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Effects of Environmental Temperatures and Carbon Dioxide Levels on Physiological Responses of Sheep

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Summary

1. The physiological responses of sheep were observed with the environmental CO_2 level adjusted to 0.03%, 1–2%, 2–3% and 6–8% and the environmental temperature controlled at 10°C, 20°C and 35°C.
2. The rectal temperature increased as the environmental temperature increased, irrespective of the CO_2 concentrations in sheep A and sheep B. On the other hand, the rectal temperature decreased as the CO_2 level increased in every tested environmental temperature.
3. A marked increase of heart rate was observed when the environmental CO_2 concentration was above 4–5%.
4. As the environmental CO_2 concentration increased, the respiration rate was only slightly changed increasing a little under the environmental temperatures of 10°C and 20°C but it remarkably decreased at the temperature of 35°C. However, the respiratory minute volume generally increased because of the increase of tidal volume whatever the respiration rate change was.
5. The CO_2 concentration in the expired air increased as the environmental CO_2 level increased. The arterial CO_2 increase was not so noticeable up to 2–3% of environmental CO_2 but it was remarkable in 6–8% CO_2.
6. The arterial blood pH was lowered by the increase of environmental CO_2.

When a ruminant is used as a experimental animal in the closed circuit type environmental controlled chamber for an extended period, the accumulated CO_2 and methane and decrease of oxygen in the air may affect the physiological activities of the ruminant. Knowleton *et al.* (1) demonstrated that the sheep can survive in air with 18% CO_2 content but that forced breathing develops and the digestive abilities are lowered to some extent. It is generally recognized that the decrease of O_2 content in the air to as low as 16% may have no harmful effect

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on animal responses, but that a slight increase of CO_2 concentration may affect them.

A series of experiments were performed in this paper to observe the effects of and mutual correlation between environmental temperature and CO_2 on the physiological reactions of sheep.

Materials and Methods

Experimental animal: Three Corridale rams were used. They were named A, B and C. Their body weights were 47, 50 and 40 kg, and their wool length 1–1.5, 1–1.5 and 5–7 cm respectively. They were preliminarily trained to be quiet in the stall which was placed in the environment controlled chamber during the experimental period.

The duration of each experiment was 8 hours starting 3 hours after the feeding in sheep A and B. In sheep C, the duration of the experiment was 3 hours starting 20 hours after feeding.

They were fed orchard grass, hay and mixed commercial concentrate so as to maintain their body weight. The ambient temperature was adjusted at 10°C, 20°C and 35°C and the relative humidity was controlled at 70% for each temperature. The CO_2 concentration in the air was controlled at the level of 0.03, 1–2, 2–3, 4–5, and 6–8%. The 0.03% CO_2 concentration means ordinary air CO_2 with no adjustment. The adjustment of CO_2 concentration was accomplished roughly by scattering the several pieces of dry ice in the chamber and finely by injecting CO_2 gas from CO_2 tanks into the chamber. The range of fluctuation of CO_2 concentration in the air was within ±1%. So the CO_2 concentration in this experiment was expressed, for example, as 1–2%. In the experiment of 6–7% CO_2, however, the upper level of CO_2 concentration sometimes reached to 8%. The data, therefore, for the range of 6–7% CO_2 was expressed as 6–8% CO_2.

In the experiment of 35°C and 6–8% CO_2 concentration the CO_2 because of mechanical failure reached nearly 10%.

When the CO_2 concentration in the air was above 5%, the investigators in the chamber had to wear aqua lung face masks to avoid abnormalities which they might have felt owing to high CO_2 concentrations.

Items for measurement: The rectal temperature (5 cm depth from anus), respiration rate and heart rate were measured by thermister, thorax pick up (a rubber tube filled with $ZnSO_4$) for respiratory movement and electrocardiogram, respectively. The above three items were measured every 10 minutes. The respiration and heart rates were shown in the data as a mean for 5 minutes of measurement.

The expired gas was collected every 30 or 60 minutes into a Douglass bag for 3 minutes. The volume of the expired gas was measured by a dry type gas meter. Through carotid loop, 5 ml of arterial blood was sampled every 30 or 60 minutes into a test tube sealed with liquid paraffin to avoid exposure to the air. The whole blood pH and CO_2 content were measured by glass-electrode pH meter and the micro diffusion method, respectively. The CO_2 concentrations in the air and in the expired gas were analysed by the Haldane method (Roken type analyser) in the experiments with sheep A and B and by infrared analyser (Fuji Elec. Co.) in that of sheep C.

The atmospheric pressure was measured by a Fortin type barometer.

Experimental design: The date of experiment for sheep A and B was in January and February, 1969 and for sheep C was from August 1964 to March 1965. The total experiment time for each sheep is shown in Table 1. Since the experiment time was different for each sheep, the number of data were accordingly different. In the experiments for sheep A and B, two days made a set. In the first day experiment, called control, the CO_2 content in the air in the chamber was not raised under one ambient temperature. In the second day, the CO_2 content in the air in the chamber was gradually increased beginning from 0.03% to 1–2%, 2–3% and 6–8% under the same ambient temperature as the first day. Each CO_2 concentration was maintained for 90 minutes.

TABLE 1. *Total Experimented Time in the Three Sheep*

CO_2 concentration in the air	Environmental temperature	10°C			20°C			35°C		
		sheep A	sheep B	sheep C	sheep A	sheep B	sheep C	sheep A	sheep B	sheep C
Control	Total exp'd time	min. 260	min. 270	min. 90	min. 270	min. 270	min. 220	min. 270	min. 270	min. 250
1–2%	Total exp'd time	90	80	—	90	90	—	90	90	—
2–3%	Total exp'd time	90	80	40	90	90	120	90	90	40
4–5%	Total exp'd time	—	—	50	—	—	280	—	—	250
6–8%	Total exp'd time	90	80	—	90	90	—	90	90	—

In the experiment on sheep C, one CO_2 concentration was imposed on the animal under one constant ambient temperature in one day experiment. One constant CO_2 level was maintained for one hour.

Results

Rectal Temperature: Under each CO_2 concentration, the rectal temperature increased significantly ($P<0.01$) as the ambient temperature increased (Fig. 1). One exception was that in sheep C when the rectal temperature tended to decrease

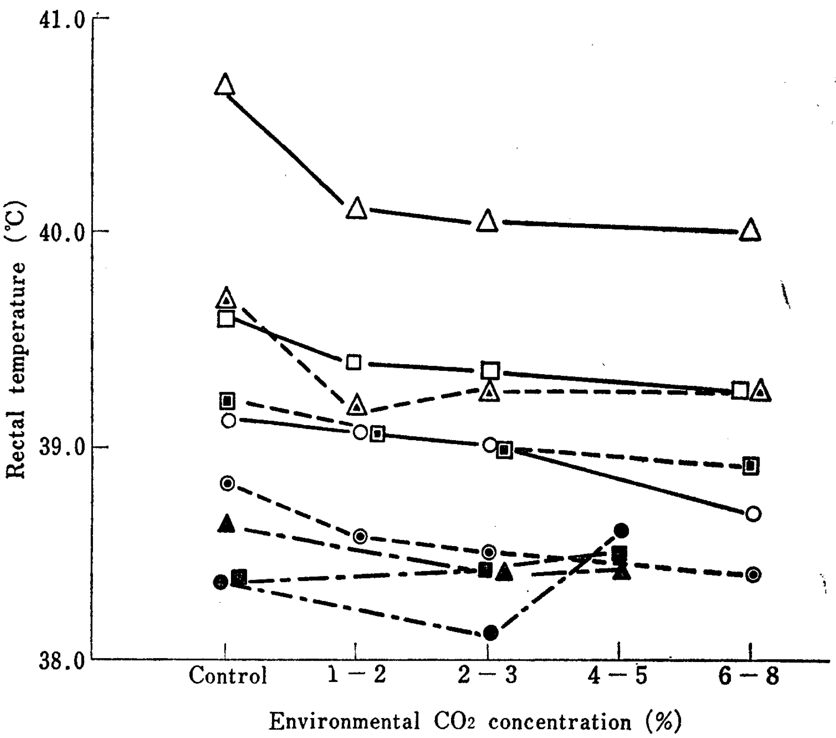

FIG. 1. Effect of environmental temperature and CO_2 concentration on rectal temperature of sheep.

	10°C	20°C	35°C
Sheep A	—○—	—□—	—△—
Sheep B	---⊙---	---▣---	---◭---
Sheep C	—·●·—	—·■·—	--·▲·--

as the ambient temperature increased when ambient CO_2 concentration was 4–5%. The reason of this might be due to low body temperature at the beginning of experiment and to the low reactibility of sheep C since the experiment of 35°C was held on February, though that of 10°C and 20°C were performed August through October.

Under the same ambient temperature, the rectal temperature decreased significantly ($P<0.05$) as the ambient CO_2 concentration increased in sheep A and sheep B. This tendency was not remarkable in sheep C because of a smaller number of experiments and of a colder season in a year.

Heart Rate: The heart rate change is shown in Fig. 2. In sheep B and C, the heart rate remained unchanged even though the ambient temperature was 35°C, if the ambient CO_2 was maintained lower than 4–5%. In sheep A, however, the heart rate increased to 141 beats/min at ambient temperature of 35°C under control CO_2 concentration. This was 70 beats/min increase from the mean heart rate of 71 beats/min at environmental temperature of 10°C and 20°C.

Under one constant environmental temperature whatever it was, the heart rate slightly increased when the ambient CO_2 concentration reached 4–5%. When the CO_2 concentration became 6–8%, a remarkable heart rate increase was

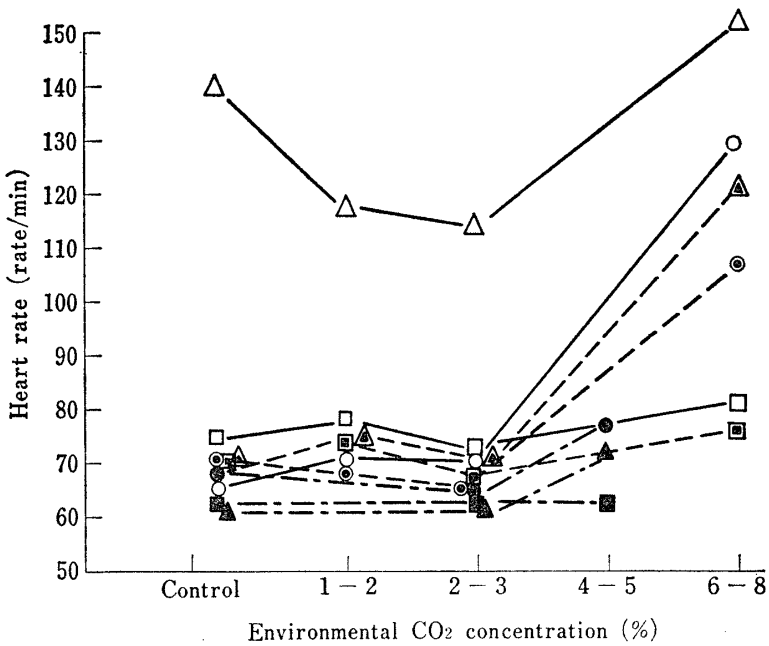

FIG. 2. Effect of environmental temperature and CO_2 concentration on heart rate of sheep.

	10°C	20°C	35°C
Sheep A	—○—	—□—	—△—
Sheep B	- - -⊙- - -	- - -▣- - -	- - -▲- - -
Sheep C	---●---	---■---	---▲---

observed, especially under the environmental temperature was 10°C and 35°C. In sheep A, different from the other two sheep, the heart rate decreased from the control level when the ambient temperature and CO_2 concentration were 35°C and 1–3% respectively. This might be caused by an extraordinary heart rate increase under 35°C and control CO_2 conditions.

Whenever the heart rate increased, the respiratory pattern also changed from shallow and fast to deep and slow.

Respiratory Function: a) Respiration rate. Whatever the CO_2 concentration in the air was, the respiratory rate clearly increased as the ambient temperature was raised. On the other hand, under one fixed temperature, the respiratory rate change accompanied with the CO_2 concentration increase was rather complicated. As the CO_2 concentration rose, the respiratory rate increased at 10°C in every sheep but it decreased (sheep A), remained unchanged (sheep B) or slightly increased (sheep C) at 20°C. At 35°C, as the CO_2 concentration increased, the respiratory rate decreased to about half of that of the control level (Fig. 3).

b) Respiratory minute volume. The minute volume was expressed as BTPS in sheep A and B, but as ATPS in sheep C, because of no measurement of atmospheric pressure in the sheep C experiment.

The minute volume increased as the ambient temperature increased, it was distinguishable especially in the case of 35°C (Fig. 4). However, the extent of minute volume increase depended on the individual sheep. The one exception was that the minute volume in 10°C was bigger than that of 20°C under 6–8%

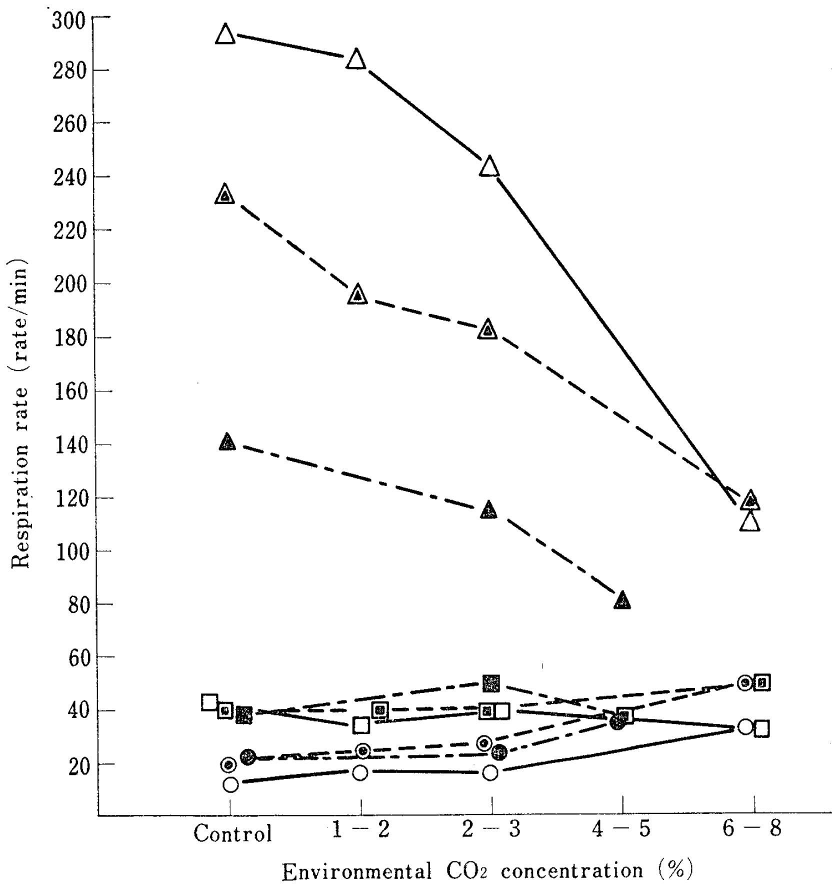

FIG. 3. Effect of environmental temperature and CO_2 concentration on respiration rate of sheep.

Sheep A —○— ; Sheep B ---⊙--- ; Sheep C ---▲--- } 10°C
—□— ; ---▣--- ; ---■--- } 20°C
—△— ; ---▲--- ; ---▲--- } 35°C

CO_2 condition in sheep B.

The CO_2 concentration increase accompanied the minute volume increase under one environmental temperature. In 6–8% CO_2 concentration, the minute volume increased about 6 times as high as that of the control CO_2 level under the temperatures of 10°C and 20°C but under 35°C it was only 1.3 times that of the control. Since the ventilation ability of the sheep had already reached maximum at 35°C under the normal CO_2 (0.03%) level, the effort on the sheep of further increase of the minute volume corresponding to the increment of the CO_2 level might be impossible physically.

In sheep A, the minute volume decreased below control level when the CO_2 and temperature were 1–3% and 35°C, respectively. This change coinciding with the decrease of heart rate may be explained that the animal in the control experiment was in a restless state.

c) Tidal volume. During the period of expired gas collection into the Douglass

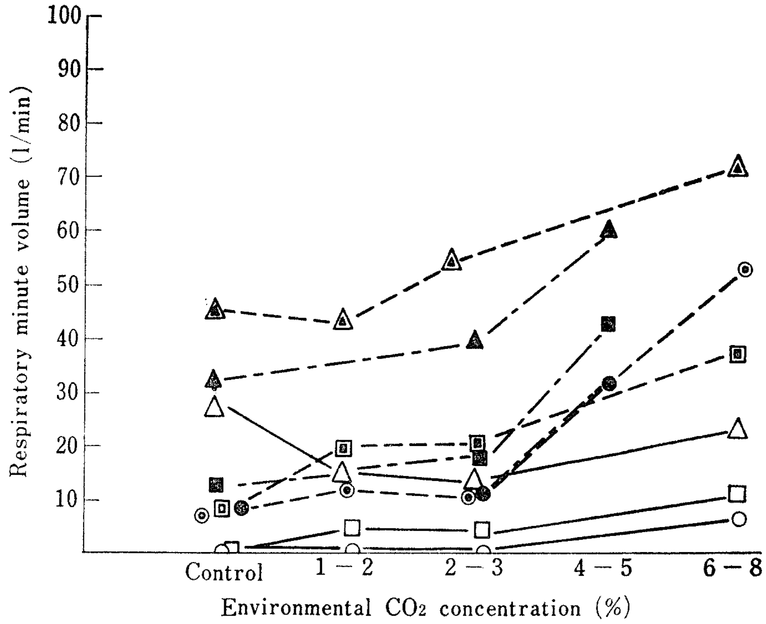

FIG. 4. Effect of environmental temperature and CO_2 concentration on respiratory minute volume of sheep.

Sheep A —○— ; —□— ; —△—
Sheep B ---◎--- 10°C ; ---▣--- 20°C ; ---▲--- 35°C
Sheep C ---●--- ; ---■--- ; ---▲---

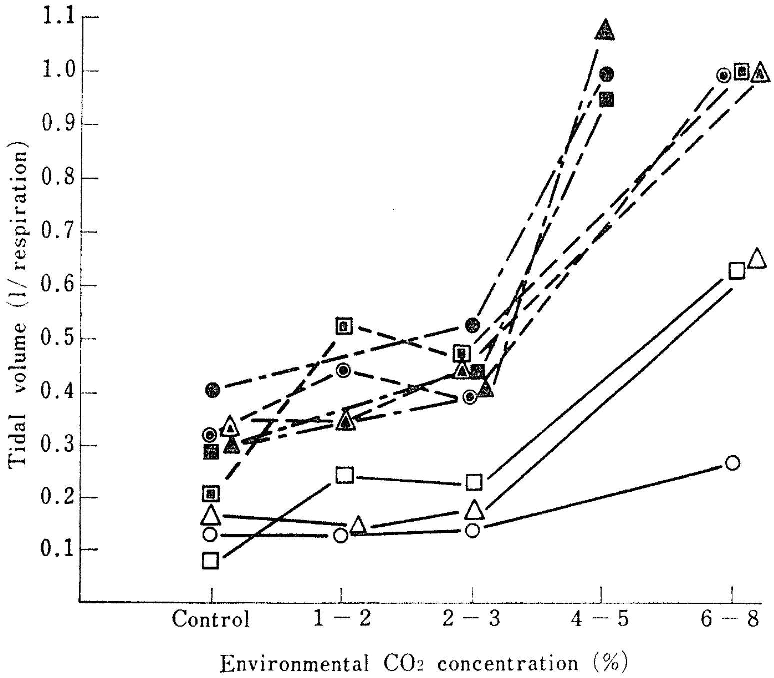

FIG. 5. Effect of environmental temperature and CO_2 concentration on tidal volume of sheep.

Sheep A —○— ; —□— ; —△—
Sheep B ---◎--- 10°C ; ---▣--- 20°C ; ---▲--- 35°C
Sheep C ---●--- ; ---■--- ; ---▲---

bag through the face mask, the respiration rate was not the same as that of the uncollected period. The tidal volume, therefore, was computed using the respiration rate taken at the expired gas collection period (Fig. 5). Under one CO_2 concentration, no one directional change of tidal volume was found as the temperature increased. Whatever the temperature was, on the other hand, the tidal volume increased as the CO_2 concentration increased from control level to 1–2% but it leveled off during the 2–3% CO_2 period, followed by a remarkable re-increment which was three times higher than the control value during the higher CO_2 concentration period. The maximum tidal volume of each sheep was obtained during the 4–5 or 6–8% CO_2 concentration period except for the value obtained in the 10°C and 6–8% CO_2 experiment on sheep A.

Respiratory and Arterial Blood CO_2 Concentrations and Arterial Blood pH: Respiratory and arterial blood CO_2 concentrations and arterial blood pH changes are summerized in Fig. 6. These data were obtained only from sheep A and B.

Respiratory CO_2 concentration was expressed as BTPS. As the temperature

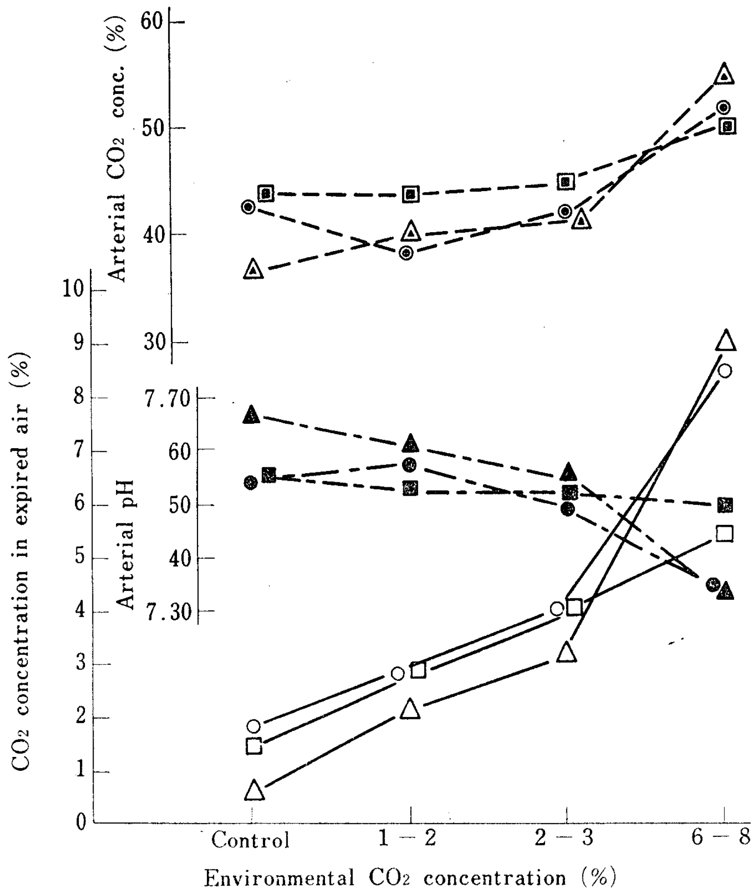

FIG. 6. Effect of environmental temperature and CO_2 concentration on CO_2 concentration in arterial blood and in expired gas and arterial pH

	10°C	20°C	35°C
Expired air CO_2 concentration	—○—	—□—	—△—
Arterial pH	-·-●-·-	-·-■-·-	-·-▲-·-
Arterial CO_2 concentration	---◉---	---▣---	---◬---

increased, respiratory CO_2 concentration decreased as high as 2–3% of environmental CO_2 concentration. Since the respiration rate increased as the temperature increased, the time required for one respiration had to be shortened, though the tidal volume did not clearly change. As a result, the insufficient gas exchange between alveolar and pulmonary artery would lead to the low expired CO_2 concentration. The expired CO_2 concentration remarkably increased as the ambient CO_2 concentration increased, whatever the ambient temperature was.

In the 6–8% ambient CO_2 concentration and 35°C experiment, the expired air CO_2 concentration reached 8.99%. This was mainly due to the high environmental CO_2 concentration which exceeded 9% because of the measuring instrument failure.
Arterial blood pH: In the control experiment, the arterial blood pH inclined to become more alkaline as the environmental temperature increased. This would be due to the respiratory alkalosis which was induced by the increased tidal volume caused by the high respiration rate in the high ambient temperature. The same tendency as above was observed up to 2–3% CO_2 concentration.

As the ambient CO_2 concentration increased, on the other hand, the blood pH was lowered in every experimental temperature. This would be explained with the reason that the increase of CO_2 absorption from the alveolar air to the blood due to the deeper respiration accompanied with a CO_2 concentration increase in the inspired air lowered the blood pH. The extent of this blood pH decrease was largest in 35°C and smallest in 20°C. In the experiment of 35°C and 6–8% (actually 9–10%) CO_2 concentration the lowest pH value (7.33) was measured.

Arterial CO_2 concentration: The CO_2 concentration changes in the arterial blood corresponded reversely to the changes of arterial blood pH. In the control experiment, when the environmental temperature increased to 35°C the blood CO_2 content decreased due to the high respiration rate. Up to 2–3% CO_2 concentration in the air, however, the CO_2 content in the blood was maintained in the normal range in every experimental temperature, because of the regulatory mechanism of deepening the respiration. On the contray, when the CO_2 concentration in the air increased to 6–8% the CO_2 content in the blood exceeded the normal range. This fact was assumed to be due to the CO_2 in the air being absorbed in the blood because of the partial pressure of CO_2 (about 55 mm Hg) in the air being higher than that in the blood (about 25 mm Hg).

Discussion

In the present experiment, the ambient CO_2 concentrations was increased by blowing pure CO_2 into the air in the closed room, therefore, the O_2 content in the air was maintained. In this regard, as for as the environmental gas content is concerned, the observed physiological responses of sheep were considered mainly due to the CO_2 content in the air.

The rise of body temperature responding to the air temperature increase was suppressed by the increase of CO_2 content in the air. This was observed even as low as 1–2% CO_2 content. The possible reasons of this phenomenon were 1) the increase of heat loss as the result of the increase of respiratory minute volume, 2) the fall of metabolic rate, 3) anesthetic effect of CO_2 on the body temperature controlling center in the brain. Chapin and Edgar (2) reported the same observation in the rat and concluded that this effect was more remarkable under low environmental temperatures. In the present experiment, however, such a cooling effect was more noticeable under a high environmental temperature. The discrepancy might be due to the differences of animal species and CO_2 concentrations.

Whether the heart rate of sheep increases or not in high (35°C) environmental temperatures with medium humidity depends on the individual animal. In the present experiment, the heart rate increase at 35°C with 70% humidity and normal CO_2 content was observed only in one sheep (sheep A). On the other hand, the heart rate of every sheep increased in response to a CO_2 concentration higher than 4%. The reason of this may be explained by the lowered blood pH due to high blood CO_2 content stimulated the chemoreceptors in the aortic, carotid bodies and the cardiovascular centers (3).

The respiration rate was regarded as a physiological index to the extent of thermal stress on the sheep because the respiration rate responded so sharply to the increase of temperature (4).

The extent of respiration rate change due to CO_2 content increase in the air is less in sheep than in man and rabbit (5) when the environmental temperature was 10°C and 20°C. However, the respiration rate of sheep remarkably decreased according to the CO_2 content increase under high temperature.

The respiration pattern changed from normal to deep as the CO_2 content in the air increased, irrespective of the temperature. It is well known that the respiratory minute volume increased as the temperature rises in order to increase the heat loss from the body in the sheep. The respiratory minute volume also increased under high CO_2 concentration in the air in order to increase the efficiency of gas exchange. When both temperature and CO_2 concentration in the air increased, the extent of respiratory minute volume increase was most remarkable.

In sheep A, apart from the other two animals, the remarkable heart rate and body temperature increases were observed in the 35°C experiment. This would be recognized as a low respiratory function of sheep A, as indicated by the low respiratory minute volume in spite of the high respiration rate.

The respiratory CO_2 content (about 1.5%) under control ambient conditions was exceedingly low compared with that of man (about 4%). The reason may be partly explained by the low CO_2 (25 mm Hg) content in the arterial blood. On the other hand, larger minute volume (10 l/min) in the experimental sheep than that of man (6 l/min) will partly conpensate for the low CO_2 content in the expired air.

As for the value of arterial CO_2 content and pH, it was assumed that the alveolar ventilatory function were effective up to 2–3% of ambient CO_2 content. Above 6 ~8% of ambient CO_2 content, however, the respiratory function could not function to maintain the arterial CO_2 content and pH within the normal range.

Mullenax and Dougherty (6) observed in sheep increases of heart rate and arterial CO_2 and decreases of respiration rate and arterial pH under 68% CO_2 and 32% O_2 conditions. The present data agreed with those data, though the extent of change was relatively small in ours. No collapse or convulsive seizures were observed in the experimental sheep in the present experiment.

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