Aust. J. Biol. Sci., 1974, **27**, 259–66

Delay in the Onset of Thermal Tachypnoea in Shorn Sheep Exposed to 42°C in Winter and Summer

M. Maskrey

Department of Physiology and Anatomy, Massey University, N.Z.; present address: Department of Physiology, University of Tasmania, G.P.O. Box 252C, Hobart, Tas. 7001.

Abstract

Shorn sheep were routinely exposed to ambient temperatures (T_a) of 14 and 42°C in a climatic chamber in winter and in summer. Rectal temperature (T_{re}) and skin temperature (T_{sk}) were measured at 14°C and the time elapsing between raising the T_a to 42°C and the onset of thermal tachypnoea was recorded. It was found that the onset of thermal tachypnoea in the heat was dependent upon the T_a to which the sheep had been previously exposed in the animal house and, in summer, the degree of fleece regrowth. There was an inverse linear relationship between the mean T_{sk} recorded immediately prior to raising the T_a and the delay in onset of thermal tachypnoea both in winter and summer. Thus, for either season, the inhibition of panting could be related to the degree of cold stimulation received from the periphery. However, a comparison of winter and summer data indicated that other factors were also involved. T_{sk} was significantly higher, and T_{re} significantly lower, in winter than in summer. These observations point towards possible seasonal changes in basal metabolic rate and thermoregulatory set-points. The results are discussed with regard to current theories concerning the mechanisms leading to the inhibition of thermal tachypnoea in shorn sheep.

Introduction

Respiratory frequency (RF) increases almost immediately when a fully fleeced sheep is exposed to a hot environment (Bligh 1959), but there is often a considerable delay before a rise in RF occurs after the sheep has been closely shorn (Bligh 1963; Phillips and Raghavan 1970; Slee 1973*a*). The length of the delay appears to be related to the area of fleece removed (Bligh 1963) and to both the length and severity of prior exposure to cold (Slee 1973*a*). Bligh (1963) has interpreted the inhibition of thermal tachypnoea in the shorn sheep as due to a long-lasting block on the respiratory centre resulting from prior stimulation of peripheral cold sensors that are exposed when the fleece is removed. Slee (1973*a*, 1973*b*) on the other hand has proposed that prior exposure to cold results in the establishment of a heat debt which has to be repaid before panting can be initiated.

The object of the present study was to examine the delay in the onset of thermal tachypnoea in shorn sheep exposed to 42°C which had been housed under winter and summer conditions. Data are also presented concerning the thermoregulatory adjustments of sheep to repeated shearing during the winter and summer while dietary intake was kept constant.

Methods

Two series of experiments were performed on each of four adult Romney ewes weighing between 40 and 48 kg. At the beginning of each series the bulk of the fleece was removed from the sheep

with shears. During the series the animals were clipped at intervals using Oster small animal clippers, pelage being removed from the entire body surface with the exception of the head, face and lower part of the leg.

The first series of experiments comprised the exposure of the sheep to 42°C at 4, 7, 10, 17 or 26 days after routine clipping of the fleece during the winter months. The sheep were first shorn at the end of April and experiments were continued until mid-July. The same four sheep were reshorn at the end of November and tested at 4, 7, 10, 17 or 26 days after clipping of the fleece until mid-February. During both series of experiments the animals were housed between tests in metabolism crates in an animal house where they were protected from wind and direct sunlight but in which they experienced seasonal variations in ambient temperature (T_a) which were monitored continuously. The sheep were fed daily with chopped hay and sheep nuts. Intake was not accurately assessed but the ration of food offered remained the same throughout winter and summer. Animals were weighed before and after each series of experiments.

For testing, the animals were placed singly in a metabolism crate in a climatic chamber measuring 2·5 by 2·5 m by 3 m high, in which the air movement was 1·6 km h^{-1}. The animals remained at a T_a of 14±1°C for 80 min, after which time T_a was raised to 42°C. The change in T_a was completed in 40 min, the rate of temperature change being similar in winter and summer. The sheep remained at 42°C until thermal tachypnoea was well established. T_a was then returned to 14°C and the animal removed from the chamber. During the whole period in the climatic chamber the rectal temperature (T_{re}) and the skin temperature (T_{sk}) were monitored continuously at 2·5-min intervals by means of copper–constantan thermocouples inserted 10 cm beyond the anal sphincter or attached to the skin surface by adhesive tape. T_{sk} was recorded from the shoulder, trunk, upper leg and pinna. The average of these temperatures was used as a measure of mean T_{sk}. All temperatures were monitored on a Riken Denshi potentiometric recorder. Respiratory movements were monitored by means of a pneumograph belt fastened around the lower thoracic margin of the sheep. These movements were converted via a tambour and lever to a kymograph record. A 1-min sample of respiratory movements was recorded every 5 min and counted. At the end of each test period measurements were made of fleece depths at seven sites on the body surface and averaged to obtain the mean fleece depth.

In the analysis of the results the regression lines were computed using the method of least squares, and the significance of differences between means was computed using Student's *t*-test.

Results

Respiratory Frequencies

The RFs of shorn sheep exposed in the climatic chamber to 14°C were very low compared with those of unshorn sheep, which generally average between 60 and 100 breaths/min at this T_a. There was also a significant difference between the RF of clipped sheep when tested in the winter (12·1±0·9 breaths/min) and the summer (20·2±2·0 breaths/min) ($P < 0·001$). Upon raising the T_a towards 42°C, RF remained low for periods of between 35 and 140 min before suddenly rising. The time interval between the onset of the rise in T_a and that of RF was taken as the delay in the onset of thermal tachypnoea.

Ambient Temperature in the Animal House

The recorded winter and summer T_a in the animal house varied greatly. In winter the daily maximum T_a recorded varied between 21°C at the beginning of the series and 12°C by mid-way through the series. Daily minimum T_a varied from 16 to 6°C over the same period. In summer the daily maximum T_a recorded varied from 19°C early in the series to 25°C mid-way through, while during the same period daily minimum T_a increased from 12 to 19°C. It was soon noticed that when sheep were tested on a day immediately after cold weather the delay in the onset of thermal tachypnoea was invariably longer than if the test day had been preceded by milder

weather. Furthermore, the average delay in onset of thermal tachypnoea was significantly longer in winter (95·5±3·3 min) than in summer (62·75±3·4 min) ($P < 0{\cdot}001$). A measure of the average T_a pertaining in the animal house in the 24 h before each test was obtained by averaging the T_a readings obtained at 1200, 1600, 2000, 2400, 0400 and 0800 h immediately preceding the test, which began at 0930 h. By plotting this average T_a against the delay in the onset of thermal tachypnoea during the test a linear relationship between prior T_a and the inhibition of panting became apparent (Fig. 1).

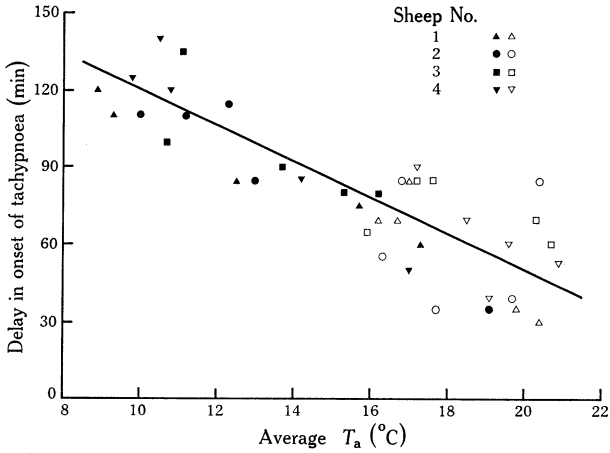


Fig. 1. Relationship between average T_a in the animal house during the 24 h preceding heat exposure and delay in the onset of thermal tachypnoea during exposure to heat in shorn sheep. The average T_a was obtained by averaging the T_a recorded in the animal house at 4-h intervals throughout the 24-h period (see text). The delay in the onset of thermal tachypnoea is the difference in time between first raising T_a towards 42°C and the first increase in RF. In this and all succeeding figures the closed symbols refer to data obtained in the winter while the open symbols refer to data obtained in the summer. Each symbol represents one heat exposure.

Fleece Regrowth

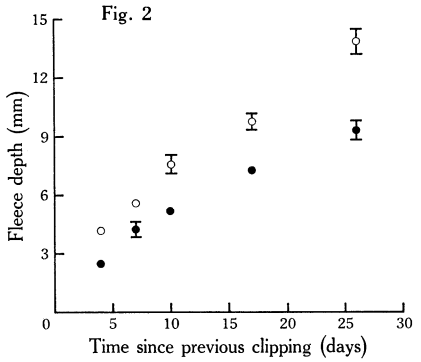
Regrowth of the fleece after clipping was more rapid in the summer than in the winter (Fig. 2). In the summer there was a continuous decrease in the delay in onset of thermal tachypnoea with increasing time after clipping, whereas in winter the delay in onset of thermal tachypnoea began to shorten with time only after 10 days had elapsed since the animals had been clipped (Fig. 3).

Initial Skin Temperatures

Plotting initial T_{sk} (the average T_{sk} of each sheep before T_a was raised) against the delay in onset of thermal tachypnoea revealed a linear relationship between these two parameters. Fig. 4 shows that the results from the winter and summer series differ in that, for a given delay in onset of thermal tachypnoea, initial T_{sk} was higher in winter than in summer. However, the slopes of the regression lines for the winter and summer data do not differ significantly. The mean initial T_{sk} for all animals was significantly greater in the winter (26·52±0·82°C) than in the summer (25·12±1·05°C) ($P < 0{\cdot}02$).

Rectal Temperatures

The mean T_{re} for all sheep measured at a T_a of 14°C before exposure to heat was greater in summer (39·30±0·4°C) than in winter (38·78±0·8°C). This difference is significant at the 5% level. Fig. 5 shows the initial T_{re} for each sheep with respect to the time elapsed since the fleece was first removed. It can be seen that when the sheep were first shorn the T_{re} increased. This increase, on average, was slightly greater in winter than in summer. During subsequent tests throughout the summer T_{re} showed a gradual fall. In the winter T_{re} initially fell at approximately the same rate as in summer, but after about 8 weeks of repeated shearing T_{re} fell steeply in all four animals, reaching levels of between 0·6 and 1·0°C below that recorded from the same animals in summer.



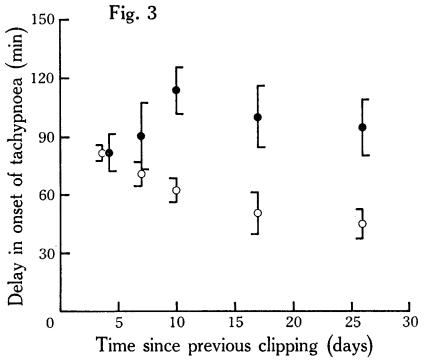


Fig. 2. Depth of the fleece at various times after clipping in winter and summer. Values for fleece depths were obtained by averaging the depth measured at each of seven sites on the body surface. Each symbol represents the mean from four sheep. Vertical lines represent standard errors of the means where these are sufficiently large to be indicated.

Fig. 3. Relationship between time elapsed after clipping and delay in onset of thermal tachypnoea in shorn sheep exposed to 42°C in winter and summer. Each symbol represents the mean from four sheep; vertical lines indicate standard errors of the means.

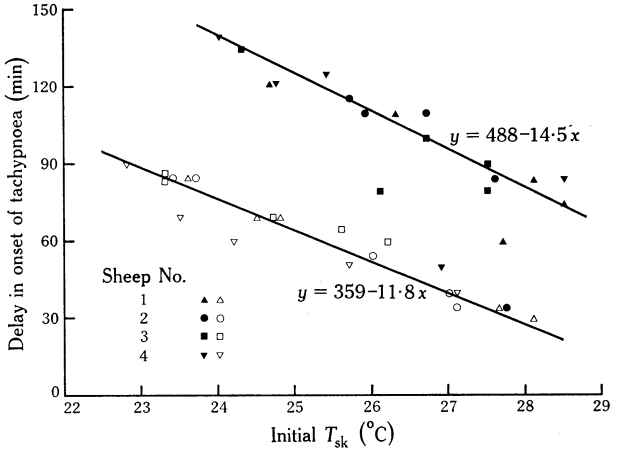


Fig. 4. Relationship between initial T_{sk} and delay in the onset of thermal tachypnoea during exposure of shorn sheep to 42°C in winter and summer. Values for initial T_{sk} were obtained by averaging the T_{sk} measured from four sites on the body surface while the animals were exposed to 14°C immediately before exposure to heat. Each symbol represents one heat exposure.

When exposed to 42°C in winter the sheep showed a rise in T_{re} during the period of exposure to heat of between 0·4 and 1·6°C (mean 0·99±0·07°C). In summer

there was little or no change in T_{re}, the maximum increase recorded being 0·7°C and the mean 0·27±0·07°C.

Body Weights

Between April and July body weight decreased in all animals. This decrease ranged between 1·0 and 2·5 kg (average 1·9 kg). Between November and February all sheep showed a weight gain of between 0·25 and 1·75 kg (average 0·7 kg).

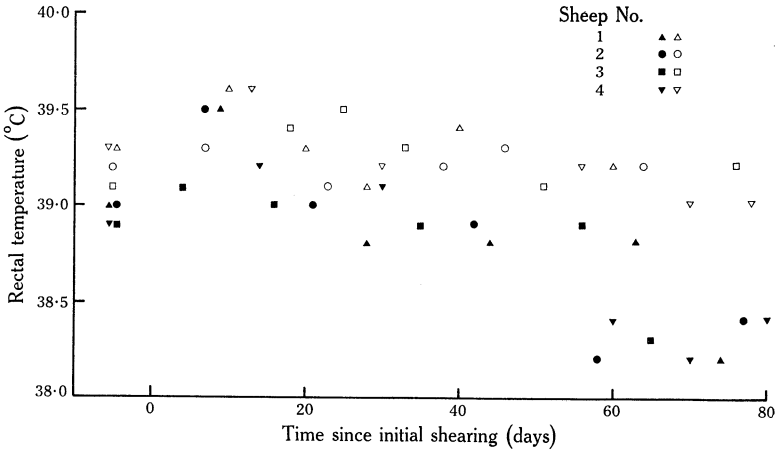


Fig. 5. Rectal temperatures of shorn sheep in winter and summer plotted with respect to the time elapsed after initial removal of the fleece. All measurements of T_{re} were made while the animals were exposed to 14°C. Zero time represents the day on which the fleece was first removed. The data represented by the vertical row of symbols to the left of the zero indicate the T_{re} of each of the sheep on the day prior to the initial shearing.

Discussion

Fig. 1 shows the correlation between the inhibition of thermal tachypnoea and the average T_a recorded in the animal house over the preceding 24 h. Slee (1973*a*) has shown that, under conditions of controlled T_a, inhibition increases with both increase in severity and duration of exposure to cold. Since the animal house T_a is plotted here as an average, it is not possible to determine from the figure whether sheep would show a longer delay before the onset of panting when exposed to roughly equal periods of warm and cold or to a constant intermediate T_a. The position is further complicated by the fact that the thermoneutral point of the sheep was presumably being shifted downwards during the gradual regrowth of the fleece, then suddenly raised again after reclipping. It is possible that during some of the warmer summer days, at least in sheep with advanced fleece regrowth, cold stimulation was completely absent. Indeed, under such conditions tachypnoea was no longer inhibited. Thus in the summer the time during which the animal was exposed to cold was probably important whereas in winter, when cold stimulation was continuous, the degree to which tachypnoea was inhibited would have been related to T_a *per se*. This may be one reason why the winter data in general show a better fit to the regression line in Fig. 1 than do the summer data.

In summer there was a correlation between the number of days that had elapsed between clipping and testing the sheep and the delay in onset of thermal tachypnoea. Such a correlation did not occur in winter until 10 days after clipping, by which time the fleece depth was 5 mm. That the regrowth of the fleece was more rapid in summer than in winter was to be expected, as it has been shown that the rate of fleece growth is governed by photoperiod (Morris 1961). It appears that in the summer the increasing amount of insulation brought about a progressive lessening of the degree of cold received from the environment, whereas in winter the fleece regrowth over the first 10 days was insufficient to combat the lower winter T_a. Winter-shorn sheep, therefore, were wholly affected by the prevailing T_a during the early stages of fleece regrowth, a finding which agrees with that of Armstrong *et al.* (1960).

Fig. 4 shows the very close linear relationship between initial T_{sk} and the delay in onset of thermal tachypnoea. It appears from the data that conditions which provide most peripheral cold stimulation in either winter or summer also produce a lower initial T_{sk}. This suggests that, under the conditions of these experiments, initial T_{sk} could be used both as an assessment of the degree of cold stimulation received from the periphery and as a predictor of the time of onset of thermal tachypnoea during exposure to heat. If this reasoning is adopted it should follow that as cold stimulation was less during summer than winter, then initial T_{sk} should be higher in the summer. As can be seen from Fig. 4 this was not the case. Instead, winter and summer tests yielded two separate sets of data which fitted two straight lines of identical slope. What is more, the mean initial T_{sk} in winter was significantly higher than in summer.

An increased T_{sk}, resulting from an increased blood flow through the periphery, is characteristic of acclimatization to cold in sheep (Sykes and Slee 1969). It is therefore tempting to suggest that the sheep in the present study had become acclimatized to cold in winter. Cold acclimatization involves an increase in basal metabolic rate, which is usually reflected in heat storage and hence in an increased T_{re} (Webster *et al.* 1969; Slee 1972). Moreover, Slee (1973*b*) has shown that acclimatization to cold brings about a reduction in the delay in onset of thermal tachypnoea upon exposure to heat. That metabolic rate initially increased during winter was evidenced by the violent shivering that occurred in newly shorn sheep during the early winter, and an initial increase in heat storage is suggested by the accompanying transient increase in T_{re} (Fig. 5). Sheep invariably show an increase in food intake upon shearing (Webster and Lynch 1966) or on exposure to low T_a (Webster *et al.* 1969), and sheep on a high plane of nutrition show greater ability to acclimatize to cold than those on a low plane (Slee and Sykes 1967). However, it is to be remembered that the dietary ration offered to shorn sheep in winter was no greater than that offered to either unshorn or summer-shorn sheep. And it seems probable that, on the number of calories received, an increased metabolic rate could only be sustained at the expense of stored material. This is supported by the weight losses incurred by winter-shorn sheep. After some weeks the animals no longer appeared to acclimatize to the winter cold, but instead their T_{re} fell as if their thermoregulatory set-point for body temperature had been changed (see Fig. 5). This must have resulted in a net saving of energy. A passive fall in body temperature is not usually seen in shorn sheep, at least during short-term exposure to cold (Webster 1966; Johnson 1971). However, a downward re-setting of the set-point for body temper-

ature in sheep has been indicated by other studies (Hales and Hutchinson 1971), and could have been induced in the present study by an insufficient calorific intake superimposed upon the repeated removal of the surface insulation afforded by the fleece.

That T_{re} should show a greater increase during exposure to 42°C in winter than in summer was to be expected. Heat loss from the upper respiratory tract takes place to an appreciable extent only during thermal tachypnoea. Therefore, the greater delays before the onset of thermal tachypnoea during exposure to heat in winter provided longer periods in which a high chamber T_a coincided with minimal respiratory evaporative cooling, during which time the heat content, and hence T_{re}, of the sheep increased.

In conclusion, if the winter and summer data are examined separately then the results would appear to support Bligh's assertion that the inhibition of thermal tachypnoea can be directly related to the degree of cold stimulation received from the periphery. However, when winter and summer data are compared it becomes apparent that the degree of peripheral cold stimulation *per se* is not the only factor involved, in which case seasonal changes in metabolic rate (Slee 1973*a*, 1973*b*) or changes in the thermoregulatory set-points for shivering and panting might play an important role in determining the time of onset of thermal tachypnoea in shorn sheep exposed to a hot environment.

Acknowledgments

The author wishes to thank Dr J. Bligh for his helpful criticism and comments during the preparation of this paper. Equipment used in the study was purchased with a grant from the scientific committee of the New Zealand Lottery Fund.

References

Armstrong, D. G., Blaxter, K. L., Clapperton, J. L., Graham, N. Mc., and Wainman, F. W. (1960). Heat production and heat emission of two breeds of sheep. *J. Agric. Sci.* **55**, 395–401.

Bligh, J. (1959). The receptors concerned in the thermal stimulus to panting in sheep. *J. Physiol. (Lond.)* **146**, 142–51.

Bligh, J. (1963). Inhibition of thermal polypnea in the closely shorn sheep. *J. Physiol. (Lond.)* **168**, 764–81.

Hales, J. R. S., and Hutchinson, J. C. D. (1971). Metabolic, respiratory and vasomotor responses to heating the scrotum of the ram. *J. Physiol. (Lond.)* **212**, 353–75.

Johnson, K. G. (1971). Body temperature lability in sheep and goats during short-term exposures to heat and cold. *J. Agric. Sci.* **77**, 267–72.

Morris, L. R. (1961). Photoperiodicity of seasonal rhythm of wool growth in sheep. *Nature (Lond.)* **190**, 102–3.

Phillips, G. D., and Raghavan, G. V. (1970). Responses of unshorn and shorn sheep to thermal stress. *J. Physiol. (Lond.)* **208**, 317–28.

Slee, J. (1972). Habituation and acclimatization of sheep to cold following exposures of varying length and severity. *J. Physiol. (Lond.)* **227**, 51–70.

Slee, J. (1973*a*). Cold-induced inhibition of thermal panting in shorn sheep. 1. Effect of intensity of cold exposure. *Anim. Prod.* **16**, 271–83.

Slee, J. (1973*b*). Cold-induced inhibition of thermal panting in shorn sheep. 2. Effect of previous acclimatization to cold. *Anim. Prod.* **17**, 9–19.

Slee, J., and Sykes, A. R. (1967). Acclimatization of Scottish Blackface sheep to cold. 1. Rectal temperature responses. *Anim. Prod.* **9**, 333–47.

Sykes, A. R., and Slee, J. (1969). Cold exposure of Southdown and Welsh Mountain sheep. 1. Effects of breed, plane of nutrition and acclimatization to cold upon resistance to body cooling. *Anim. Prod.* **11**, 65–75.

Webster, A. J. F. (1966). The establishment of thermal equilibrium in sheep exposed to cold environments. *Res. Vet. Sci.* **7**, 454–65.

Webster, M. E. D., and Lynch, J. J. (1966). Some physiological and behavioural consequences of shearing. *Proc. Aust. Soc. Anim. Prod.* **6**, 234–9.

Webster, A. J. F., Hicks, A. M., and Hays, F. L. (1969). Cold climate and cold temperature induced changes in the heat production and thermal insulation of sheep. *Can. J. Physiol. Pharmacol.* **47**, 553–62.

Manuscript received 26 November 1973