15 – 20% that has been reported by McDonald *et al.* (1998) as occurring across a range of farming systems in New Zealand. The mortality rate to weaning occurring on the steep hill country at Whatawhata of 18% exceeded that of 4% on flat irrigable land at Winchmore with a 3% greater mortality in male than female lambs between birth and weaning, at both locations. A trend that aligns with that reported by Skjervold (1979), of a differential loss of predominantly males in early life, with the sex ratio potentially providing an indication of the prevailing environmental stress.

Within current New Zealand sheep farming systems producing lambs for meat, there is a potential economic advantage from farming ram lambs for slaughter before one year of age on the grounds of intact ram lambs growing faster than ewe lambs (Kirton & Morris, 1989), the meat classification system taking no account of sex for sheep before they erupt their first pair of permanent incisors at about one year of age (Kirton, 1989) and the eating quality of ewe and ram carcasses of the same weight being similar (Purchas, 1989).

In light of the data collected by Skjervold (1979), Kent (1995) and in this study, it is unlikely that it would be possible for an individual sheep farmer to consistently influence the sex ratio of his lamb crop through changes in his flock management so as to influence his net returns from meat.

### ACKNOWLEDGEMENTS

To field staff at Whatawhata Research Centre and at Winchmore Research Station, for assistance in the collection of field data and to Sharon Hickey for collation of the records for the current analysis. Maintenance of the flock after 1992 and the current analysis was funded by the Foundation for Research, Science and Technology (UOAX0808).

### REFERENCES

- Barker, D.J.P. 2007: The origins of the developmental origins theory. *Journal of Internal Medicine* **261**(5): 412-417.
- Clopper, C.J.; Pearson, E.S. 1934: The use of confidence or fiducial limits illustrated in the case of the binomial. *Biometrika* **26**: 404-413.
- Clutton-Brock, T.H.; Iason, G.R. 1986: Sex ratio variation in mammals. *Quarterly Review of Biology* **61**: 339-374.
- Grant, V.J.; Chamley, L.W. 2010: Can mammalian mothers influence the sex of their offspring peri-conceptually? *Reproduction* **140**: 425-433.
- Green, M.P.; Spate, L.D.; Parks, T.E.; Kimura, K.; Murphy, C.N.; Williams, J.E.; Kerley, M.S.; Green, J.A.; Keisler, D.H.; Roberts, R.M. 2008: Nutritional skewing of conceptus sex in sheep: effects of a maternal diet enriched in rumen-protected polyunsaturated fatty acids (PUFA). *Reproductive Biology and Endocrinology* **6**:21. doi:10.1186/1477-7827-6-21.
- Hewinson, A.J.M.; Gaillard, J-M. 1999: Successful sons or advantaged daughters? The Trivers-Willard model and sex-biased maternal investment in ungulates. *Trends in Ecology and Evolution* **14**: 229-234.
- Hogg, J.T.; Hass, C.C.; Jenni, D.A. 1992: Sex-biased maternal expenditure in rocky mountain bighorn sheep. *Behavioural Ecology and Sociobiology* **31**: 243-251.
- Kent, J.P. 1995: Birth sex ratios in sheep over nine lambing seasons: years 7-9 and the effects of ageing. *Behavioural Ecology and Sociobiology* **36**: 101-104.
- Kirton, A.H. 1989: Principles of classification and grading. In: Purchas, R.W.; Butler-Hogg, B.W.; Davies, A.S. eds. Meat Production and processing. New Zealand Society of Animal Production, Hamilton, New Zealand. Occasional Publication Number 11, pp. 143-157.
- Kirton, A.H.; Morris, C.A. 1989: The effect of mature size, sex and breed on patterns of change during growth and development. In: Purchas, R.W.; Butler-Hogg, B.W.; Davies, A.S. eds. Meat Production and processing. New Zealand Society of Animal Production, Hamilton, New Zealand. Occasional Publication Number 11, pp. 73-85.
- McDonald, M.F.; Barrell, G.K.; Xu, Z.Z. 1998: Modifying reproductive processes. In: Fielden, E.D.; Smith, J.F. eds. Reproductive management of grazing ruminants in New Zealand. New Zealand Society of Animal Production, Hamilton, New Zealand. Occasional Publication Number 12, p. 77-90.
- Mittwoch, U. 1996: Differential implantation rates and variations in the sex ratio. *Human Reproduction* **11**:8-9.
- Payne, R.W.; Murray, D.A.; Harding, S.A.; Baird, D.B.; Soutar, D.M. 2009: GenStat for Windows, 12th Edition. Introduction. VSN International Ltd., Hemel Hempsted, Hertfordshire, UK.
- Purchas, R.W. 1989: On-farm factors affecting meat quality characteristics. In: Purchas, R.W.; Butler-Hogg, B.W.; Davies, A.S. eds. Meat Production and processing. New Zealand Society of Animal Production, Hamilton, New Zealand. Occasional Publication Number 11, p. 159-171.
- Rosenfeld, C.J.; Roberts, R.M. 2004: Maternal diet and other factors affecting offspring sex ratio: A review. *Biology of Reproduction* **71**: 1063-1070.
- Skjervold, H. 1979: Causes of variation in the sex ratio and sex combination in multiple births in sheep. *Livestock Production Science* **6**: 387-396.
- Skjervold, H.; James, J.W. 1979: Causes of variation in the sex ratio in dairy cattle. *Journal of Animal Breeding and Genetics* **95**: 293-305.
- Sumner, R.M.W.; Clarke, J.N.; Cullen, N.G. 2007: Effect of divergent selection for wool bulk on live weight and wool characteristics in Perendale sheep. *Proceedings of the New Zealand Society of Animal Production* **67**: 180-185.
- Sumner, R.M.W.; Morris, C.A.; Hickey, S.M.; Sheppard, A.M. 2010: Genetic and environmental relationships between live weight change over the summer in Perendale ewes and the lifetime live weight profiles of their progeny. *Proceedings of the New Zealand Society of Animal Production* **70**: 165-170.
- Trivers, R.L.; Willard, D.E. 1973: Natural selection of parental ability to vary the sex ratio of offspring. *Science* **179**: 90-92.