Continuous measurement of heart rate as an indicator of the energy expenditure of sheep

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1. The relationship between the heart rate and the energy expenditure of four sheep, S_6, S_7, S_8 and S_1, was studied under conditions known to increase energy metabolism.

2. A close relationship between heart rate and energy expenditure was shown to exist in three of the four sheep tested when energy expenditure was increased by cold exposure and by increased levels of food intake.

3. The source and magnitude of the errors associated with this relationship were studied by analysis of the variation occurring in the O_2 pulse (ml O_2/heart beat) of the sheep in response to factors other than those directly related to changes in heart rate. In two sheep, S_8 and S_6, variations in O_2 pulse were random. The errors associated with the estimation, from heart rate measurements, of the energy expenditure of these sheep were $\pm 6{\cdot}8\%$ and $\pm 8{\cdot}1\%$ respectively. In the other two sheep, S_7 and S_1, O_2 pulse tended to vary significantly during the experiments, in a way that was not directly related to changes in heart rate. The errors of the relationship in these sheep were $\pm 8{\cdot}6\%$ and $\pm 13{\cdot}8\%$ respectively.

4. Indirect evidence was obtained to suggest that continuous measurements of heart rate continued to reflect with reasonable accuracy the energy expenditure of the three sheep, S_6, S_7 and S_8 when they were standing and lying and when they were eating.

5. Direct measurements were made of the O_2 consumption and heart rate of sheep S_7 and S_1 during the act of eating. The energy expenditure of sheep S_7 estimated from its O_2 consumption was close to that estimated from measurements of its heart rate. Large errors were noted between these two estimates in sheep S_1.

6. It was concluded that sheep S_8 and S_6 would be suitable for long-term experiments designed to predict energy expenditure from heart rate measurements made in the field. Sheep S_7 was considered to be of limited value for short-term experiments. Sheep S_1 was considered to be unsuitable.

Much information is available to describe the amount of feed energy required to maintain sheep that are restrained in metabolism cages or respiration chambers. However, much less is known of the energy requirements of sheep grazing out-of-doors, on free range, and exposed to the full effects of the environment. Blaxter (1962) estimated from observations made in respiration chambers that the energy cost of the activity performed by sheep eating a maintenance ration in a thermoneutral environment would increase their total energy expenditure by about 11 %. Graham (1964) predicted on the basis of his experiments that sheep on free range would expend about 25 % more energy than those receiving similar rations in respiration chambers. Several workers have compared the energy requirements of sheep kept indoors in pens and of sheep at pasture, by measuring the intake of digestible organic matter necessary to maintain each group at constant live weight; increased energy requirements have been found for the free-ranging sheep, varying from 25 % (Langlands, Corbett, McDonald & Reid, 1963) to 33–275 % (Lambourne & Reardon, 1963).

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The higher values found in the latter experiments were associated with periods of severe weather and indicate the possible magnitude of the direct effect of cold stresses on the energy requirements of sheep. The best available estimate of the magnitude of these effects is given in the form of a general equation which relates heat losses from sheep to certain measurable characteristics of the outdoor environment (Blaxter, Joyce & Park, 1966).

Discrepancies exist between available estimates of the energy cost of the activity performed by sheep in natural environments. There are also difficulties in relating heat losses from sheep exposed to fluctuating environments to their heat production (Webster, 1966). The need was felt accordingly for a different approach to the estimation of the energy expenditure of the grazing sheep. It is well known that a relationship exists between the heart rate and the O_2 consumption and thus the heat production of man and animals (Henderson & Prince, 1914; Brody, 1945). Several workers have used this relationship to predict from measurements of heart rate, the heat production of men exposed to a variety of conditions (Read, 1924; Lundgren, 1946; Malhotra, Sen Gupta & Rai, 1963). Relatively little information is available, however, to describe the relationship between the heart rate and the heat production of ruminants under conditions other than those of basal metabolism (Blaxter, 1948; Blaxter & Wood, 1951). The present experiments were carried out to determine the extent to which continuous measurements of heart rate could be used to predict the energy expenditure of individual sheep exposed to cold, fluctuating environments similar to those that they might encounter naturally out-of-doors.

EXPERIMENTAL

Animals and rations

Four adult wether sheep of the Suffolk breed, S_6, S_7, S_8, and S_1, were used as experimental animals. All the sheep had been trained previously to become accustomed to the experimental apparatus (Webster & Blaxter, 1966). During most of the experiments, the sheep were fed a standard ration of 800 g dried grass daily in two meals. It was calculated that this amount would prevent them from losing or gaining weight. In some experiments, as indicated below, this ration was increased by the addition of a concentrate mixture in amounts of 400 g or 800 g/day.

Determination of metabolic rate

A ventilated-mask method (Webster, 1966) was used to measure the respiratory exchange of the sheep in all the early experiments. Heat production, Hp (kcal/h), was determined from measurements of O_2 consumption, and CO_2 and CH_4 production (l./h) using the conversion factors of Brouwer (1965):

$$Hp = O_2 \times 3{\cdot}866 + CO_2 \times 1{\cdot}200 - CH_4 \times 0{\cdot}518.$$

This equation slightly overestimates the true heat production of the sheep because no account is taken of the loss of nitrogen in the urine. However, all the determinations of metabolic rate were made over periods of 10–20 min. Measurements of urinary N could clearly not be included in determinations of metabolic rate made over such short periods, particularly in view of the large changes that occurred in the metabolic rate of the animals during the course of most of the experiments.

Sheep S_7 and S_1 were later tracheostomized by the method of Blaxter & Joyce (1963) to permit determinations of their heat production to be made while they were feeding. The air expired by animals tracheostomized by this technique included only a small fraction of the CO_2 and CH_4 arising from the gut. Accordingly, in these experiments Hp was calculated from O_2 consumption alone using the conversion factor of Blaxter & Joyce (1963):

$$\text{Hp} = O_2 \text{ consumption (l./h)} \times 4{\cdot}68.$$

Measurement of heart rate

A method based on electrocardiography was used. A cardiotachometer similar to that described by Beakley & Findlay (1949) was used to record heart rate in double beats/min. In the first series of experiments, three skin surface electrodes placed around the thorax of the sheep were used to record the cardiac potentials. The fleece of the sheep was clipped at the points of contact of the three electrodes and Cambridge electrode jelly was used to ensure good electrical contact. Continuous records of the heart rate of sheep could be obtained by this method only if the animals were restrained in the standing position and remained quiet; interference arising from muscle movement tended to obscure the cardiac signal. In later experiments three stainless-steel wire electrodes were chronically implanted subperiostially on to the fifth rib at a point close to the apex beat of the heart, and to the spinous processes of the third and fourth thoracic vertebrae. Implantation of the electrodes was carried out under general anaesthesia induced by pentobarbitone sodium (Sagatal; May and Baker) and maintained with halothane (Fluothane; ICI). The best ECG signal from the sheep was obtained when the earthed lead to the cardiotachometer was connected to the spinous process of the third thoracic vertebra. Disturbances of the signal obtained in this way due to movement of the animal were very small, so that it was possible to obtain a satisfactory recording of heart rate that was not affected by moderate activity such as walking and eating. Extreme activity, such as running or violent shaking, was liable to give rise to disturbances of the base-line and thus to false counts. In the experiments in which chronically implanted electrodes were used, the voltage output from the heart rate meter circuit in the cardiotachometer was connected through suitable resistances to a 2 mV Honeywell-Brown-Electronik recorder so that full-scale deflexion on the recorder was equivalent to a heart rate of 180 beats/min. In this way a continuous, permanent record of heart rate could be obtained.

Experimental environments

The first two series of experiments were carried out in a refrigerated room in which air temperature could be controlled between $-10°$ and $+10°$ (Webster, 1966). The final series of experiments was done in another refrigerated room, the temperature of which could be thermostatically controlled between $-8°$ and $+10°$. A battery of fans built into the end of a small wind-tunnel could be used to create a mean air velocity over the sheep of 9·9 miles/h. Four infrared heaters sited above the sheep at an angle of about 60° could be switched on to simulate the ameliorating effects of sunshine in cold environments.

Experiments

Four series of experiments were performed.

Series A. A total of fifty-one simultaneous determinations of the heart rate and respiratory exchange of each sheep was made at air temperatures which ranged from the thermoneutral zone to values cold enough to induce a rise in metabolic rate of over 100%. The sheep received a maintenance ration of 800 g dried grass daily throughout these experiments. When these determinations had been made, the ration fed to the sheep was increased by the addition of 400 g concentrates daily. After they had received this ration for a week they were exposed to a thermoneutral environment and ten further determinations of heart rate and respiratory exchange were made. The ration was then increased again, so that each sheep received daily 800 g dried grass and 800 g concentrates, and after 1 week another eleven determinations were made.

Series B. Each sheep was held in the small refrigerated room for a period of 18 days. Air temperature was maintained at a value just below the calculated critical temperature for each sheep, and was reduced by 2° at the end of the 1st and of the 2nd weeks to ensure that the thermal demand of the environment remained approximately constant although the fleece of each sheep was growing. The sheep were restrained in a standing position at about 10.00 h on 4 days each week. Four 15 min determinations of respiratory exchange and heart rate were made between 11.15 h and 12.15 h and another four between 14.15 h and 15.15 h. The sheep were given 800 g dried grass daily in two meals at 05.30 h and 16.00 h.

Series C. Sheep S_6, S_7 and S_8 were each exposed for 8 h periods to five different types of environment in a large refrigerated room. Air temperature was maintained at about 0°. The thermal demand of the environment was increased by switching on the fans (referred to hereafter as windy conditions), and reduced by switching on the infrared heaters (referred to herafter as sunny conditions). The sheep were given 200 g dried grass at the beginning of the 3rd and 7th hours of each experiment. In the 1st and the 8th hours of each experiment the sheep were always exposed to an air temperature of 0° with no appreciable air movement and the infrared heaters off (control conditions). In the middle 6 h of the experiment the sheep were exposed to varying conditions of sun and wind. The skin surface temperatures of the trunk and the extremities of the sheep and the time spent by them in standing and lying were recorded throughout these experiments. No measurements were made of respiratory exchange, but a continuous record of heart rate was obtained from electrodes implanted subperiostially. The direct effects of these fluctuating cold environments on the heart rate and estimated energy expenditures of the sheep will be reported elsewhere.

Series D. Sheep S_7 and S_1 were tracheostomized to permit determinations of O_2 consumption to be made during the act of eating. The heart rate and the O_2 consumption of each of these sheep were determined continuously on four occasions over a period of 150 min. The sheep were fed 400 g dried grass on each occasion after 60 min. Collections of expired air were all of 10 min duration in these experiments. The first two experiments on each sheep were carried out on successive days. Before this, the sheep had been receiving hay and concentrates *ad lib.* After the first two experiments, the sheep were fed a standard ration of 800 g dried grass daily for a period of 1 week before the last two experiments were performed.

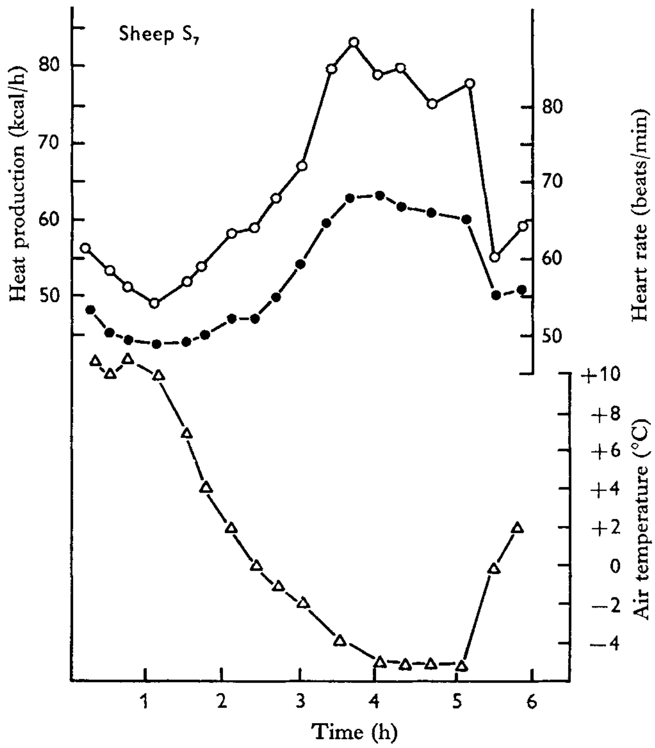

Fig. 1. Effect of varying air temperature (△) on the heart rate (●) and the heat production (○) of sheep S_7.

RESULTS

Effects of cold environments

Fig. 1 shows the results of a typical experiment in which sheep S_7 was exposed to an environment in which air temperature was first lowered gradually and then increased. The figure shows that the variation that occurred in the heat production of the animal as air temperature was altered was very similar to the variation that was noted in its heart rate, and indicates clearly that a relationship between heat production and heart rate could be detected in the presence of a stimulus of varying intensity. The results of the fifty-one simultaneous determinations of the heart rate and the heat production made for each sheep in the first series of experiments are shown in Fig. 2. In this series the sheep were given a constant ration of dried grass and exposed to air

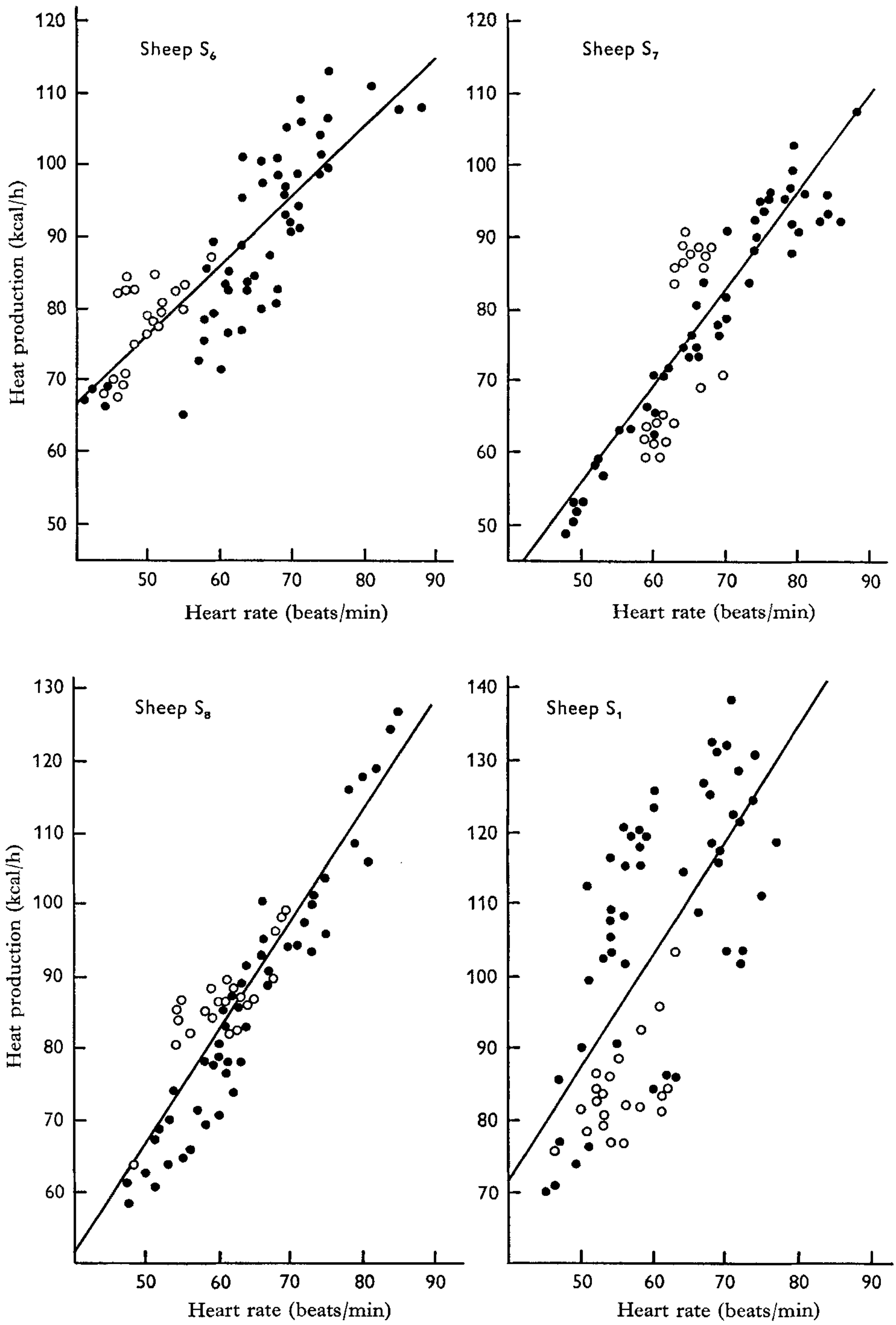

Fig. 2. Relationship between the heart rate and the heat production of four sheep during exposure to cold environments (●) and during periods of increased food consumption (○). The regression lines show the effect of exposure to cold (see Table 1).

temperatures that ranged from the thermoneutral zone to values cold enough to induce large rises in metabolic rate. It is clear from Fig. 2 that a linear relationship existed between the heart rate and the heat production of the individual sheep within the range measured. It is equally clear that the amount of variation associated with the relationship varied between individual sheep.

Table 1. *Regression of heat production on heart rate in four sheep during exposure to cold environments and in a thermoneutral environment at three levels of feeding*

Sheep	No. of expts	Regression	SE of regression coefficient	SE of estimate
		Exposure to cold		
S_6	51	$y = 1.13x+15.96$	±0.108	±7.28
S_7	51	$y = 1.34x-12.37$	±0.058	±4.54
S_8	51	$y = 1.67x-20.80$	±0.068	±4.88
S_1	51	$y = 1.28x+31.05$	±0.202	±13.45
		Effects of feeding		
S_6	29	$y = 0.63x+45.63$	±0.206	±6.08
S_7	29	$y = 1.89x-44.12$	±0.303	±8.72
S_8	29	$y = 1.41x-0.61$	±0.184	±6.22
S_1	25	$y = 1.07x+24.53$	±0.205	±5.05

y = heat production (kcal/h), x = heart rate (beats/min).

The regression equations relating heat production to heart rate in these experiments are given in Table 1. All these regressions were very highly significant statistically ($P < 0.001$). The standard error of the regression coefficients and the standard errors of the estimates were small for sheep S_7 and S_8, slightly larger for sheep S_6 and considerably larger for sheep S_1. The low skin temperature of the extremities of the sheep that was noted in many of the individual experiments was taken to mean that the peripheral vessels of the sheep were constricted. Cold-induced vasodilation of the ears occurred frequently, however, at air temperatures of $-10°$ although on no occasion was it recorded in the shanks. When the sheep were exposed to thermoneutral environments the skin temperature of their extremities was often well above air temperature. There is no suggestion, however, from the individual results that variations in peripheral blood flow in any way affected the relationship between heart rate and heat production as determined in these experiments over 20 min periods.

Effects of increased food consumption

The results of the twenty-one simultaneous determinations of heart rate and heat production made for each sheep in the first series of experiments when their ration of 800 g dried grass was increased by the addition of 400 g and 800 g concentrates in two stages are shown in Fig. 2. These twenty-one determinations and a further eight determinations made in a thermoneutral environment for sheep S_6, S_7 and S_8, when they were receiving 800 g dried grass only, have been used to derive linear regression equations relating heat production to heart rate which are also shown in Table 1. Only four determinations were made for sheep S_1 in a thermoneutral environment when it was receiving 800 g dried grass. The range of heart rate and heat production over which the determinations were made was much smaller than that recorded in cold environments and the standard errors of the regression coefficients were larger for all the sheep. Even so, the regression coefficients for sheep S_6 and S_7 in particular appear to differ markedly from those determined in cold environments. The extent of these differences is discussed below. The weights of the four sheep increased during these experiments by 2·8–6·2 kg, but these increases in weight appeared to have no significant effects on the relationship. The individual differences between the regression coefficients and the intercepts derived for individual sheep in cold environments and during periods of increased food consumption appeared to be random.

Table 2. *Pooled linear regression of (A) heat production and (B) O_2 consumption on heart rate in four sheep*

Sheep	Regression*	SE of regression coefficient	SE of estimate	Percentage error of $\bar{y}$
		A		
S_6	$y = 0.95x+29.10$	±0·076	±7·02	±8·10
S_7	$y = 1.36x-12.40$	±0·083	±6·75	±8·64
S_8	$y = 1.53x-10.01$	±0·079	±5·92	±6·85
S_1	$y = 1.56x+9.15$	±0·202	±14·08	±13·82
		B		
S_6	$y = 0.20x+5.48$	±0·016	±1·47	±8·30
S_7	$y = 0.29x-3.26$	±0·016	±1·33	±8·27
S_8	$y = 0.32x-2.48$	±0·015	±1·13	±6·37
S_1	$y = 0.34x+0.64$	±0·045	±3·14	±14·92

* x = heart rate (beats/min); y = (*A*) heat production (kcal/h), (*B*) O_2 consumption (l./h). Seventy-two observations were made for each animal.

Overall relationship between the heart rate and the heat production of sheep

Table 1 showed that differences existed between the regression equations derived for individual sheep during cold exposure and at different levels of feeding in a thermoneutral environment. However, in only one sheep, S_7, was the difference between the regression coefficients statistically significant ($P < 0.05$). If the seventy-two determinations made for each sheep in cold environments and at three levels of feeding in a thermoneutral environment are pooled as shown in Table 2, then the errors associated with the estimation of heat production from heart rate were markedly increased only in this one sheep. Table 2 includes also the regression equations which describe the overall relationship between the heart rate and the O_2 consumption of the four sheep. It is clear from this table that the errors associated with this relationship were not significantly different from those associated with the relationship between heart rate and heat production as estimated from O_2 consumption and CO_2 and CH_4 production. In the last column in Table 2, the percentage error attached to the estimate of $\bar{y}$, the mean heat production, is shown to have varied from ±6·8% for sheep S_8 to ±13·8% for sheep S_1. The errors associated with the estimation of the heat production of the three sheep S_6, S_7, and S_8 from heart-rate measurements were not very much higher than the residual variation associated with estimates made of the heat production of the same sheep from 20 min measurements of their respiratory exchange (Webster & Blaxter, 1966). The errors associated with the estimation of the heat production of sheep S_1 from measurements of its heart rate were considerably in excess of the residual variation that was associated with direct determinations of its respiratory exchange.

Variations in O_2 pulse

The expression 'O_2 pulse', which is the volume of O_2 consumed per heart beat, was used by Henderson & Prince (1914) to describe the relationship between O_2 consumption (ml/min) and heart rate (beats/min). If the O_2 pulse of an animal does not vary over the physiological range of heart rate, or if it varies in a systematic fashion with heart rate, then the errors associated with the relationship between heart rate and O_2 consumption, and thus heat production, will be small. The extent of the variation associated with measurements of O_2 pulse that is not directly associated with changes in heart rate will determine the accuracy of the relationship between heart rate and O_2 consumption.

Table 3 summarizes partial regression coefficients derived for each sheep from the seventy-two individual determinations of O_2 pulse; they separate the joint effects, on O_2 pulse, of heart rate and duration of exposure of the animal to the conditions of the experiment. The table shows that in all the sheep there was a statistically significant effect of heart rate on O_2 pulse. In two sheep, S_7 and S_8, the O_2 pulse increased with increasing heart rate, and in the other two it decreased. The effect was most significant in sheep S_6. In sheep S_6 and S_8 there was no significant effect of duration of exposure on O_2 pulse. These were the two sheep that had the smallest errors attached to the prediction of their heat production from heart rate measurements. In sheep S_7 a slight, but statistically significant ($P < 0.05$) increase in O_2 pulse occurred during the course of the experimental period. Sheep S_1 showed a marked and very highly significant ($P < 0.001$) increase in O_2 pulse during the experimental periods. As these two sheep accustomed themselves to the conditions of the experiment, therefore, they were able to absorb more O_2 from the pulmonary circulation per heart beat, whatever the magnitude of the stimulus to increased metabolism. The existence of this trend within a day in two out of four sheep suggested that, over longer periods, more marked trends might occur which would introduce further errors into the estimation of O_2 consumption from heart rate measurements.

The results of the experiments in series B, which were carried out to discover whether such trends existed when the sheep were exposed for 3 weeks to a constant mild cold stress, are summarized in Table 4. The table shows that in only one sheep, S_7, was there any significant tendency for O_2 pulse to alter during this period. The O_2 pulse of this sheep increased by 0·9 ml/heart beat during the 3 weeks for which it was exposed to the cold environment. The individual results indicate, however, that most of this increase took place in the 1st week; O_2 pulse remained approximately constant thereafter at about 5.0 ± 0.2 ml/heart beat.

Table 3. *Analysis of partial regression coefficients describing the significance of the joint effects of heart rate (beats/min) and duration of exposure (min) on* O_2 *pulse (ml* O_2*/heart beat)*

(Results of seventy-two observations made for each sheep in series A)

	Heart rate				Duration of exposure			
Sheep	Regression coefficient	SE of regression coefficient	t	Significance	Regression coefficient	SE of regression coefficient	t	Significance
S_6	−0·026	±0·0051	5·56	***	−0·0002	±0·0001	0·48	NS
S_7	+0·012	±0·0041	3·02	**	+0·0008	±0·0004	2·26	*
S_8	+0·010	±0·0040	2·42	*	+0·0005	±0·0003	1·62	NS
S_1	−0·021	±0·0098	2·22	*	+0·0052	±0·0007	7·90	***

NS, not significant. * $P < 0·05$, ** $P < 0·01$, *** $P < 0·001$.

Table 4. *Analysis of partial regression coefficients describing the significance of the joint effects of mean heart rate (beats/min) and duration of exposure (days) on mean* O_2 *pulse/day (ml* O_2*/heart beat day)*

(Results of ninety-six observations made for each sheep in series B)

	Heart rate				Duration of exposure			
Sheep	Regression coefficient	SE of regression coefficient	t	Significance	Regression coefficient	SE of regression coefficient	t	Significance
S_6	−0·004	±0·079	0·01	NS	−0·018	±0·046	0·43	NS
S_7	−0·023	±0·036	2·31	*	+0·050	±0·014	3·81	**
S_8	−0·077	±0·046	0·36	NS	+0·013	±0·034	0·42	NS
S_1	+0·125	±0·053	2·53	*	+0·032	±0·021	1·62	NS

NS not significant. * $P < 0·05$, ** $P < 0·01$.

Effects of standing and lying

In the experiments in series C, in which sheep S_6, S_7 and S_8 were exposed to different degrees of cold stress, the sheep were not restrained in a standing position but were able to stand up and to lie down at will. In the hours in which they were not fed, sheep S_7 lay down on average for 31 min, S_8 for 32 min, and S_6 for 49 min. Continuous records of the heart rates of sheep S_7 and S_8 recorded when they were standing and when they were lying in control, sunny and windy environments were integrated with a planimeter to obtain the mean values shown in Table 5. Records of heart rate made during the hours when the sheep were fed were not included. Effects of eating on heart rate are not therefore considered in this section. The results show that the heart rate of the sheep when they were standing was always greater than when they were lying. This increase was always highly significant statistically ($P < 0.01$). There were, however, no statistically significant differences between the measured increments in heart rate due to standing over lying as determined in the three environmental conditions, control, sunny and windy. Table 5 also shows the mean heat production of the sheep as estimated from their heart rates using the pooled regression equations given in Table 2. According to these estimates, the energy cost of standing in these experiments was 4·5 kcal/kg per 24 h for sheep S_7, and 3·7 kcal/kg per 24 h for sheep S_8. The same two sheep had previously been used to estimate the energy cost of standing by direct measurement of their respiratory exchange (Webster & Valks, 1966). Mean daily measurements ranged from 1·7 to 4·7 kcal/kg per 24 h for sheep S_7, the overall mean being 3·1 kcal/kg per 24 h, and from 1·1 to 3·9 kcal/kg per 24 h for sheep S_8, the overall mean being 2·2 kcal/kg per 24 h. The present estimates, from heart rate measurements, of the energy costs of standing are thus similar to the higher values determined by direct experiment. This is not surprising because the animals in the direct experiments were wearing face masks, were always in thermoneutral environments, and were restrained in such a way as to limit their activity as far as possible. In the present experiments the sheep, which were not tightly restrained, frequently sniffed, scratched, shook or nibbled and generally displayed more activity than they had done in the previous experiments. For this reason the results for sheep S_6 were not included. It has been already stated that this sheep lay down on average for 49 min/h. During the brief periods in which it stood up it usually showed considerable activity and heart rate was nearly always greatly in excess of that recorded when it was lying down. The results obtained with sheep S_7 and S_8 suggest, however, that, although the true energy cost of standing has been slightly overestimated in the present experiments, this was because of the level of activity displayed by the sheep. The results provide good indirect evidence to support the conclusion that the heart rate of these sheep could be used equally well to predict heat production whether they were standing up or lying down.

Effects of eating

The mean heart rates of the sheep determined during the hours in which they were and were not fed are shown in Table 6. From these values the energy cost of eating has again been estimated from the pooled regression equations given in Table 2.

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Table 5. *Energy cost to two sheep of standing compared with that of lying, estimated in three environments from measurements of heart rate*

Sheep	Environment	Mean heart rate (beats/min)		Estimated heat production (kcal/h)*		% increase in heat production on standing	Energy cost of standing (kcal/kg per 24 h)
		Standing	Lying	Standing	Lying		
S_7	C	75 (±7·1)	67 (±3·6)	89	79	11·9	3·9
	W	75 (±5·1)	66 (±6·9)	89	77	13·6	4·4
	S	76 (±5·8)	65 (±4·1)	91	76	16·9	5·1
Mean				90	77	14·1	4·5
S_8	C	64 (±4·7)	58 (±3·5)	88	79	9·2	3·5
	W	61 (±3·2)	54 (±4·6)	83	73	10·7	4·0
	S	64 (±3·6)	58 (±2·9)	88	79	9·2	3·5
Mean				86	77	9·7	3·7
Overall mean				88	77	11·9	4·1

C = air temperature of 0°; W = air temperature of 0° and air movement of 9·9 miles/h; S = air temperature of 0° and infrared heaters on.
Figures in parentheses are standard deviations.

* See Table 2.

Table 6. *Energy cost to three sheep of eating 200 g dried grass, estimated from their mean heart rates determined during the hours in which they were and were not fed*

Sheep	Mean heart rate (beats/min)		Estimated heat production (kcal/h)*		Time spent eating (min)	Estimated energy cost of eating		
	Fed	Not fed	Fed	Not fed		cal/g food	kcal/min spent eating	cal/kg body-wt min spent eating
S_8	74 (±4·8)	62 (±4·9)	103	85	12	85	1·4	22
S_7	83 (±4·8)	70 (±5·1)	100	83	13	90	1·3	22
S_6	80 (±7·7)	59 (±7·3)	105	85	14	100	1·4	23
Mean			103	84	13	92	1·4	22

Figures in parentheses are standard deviations.

* See Table 2.

The results show that there was very good agreement between individual estimates of the energy cost of eating in the three sheep. This was possibly fortuitous. The estimated energy cost of eating was 92 cal/g food consumed. Previously published estimates of the energy cost of eating dried grass range from 40 cal/g (Blaxter, 1960) to 120 cal/g (Armstrong, Blaxter & Graham, 1957). The results given in Table 6 suggest therefore that heart rate continued to reflect with reasonable accuracy the changes that occurred in the heat production of these sheep during the time they were eating.

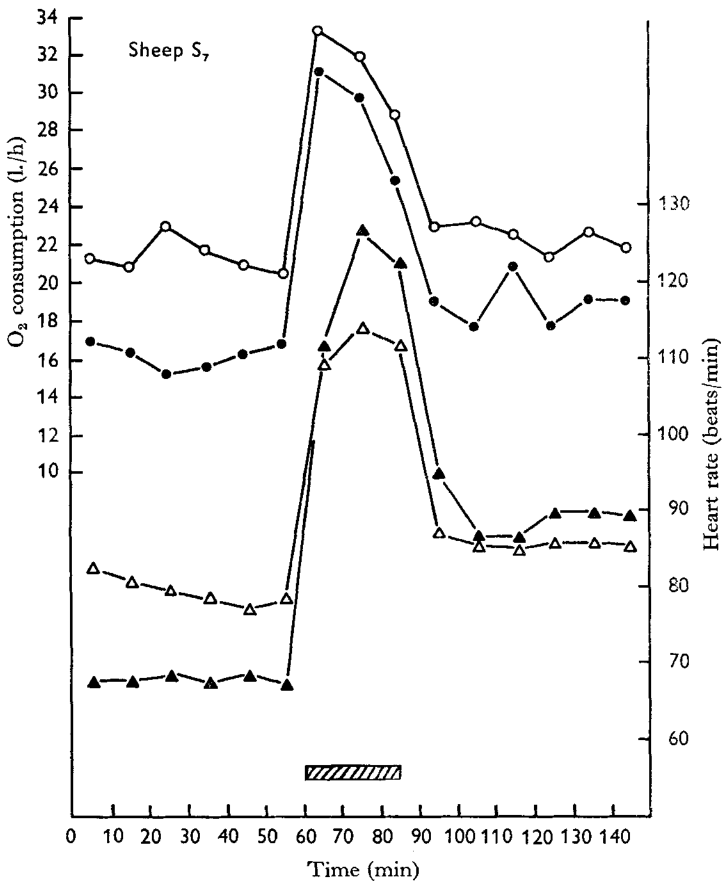

Fig. 3. Effect of eating on the heart rate (△, first series; ▲, second series) and oxygen consumption (○, first series; ●, second series) of sheep S_7. Shaded area shows time of eating.

Sheep S_1 and S_7 were subsequently tracheostomized so that direct, simultaneous measurements of their heart rate and O_2 consumption could be made during the act of eating. It has already been stated that these were the two sheep which showed the greatest errors associated with the estimation of their heat production from heart rate measurements. However, previous reports had indicated that survival of tracheostomized sheep for periods of more than 9 months was rare (Cresswell & Harris, 1961; Blaxter & Joyce, 1963). It was decided therefore not to tracheostomize sheep S_6 and S_8

because of their potential value as suitable sheep for use in later experiments designed to predict energy expenditure from heart rate measurements made out-of-doors. Fig. 3 illustrates the effect of eating on the O_2 consumption and the heart rate of sheep S_7. The figure gives the mean values obtained for O_2 consumption and heart rate in the first two experiments performed after a week in which the sheep had been fed hay and concentrates *ad lib.*, and the mean values obtained in the last two experiments performed after the sheep had been receiving a maintenance ration of 800 g dried grass for 1 week. Both the resting O_2 consumption and heart rate of sheep S_7 were higher in the former experiments than in the latter. The figure also shows that both the O_2 consumption and the heart rate of the sheep increased markedly as soon as they began to feed. The absolute values recorded for the O_2 consumption of the sheep during the act of eating were similar in both pairs of experiments. The increase

Table 7. *Effect of eating on the heart rate, oxygen consumption and estimated heat production of two sheep*

(Each figure represents the mean of four experiments)

Sheep		Heart rate (beats/min)	O_2 consumption (l./h)	Estimated heat production (kcal/h)	
				From O_2 consumption	From heart rate†
S_7	Before meal	74	18·8	88·2	88·2
	During meal	112	27·9	130	139
	After meal	88	20·9	97·8	107
S_1	Before meal	70	20·4	95·5	118
	During meal	109	29·7	139	179
	After meal	78	21·3	99·7	131

* Heat produced = O_2 consumption (l./h) × 4·68.
† See Table 2.

in O_2 consumption noted during eating was therefore greater in the second series of experiments. The heart rate during eating was rather higher in the second series of experiments. The results showed that the O_2 consumption of the sheep during the act of eating rose to about 32 l./h in the first 10 min of eating and fell slowly thereafter to about 28 l./h. The increase in heart rate during eating was more gradual, reaching a peak after about 15 min. After the sheep had finished eating, O_2 consumption and heart rate both fell. The O_2 consumption fell to values not markedly different from those observed before the meal, but heart rate remained 10–20 beats/min higher than that recorded before the meal. These results agree closely with those of Blaxter & Joyce (1963) and of Young (1966) who observed a substantial increase in the rate of energy expenditure of tracheostomized sheep during eating which did not persist into the postprandial period. Clearly, a relationship between heart rate and heat production existed in sheep S_7 during the act of eating. However, if Fig. 3 is compared with Fig. 1 it can be seen that the relationship was much less exact than when the heart rate and heat production of the same sheep were elevated by increasing cold stress.

Even so, Table 7 shows that the mean heat production of sheep S_7 during feeding as estimated from measurements of its O_2 consumption was 130 kcal/h. The mean heat production as estimated from measurements of its heart rate from the regression equation given in Table 2 was 139 kcal/h. For this sheep, therefore, the differences between the observed and predicted values for heat production during the act of eating were small. Table 7 also shows, however, that the differences between the observed and predicted values for the heat production of sheep S_1 during eating were very large indeed. These few direct measurements tend to confirm the observation made from indirect experiments that the heat production of sheep S_7 could be predicted with reasonable accuracy from heart rate measurements while it was feeding, whereas the errors associated with the relationship in sheep S_1 were so large as to make such predictions worthless.

DISCUSSION

The results of the experiments show that a close relationship existed between the heart rate and the heat production of three of the four sheep tested in the presence of different and fluctuating stimuli to increased metabolism. The results obtained during exposure of the sheep to cold environments and those obtained in a thermoneutral environment at three levels of feeding were pooled and linear regression equations were derived to describe the overall relationship.

The range of heart rates and heat productions over which these measurements were made was, however, relatively small. The heart rate of the sheep during these determinations never exceeded 90 beats/min. It is not possible therefore to state how accurately the linear relationship between heart rate and heat production would hold at heart rates, for example, in excess of 100 beats/min such as those recorded during feeding or during exercise. However, Wyndham, Strydom, Maritz, Morrison, Peter & Potgeiter (1959) showed that a linear relationship existed between the heart rate and O_2 consumption of individual men during exercise, until heart rate approached an upper limit of about 180 beats/min. This suggests that the linear relationships obtained for the individual sheep in the present experiments may persist at values for heart rate considerably in excess of those on which the present linear regression equations were based. The reasonably good agreement between values predicted for the heat production of sheep S_7 from O_2 consumption and from heart rate measurements made during feeding when heart rate was over 100 beats/min lends support to this conclusion.

It was shown that considerable day-to-day variation occurred in the O_2 pulse of all four sheep. Such variation was, of course, included in the errors associated with the original seventy-two determinations of the heart rate and heat production of the sheep which were made on 6 days over a period of about 6 weeks. In the three sheep S_6, S_8 and S_1 there was no evidence to suggest that the day-to-day variation represented any tendency for their cardiorespiratory performance, as indicated by changes in O_2 pulse, to alter in any systematic fashion during continuous exposure to a cold environment. The O_2 pulse of sheep S_7, however, did increase markedly during the 1st week of exposure to a constant cold environment. In sheep S_1 there was a significant tendency for O_2 pulse to increase during the course of each day. In view of the existence of these trends in the O_2 pulse of the sheep S_7 and S_1 it is not surprising that these should have been the two sheep which showed the largest errors associated with the pooled estimates of their heat production from the experiments in series A.

Sheep S_8 and S_6 showed no significant trends in O_2 pulse that were not associated with changes in heart rate. The effect of the total random variation in the O_2 pulse of these two sheep was to introduce errors into the estimation of their heat production from heart rate measurements of $\pm 6{\cdot}8\%$ and $\pm 8{\cdot}1\%$ respectively. It is reasonable to assume therefore that simultaneous determinations of the heart rate and heat production of these two sheep made over a number of days might be used thereafter to predict heat production from heart rate measurements, certainly for 3 weeks, and possibly for much longer periods, without significantly altering these errors. The error term for sheep S_7 was $\pm 8{\cdot}6\%$ and for sheep S_1 $\pm 13{\cdot}8\%$. When the errors associated with the tendency for the O_2 pulse of sheep S_1 to increase during the course of each day were removed by partial regression analysis, the random error term was reduced only to $\pm 11{\cdot}6\%$ which was still considerably greater than that found for the other three sheep. Sheep S_1 was therefore considered to be unsuitable for use in experiments designed to predict heat production from heart rate in cold environments. The large discrepancy noted between the measured and the predicted heat production of this sheep during the act of eating reinforces this conclusion. Much of the discrepancy between the heat production and heart rate of sheep S_1 can be attributed to the fact that this animal was of an unusually nervous disposition and often showed marked, transient increases in heart rate when disturbed by the sound or appearance of people. Such nervous reactions were not noted in the other three sheep. The relatively small random variation associated with measurements of the O_2 pulse of sheep S_7 suggests that it could be used in such experiments if it were recalibrated for heat production with respect to heart rate at frequent intervals.

In three of the four sheep tested, then, the errors of the relationship between heart rate and heat production were less than $\pm 10\%$. These errors, though considerable, are small in comparison with the very large discrepancies that exist between the different available estimates of the increased energy requirements of grazing sheep over sheep fed indoors in pens. Clearly, therefore, the technique of using continuous measurements of heart rate to indicate the heat production of sheep has an application to studies in the energy metabolism of the free-ranging animal.

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