These findings raised questions of a fundamental nature concerning the nature and magnitude of the energy reserves of lambs at birth, the rate at which these reserves are depleted and the effect of such depletion on behaviour.

III. ENERGY BALANCE IN THE YOUNG LAMBS

(a) Energy reserves

The fat and glycogen reserves at birth were estimated by comparing the body composition of lambs starved to death with that of lambs killed at birth; most depot fat and all glycogen appeared to be exhausted at death from starvation (Alexander 1962a). Protein reserves were not exhausted since nitrogen catabolism continued to increase throughout the period of starvation. However, protein utilization was never sufficient to supply the energy needs of a starving lamb after fat and glycogen reserves were exhausted.

In lambs from ewes fed adequately throughout pregnancy, energy reserves in the form of fat and glycogen were estimated to be 165 and 40 $kcal\,kg^{-1}$ respectively. In lambs from' ewes poorly fed in late pregnancy the estimate for glycogen was also 40 $kcal\,kg^{-1}$, but the fat reserve, 72 $kcal\,kg^{-1}$, was strikingly different. Current work suggests that this reduction in fat reserves, due to poor prenatal nutrition during the last third of gestation, is less marked when the under-nutrition extends throughout the last two thirds of pregnancy. When the energy equivalent of the protein catabolised during starvation is added to the calories derived from fat and glycogen, the estimated total useful reserves are 250 $kcal\,kg^{-1}$ in lambs well fed prenatally, and about 130 $kcal\,kg^{-1}$ in lambs poorly fed in the late foetal period. These estimates agree with those obtained by measurement of oxygen consumption throughout starvation. Starved lambs survived for 16 hours to 5 days depending upon prenatal nutrition and air temperature.

(b) Energy expenditure

The metabolic rate (heat production) of lambs under various combinations of air temperature and coat condition has been measured in a climatic respiration chamber (Alexander 1962b). In homeothermic animals, such as the young lamb, metabolic rate increases in response to an increase in heat loss, so that body temperature is stabilized. Heat loss is increased when air temperature falls, and when air movement or evaporation from the coat increase. Figure 1 provides a basis for equating these variables in terms of heat loss; for example., the heat loss is the same for a dry lamb in "still" air at-32°C as for the same lamb, wet, in a wind of 550 cm sec^{-1} (about 12 m.p.h.) at 13°C. Fortunately only about 30% of the latent heat of vaporization is drawn from the lamb.

The heat loss from a lamb depends on its thermal insulation as well as on the environment. The advantage of a good coat is apparent from Figure 1.

Fig. 1.-Climatic limits to the maintenance of homeothermy in lambs less than 24 hr old. The figures for heat production are taken from Alexander (1962b); those for summit metabolism are from Alexander (1962c). The numbers at the points of intersection are the ambient temperatures below which body temperature would begin to fall (* point of intersection not shown). The sloping dotted lines represent extrapolations or conditions under which few results were obtained such as at low temepratures on wet lambs with hairy coats.

The horizontal dotted lines represent the summit metabolism (from Fig. 2).

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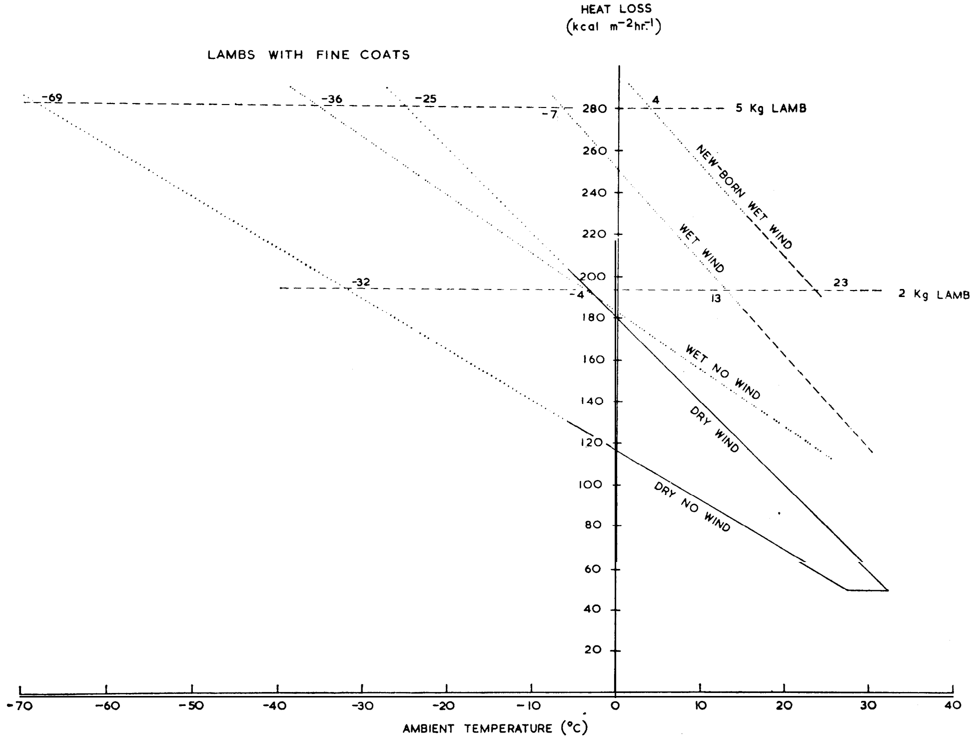
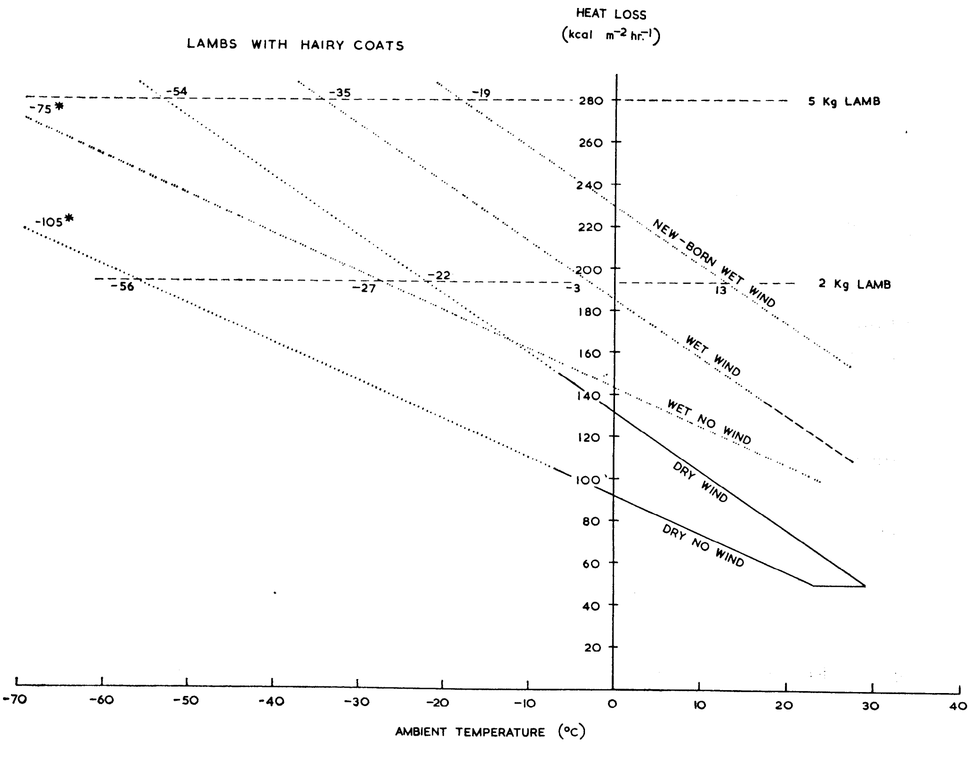

HEAT LOSS
(kcal m⁻²hr.⁻¹)
LAMBS WITH FINE COATS
-69
-36
-25
-7
4
5 Kg LAMB
NEW-BORN WET WIND
WET WIND
-32
-4
13
23
2 Kg LAMB
WET NO WIND
DRY WIND
DRY NO WIND
280
260
240
220
200
180
160
140
120
100
80
60
40
20
-70
-60
-50
-40
-30
-20
-10
0
10
20
30
40
AMBIENT TEMPERATURE (°C)


HEAT LOSS
(kcal m⁻² hr.⁻¹)
LAMBS WITH HAIRY COATS
-54
-35
-19
-75*
5 Kg LAMB
-105*
-22
-56
-27
-3
13
2 Kg LAMB
NEW-BORN WET WIND
WET WIND
WET NO WIND
DRY WIND
DRY NO WIND
280
260
240
220
200
180
160
140
120
100
80
60
40
20
-70
-60
-50
-40
-30
-20
-10
0
10
20
30
40
AMBIENT TEMPERATURE (°C)

The ability of a lamb to maintain a normal body temperature will depend, in part, on its capacity to produce heat. This capacity (summit metabolism) has been estimated by measuring heat production at low air temperature, when body temperature, monitored by thermocouple, has been induced to fall slowly by controlled air movement (Alexander 1962c). In young lambs summit metabolism. per unit of body weight, proved to be fairly constant over the whole range of body weight (Figure 2), but when expressed on the basis of surface area the rate was higher in large than in small lambs. Since heat loss is proportional to surface area, small lambs would be expected to begin cooling under milder conditions than large lambs (Figure 1). These measurements provide estimates of the climatic limits to homeothermy in young lambs (Figure 1).

In normal lambs from adequately fed ewes, summit metabolism. which is about five times the basal rate, may be achieved within minutes of birth. However, there is evidence (Alexander 1962c, and unpublished data) that some lambs poorly fed prenatally or subjected to a prolonged birth process are slow to develop the ability to produce heat at high rates. The ingestion of milk does not increase summit metabolic rate, but its maintenance depends upon adequate nutrition. Fasting and prolonged exposure to cold result in a decrease in summit metabolism (Alexander 1962c). In comparison with adults of the few other species in which summit metabolism has been estimated, the lamb possesses a remarkably well developed "chemical" method of regulating body temperature.

Little is known about the heat-conserving mechanisms in the lamb, but observations on skin-temperature suggest that the peripheral vasomotor mechanisms are as well-developed at birth as in the adult sheep. The only obvious improvement in heat conservation with advancing age results from the increasing insulation of the growing fleece. The declining ratio of surface area : mass may also be an advantage, depending upon how summit metabolism changes with age, but this remains to be determined.

These results show that temperature regulation in the lamb is very well developed at birth. They also show clearly that particularly for small lambs the climatic limits to homeothermy, at the "cold end" of the scale, will be exceeded during a winter or spring lambing in many parts of Australia.

IV. BEHAVIOUR OF EWES AND LAMBS

Behaviour was studied to provide an answer to the question, "Is failure to suck due to the ewe or to the lamb?"

(a) Maternal behaviour

Ewes were observed constantly during parturition, and during the subsequent 12 or more hours. The normal pattern of behaviour and various aberrant patterns

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Legend Fig. 2

Fig. 2.--Relation of summit metabolism to body weight in Merino lambs less than 9 hr old.

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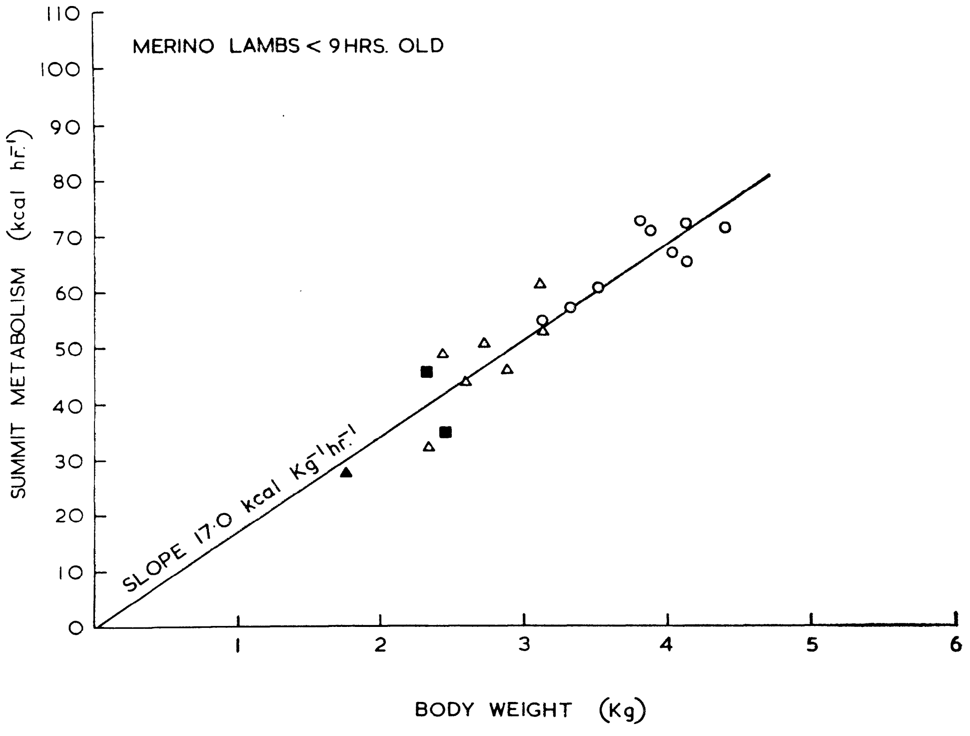
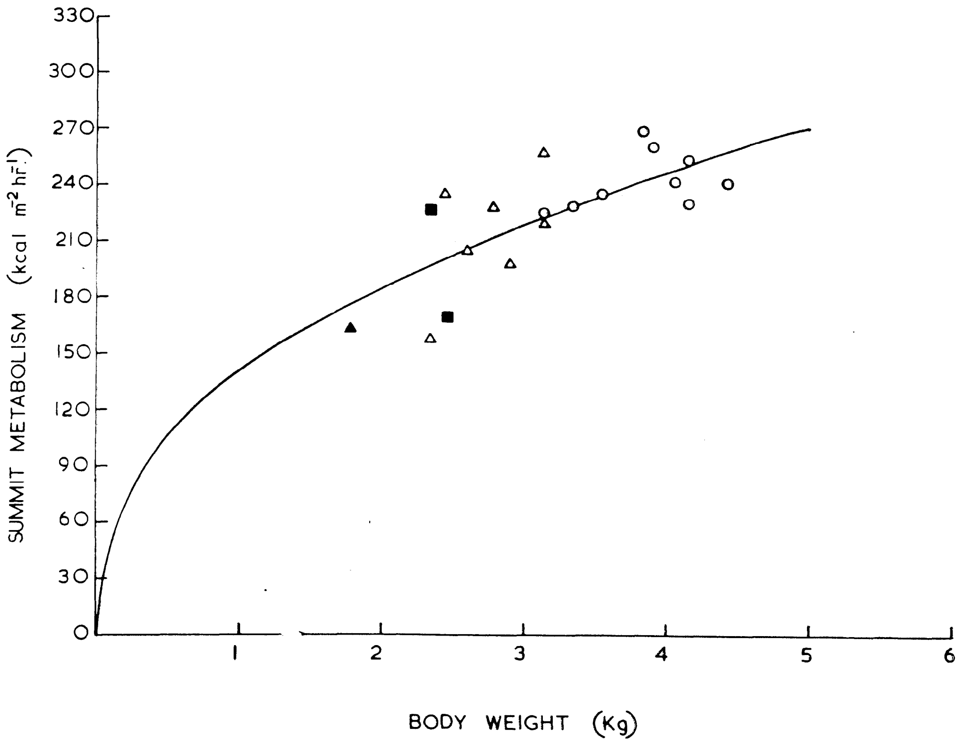

MERINO LAMBS < 9 HRS. OLD
SUMMIT METABOLISM (kcal hr⁻¹)
SLOPE 17·0 kcal Kg⁻¹ hr⁻¹
BODY WEIGHT (Kg)
0
10
20
30
40
50
60
70
80
90
100
110
1
2
3
4
5
6


SUMMIT METABOLISM (kcal m⁻² hr⁻¹)
BODY WEIGHT (Kg)
0
30
60
90
120
150
180
210
240
270
300
330
1
2
3
4
5
6

observed in maiden Merino ewes, e.g. butting and rotating away from the approach of the lambs were described by Alexander (1960). The aberrant patterns usually disappeared after several hours. Desertion was associated with prolonged parturition, high birth weight and high bodily condition of ewes, and these three conditions were inter-related. Undernourished ewes were frequently exhausted by parturition and remained recumbent for some time; the lambs sometimes wandered away and became lost before the ewe got to its feet.

More recently, the role of the ewe in facilitating the sucking drive of lambs has been studied. Two aspects of behaviour were examined, namely, spatial orientation of the ewe towards the lamb and maternal grooming, i.e. licking of the lamb by the ewe. Grooming and orientation were prevented at the same time by fastening the head of the ewe to a frame and denying the lamb access to the area in front of the frame. Lambs of these ewes were less active than control lambs and were slower to suck for the first time. These results suggest that the progress of the lamb may be retarded if maternal care is indifferent, but the importance of grooming relative to that of orientation is not yet clear.

(b) Behaviour of lambs

(i) Effect of age and experience

Continuous observations on lambs born in yards (Alexander 1958) suggested that the sucking drive and the chances of ever sucking successfully were reduced if lambs had not sucked by six hours after birth. A study (unpublished data) was therefore made, under controlled conditions, of the changes in sucking drive that occur with age. Since the drive would be affected by satiety and by conditioning in lambs which sucked successfully, observations were made on lambs prevented from sucking by a cover over the maternal udder. The frequency of attempts to reach the udder or to suck declined markedly during the first four hours of life (Figure 3). When the cover was removed at 6-24 hr after birth, fewer lambs

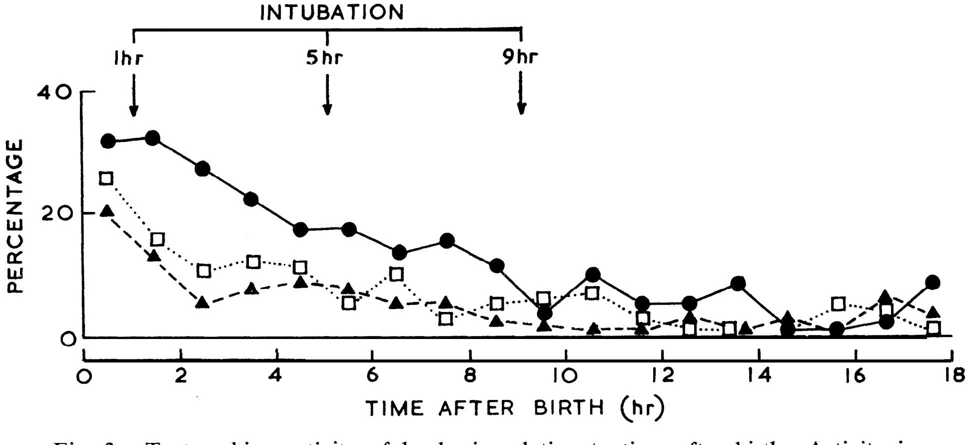


Fig. 3.—Teat seeking activity of lambs in relation to time after birth. Activity is expressed as the percentage of observations in which lambs were seeking to suck.
● udder of ewe covered.
□ lamb allowed to suck *ad lib.*
▲ lamb given 300 ml of milk by stomach tube at 1, 5 and 9 hr after birth.

They included good prenatal nutrition, close confinement of ewe and lamb, temperate air temperatures of about 21°C (in (i) above), short labour and good maternal behaviour; ewes not satisfying the last two criteria were rejected. Under less favourable conditions such as in the paddock, the effect of the treatments would almost certainly have been more marked.

V. FIELD IMPLICATIONS

Although made under laboratory conditions, these studies assist interpretation of field observations.

They show that exhaustion of energy reserves may contribute to the high incidence of deaths observed during the first three days of life (Moule, Jackson and Young 1956), thus supporting the conclusion of Moule (1954), McFarlane (1955), Safford and Hoversland (1960) and others, that starvation is a major cause of death.

They provide some physiological reasons for the high mortality amongst small lambs (Moule, Jackson and Young 1956). Not only is summit metabolism per unit area low in lambs of low birth weight, but the insulation of the coat may also be low, since the density of secondary wool fibres is related to birth weight (Alexander, unpublished). No doubt many other physiological explanations of this mortality pattern will also be found.

Further, the results explain why lambs die during inclement weather and they provide a semi-quantitative basis on which to assess the need for shelter. However, the manner in which adequate shelter may be provided requires definition.

They show some of the ways in which poor prenatal nutrition reduces the chances of survival. When nutrition of the pregnant ewe is inadequate, gestation may be shortened (Alexander 1956), birth weight is low and vigour of the newborn lamb is poor (Thomson and Thomson 1949), the energy reserves are reduced, metabolic rate may be slow to increase to summit levels in response to cold (see also Alexander and McCance 1958), the onset of lactation is delayed (McCance and Alexander 1959), maternal exhaustion delays successful suckling and the lambs are slow to stand and suck for the first time (Alexander 1958). The work of Everitt and Taplin (1964) shows that prenatal undernutrition reduces the amount of wool per unit area of skin at birth and hence presumably decreases insulation.

The author's results also suggest that lambs well insulated by a long (hairy) birth coat would have a greater chance of survival than lambs with a short (fine) coat (Alexander 1962c). The superiority of the hairy coat in providing insulation cannot be disputed, but so far there are no data from the field to show that hairy coats provide a survival advantage. In fact, field data suggest there is no advantage (Davies 1964), or that a hairy coat is even a disadvantage (Purser, personal communication), presumably because of some correlate. However, a difference in mortality would be expected only when deaths were due to cold and when climatic conditions were not so severe as to adversely affect all lambs.

The findings presented in this paper do not show the relative importance of the various causes of death in the field, but they do show that a high mortality can readily be accounted for by the vulnerability of the lamb to the circumstances of its birth, such as poor maternal behaviour, inadequate prenatal nutrition, inclement weather and other environmental factors. Indeed, the low incidence of infectious disease and other pathological conditions as causes of death (e.g. Hughes *et al*. 1964) suggests that most of the lamb mortality in Australia can be accounted for by these behavioural and physiological factors.

VI. CONCLUSION

The immediate object of these studies was to find out why lambs die, not to investigate methods of preventing deaths. However, the results suggest that survival depends largely on the standard of animal husbandry practised the improvement of these standards by the use of information such as discussed here, will no doubt present many problems. The results also point the way for future work.

The physiology and behaviour of the lamb dwarfed by placental insufficiency, by prenatal undernutrition, by heat, by competition with litter mates, or by disease invite investigation.

The physiological basis of the drive to suck is unexplored in the sheep and in any other species and the basis of maternal behaviour in mammals is far from understood; even the role of the "mothering hormone", prolactin, is in doubt (Lott and Fuchs 1962).

While these problems may remain unsolved for many years, useful genetic differences in maternal behaviour of ewes and in sucking drive of lambs may be found by the application of objective yard-sticks developed during these studies. Utilization of such differences could lead to improved survival in the Australian lamb crop in the foreseeable future.

VII ACKNOWLEDGMENTS

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