

RESPIRATORY AND CARDIOVASCULAR RESPONSES OF THE EXERCISING CHICKEN TO SPINAL CORD COOLING AT DIFFERENT AMBIENT TEMPERATURES

II. RESPIRATORY RESPONSES

By M. GLEESON*, G. M. BARNAS† AND W. RAUTENBERG

*Ruhr-Universität Bochum, Arbeitsgruppe Temperaturregulation,
D-4630 Bochum, F.R.G.*

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SUMMARY

1. We measured oxygen consumption (\dot{V}_{O_2}), carbon dioxide production (\dot{V}_{CO_2}), minute volume (\dot{V}_E), respiratory frequency (f) and tidal volume (V_T) of chickens during 15 min treadmill exercise at 0.5 m s^{-1} and 0.8 m s^{-1} at thermoneutral (23°C), low (9°C) and high (34°C) ambient temperature (T_a); the vertebral canal was cooled to 34°C during the middle 5 min of each exercise period. Temperatures of the vertebral canal (T_{vc}) and rectum (T_{re}) were also measured.

2. Exercise at 0.5 m s^{-1} caused increases in O_2 consumption, CO_2 production, minute volume and tidal volume compared to resting controls at each T_a . Minute volume and respiratory frequency were higher and tidal volume was lower in birds exercising at 34°C than at 23 or 9°C .

3. Spinal cord cooling during exercise (0.5 m s^{-1}) at 9°C caused further increases in O_2 consumption, tidal volume and respiratory frequency almost equivalent to those produced by an increase in the running speed to 0.8 m s^{-1} .

4. Spinal cord cooling during exercise (0.5 m s^{-1}) at 23°C did not significantly affect O_2 consumption, CO_2 production, minute volume, tidal volume or respiratory frequency.

5. Spinal cord cooling during exercise (0.5 m s^{-1}) at 34°C did not affect O_2 consumption or CO_2 production, but caused decreases in minute volume and respiratory frequency and an increase in tidal volume.

6. We conclude that the domestic fowl exhibits spinal thermosensitivity during exercise, although these responses appear to be smaller than those previously reported for the resting bird. Decreased external temperature potentiates the effects of spinal cord cooling during exercise.

INTRODUCTION

The ventilatory response of birds to exercise (both running and flying) is markedly influenced by changes in body temperature which may result from the

* Present address: Department of Veterinary Physiology, Royal (Dick) School of Veterinary Studies, University of Edinburgh, Edinburgh EH9 1QH, Scotland.

† Stipendiat of the German Humboldt-Stiftung.

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storage of metabolic heat (Kiley, Kuhlmann & Fedde, 1979; Hudson & Bernstein, 1981; Brackenbury, Gleeson & Avery, 1982a). The influence of thermal stimulation on ventilatory pattern is governed by exercise intensity and duration and by ambient temperature. For example, in domestic fowl exercise produces an initial increase in both respiratory frequency and tidal volume, but as exercise continues and body temperature begins to rise (this effect being more pronounced at elevated ambient temperatures) the respiratory pattern becomes more rapid and shallow and the birds become hypocapnic as a result of thermal hyperventilation (Gleeson & Brackenbury, 1984). If domestic fowl undergo exercise of moderate intensity at low ambient temperature, under conditions in which body temperature does not rise, there is no sign of thermal influence on respiratory pattern and the birds maintain an isocapnic hyperpnea.

In resting domestic fowl, thermoregulatory respiratory responses to elevated ambient temperature (panting) can be inhibited if the spinal cord temperature is cooled (Richards & Avery, 1978; Barnas, Gleeson & Rautenberg, 1984). In addition, cooling the spinal cord at thermoneutral or low ambient temperatures in resting domestic fowl causes shivering and an increased O_2 consumption. The magnitude of these responses is greater at low ambient temperature (Barnas *et al.* 1984). Increases in minute volume were linearly related to increases in O_2 consumption. The increased minute volume was achieved by coupled increases in respiratory frequency and tidal volume, comparable to those observed during low intensity exercise at low ambient temperature in domestic fowl (Gleeson & Brackenbury, 1984). In birds, spinal cord temperature sensors are thought to exert the dominant influence on the thermoregulatory centre and on the intensity of thermoregulatory effector responses (Rautenberg, Necker & May, 1972; Richards, 1975).

In this study we have investigated the thermosensitivity of the spinal cord of the male domestic fowl during moderate exercise when exposed to high, thermoneutral and low ambient temperatures in order to examine the relative importance of spinal cord and external thermal stimuli in respiratory control during exercise hyperpnea.

METHODS

Animals and experimental training

Six white Leghorn cockerels (*Gallus domesticus*) 16–19 weeks of age and weighing 1.3 ± 0.1 kg were used. Housing and training regimes and the implantation of vertebral thermodes (nylon tubes), arterial and venous catheters were as described previously (Barnas, Gleeson & Rautenberg, 1985).

Experimental measurements

Temperatures of the rectum (T_{re}) and the vertebral canal (T_{vc}) were measured with copper constantan thermocouples (Fine Wire, California, OUS) either placed 8 cm into the rectum or inserted into the previously placed cannula in the vertebral canal. These temperatures, as well as that of the ambient air (T_a) in the treadmill cage, were recorded on a multipoint recorder (Phillips, PM 8235). The measurements of arterial blood pressure, heart rate, blood gases and pH have been previously described and reported (Barnas *et al.* 1985).

Respiration was measured in the following way: the cockerel's head was placed in a $12 \times 5.5 \times 10$ cm helmet made of light but rigid clear plastic. A rubber surgical glove, cut at the finger protrusions and attached to the round opening for the head on the bottom of the helmet, encircled the cockerel's neck. A rubber condom (Sicher, London), cut at the tip, was placed over the surgical glove to form a loose but air-tight sealed collar along about half of the neck. The helmet therefore completely enclosed the cockerel's head with no openings to the outside except for (i) a gas outlet, (ii) an air inlet, and (iii) a closable opening for calibration purposes. The gas was drawn from the helmet at a constant rate of 61 min^{-1} measured continuously by a dry gas meter after drying. The PO_2 and PCO_2 of the dried gas were measured by an O_2 analyser (Beckman, OM-11) and a CO_2 analyser (Leybold-Heraeus, Binos) respectively, and recorded continuously on a two-channel pen recorder (Phillips). A Fleisch pneumotachograph (size 2) was attached *via* a 25 cm long tube to the air inlet of the helmet and secured into a stationary position. The cockerel's respiratory movements caused oscillations in flow of the air entering the helmet *via* the pneumotachograph which were added and subtracted from the base flow of 61 min^{-1} drawn through the pneumotachograph and helmet. These flow changes were measured by a pneumotachometer (Gould) and recorded on a penwriter (Gould, Brush 2209). The constant flow entering the helmet was electronically offset to zero – allowing the oscillating flow signal to be integrated (Gould pneumotachometer) to obtain the tidal volume. For calibration purposes a machine-driven pump cycled known volumes in and out of the helmet at frequencies up to 4 Hz. No diminishing of the measured tidal volume signal was observed at the high frequencies. In cases where the cockerel was killed after the experiment, the pneumotachometer was calibrated with the animal's head inside the helmet; otherwise a closed flask of approximately comparable size was substituted during the calibration.

The helmet weighed 25 g and so to aid running performance during the experiments the helmet was supported by a spring attached to a moveable Teflon ring which ran along a brass rail attached to the treadmill cage ceiling.

Experimental procedure

The experimental protocol is described in the previous paper (Barnas *et al.* 1985). In the Results, data on T_{re} , \dot{V}_{O_2} , \dot{V}_{O_2} , R , \dot{V}_{E} , f and \dot{V}_{T} are presented from measurements made at the 4th, 9th or 14th minute of exercise to coincide with the blood sampling and measurements made in the previous paper (Barnas *et al.* 1985).

Data analysis

Oxygen consumption (\dot{V}_{O_2}) and carbon dioxide production (\dot{V}_{CO_2}) were calculated from the corrected volume of gas (STPD) flow and gas concentrations of the air leaving the helmet. Minute volume (\dot{V}_{E} in BTPS) was calculated as the product of tidal volume (V_{T}) and respiratory frequency (f). Respiratory exchange ratio (R) was also calculated.

Paired *t*-tests were performed on the differences between every measured variable caused by spinal cord cooling, exercise and changes in T_{a} . Differences between means were considered significant at $P < 0.05$. Results are expressed as mean \pm S.E.M.

RESULTS

Resting values

Resting \dot{V}_{O_2} was not significantly affected by T_a . The mean values (\pm s.e.) at each T_a were 21.6 ± 1.0 , 20.8 ± 0.8 and 20.1 ± 1.7 ml kg⁻¹ min⁻¹ at 9, 23 and 34°C respectively. This seems somewhat surprising in view of the fact that birds, like mammals, are homeotherms, but it is probable that the cockerels were not in a true resting state: our resting values of \dot{V}_{O_2} of the cockerels are considerably higher than the 9.5 ml O₂ kg⁻¹ min⁻¹ measured in resting cockerels at 20°C by Brackenbury & Avery (1980). The higher \dot{V}_{O_2} values we obtained at rest could be due to the anticipation of exercise by the birds. These animals were regularly trained and the resting measurements were taken while the birds were sitting on the treadmill. Their already elevated \dot{V}_{O_2} may have masked any effects of T_a on resting \dot{V}_{O_2} measured under these conditions.

Rectal temperature (T_{re}) was significantly higher at T_a of 34°C than at either of the lower T_a values (Fig. 1). At 34°C, the birds exhibited varying degrees of thermal panting: minute volume (\dot{V}_E) and respiratory frequency (f) increased markedly and tidal volume (V_T) decreased, compared to resting controls at either of the lower T_a .

Effects of exercise and spinal cord cooling at T_a of 23°C

Exercise at 0.5 ms⁻¹ at 23°C caused a small gradual increase in T_{re} (Fig. 1). O₂ consumption (\dot{V}_{O_2}) increased 2.6 times during exercise compared to resting con-

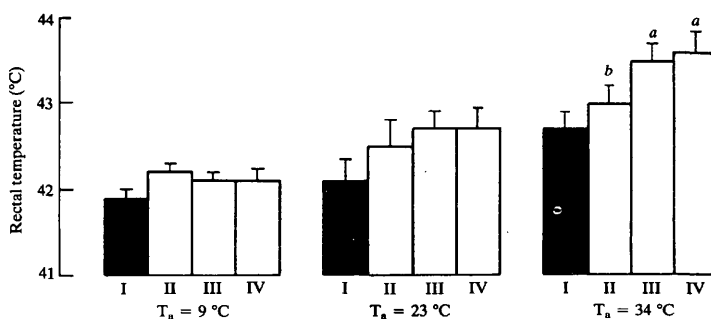


Fig. 1. Rectal temperature in cockerels at rest (I) and during the 4th (II), 9th (III, plus spinal cord cooling) and 14th (IV) minute of exercise at 0.5 ms⁻¹. Measurements were made at ambient temperature (T_a) of 9, 23 or 34°C. Vertical bars indicate \pm 1 s.e. Data from five birds. Significant differences ($P < 0.05$) between exercising variables calculated from paired t -tests of corresponding values from each cockerel are indicated in letters above the s.e. bars: a = different from exercising 4th minute control (II); b = different from exercising 14th minute control (IV).

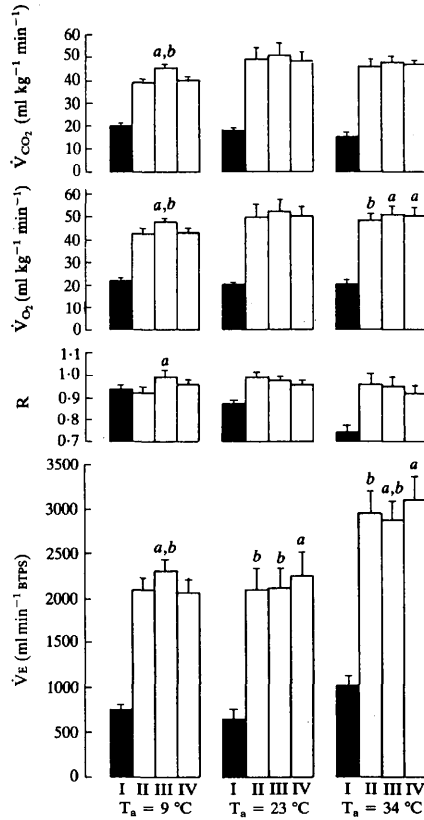


Fig. 2. Carbon dioxide production (\dot{V}_{CO_2}), oxygen consumption (\dot{V}_{O_2}), respiratory exchange ratio (R) and minute volume (\dot{V}_E) in cockerels at rest (I) and during the 4th (II), 9th (III) and 14th (IV) minute of exercise at 0.5 m s^{-1} showing the effect of spinal cord cooling. Measurements were made at ambient temperature (T_a) of 9, 23 or 34°C . Vertical bars indicate $\pm 1 \text{ s.e.}$. Data from five birds. Significant differences ($P < 0.05$) between exercising variables calculated from paired t -tests of corresponding values from each cockerel are indicated in letters above the s.e. bars: a = different from exercising 4th minute control (II); b = different from exercising 14th minute control (IV).

trols. CO_2 production (\dot{V}_{CO_2}), respiratory exchange ratio (R) and minute volume (\dot{V}_E) were also significantly increased during exercise (Fig. 2). The increased \dot{V}_E during exercise was achieved by an increased respiratory frequency (f) and increased tidal volume (V_T) (Fig. 3). Values of \dot{V}_E and f were higher and V_T lower in

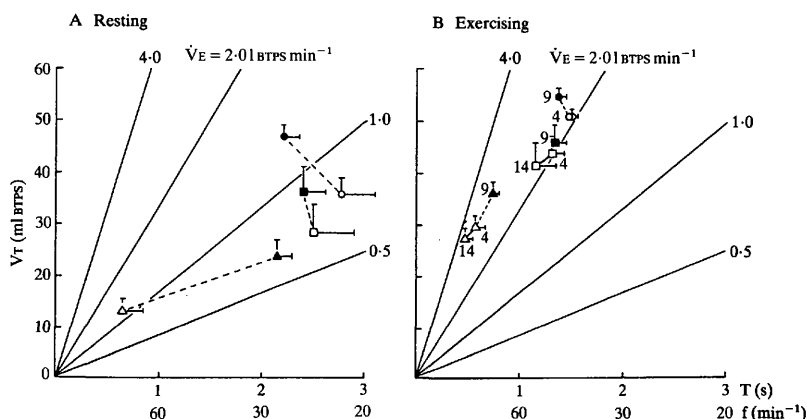


Fig. 3. Ventilatory variables of domestic fowl (A) at rest and (B) during exercise at 0.5 m s^{-1} , showing the effects of spinal cord cooling. Measurements made at ambient temperature (T_a) of 9°C (circles), 23°C (squares) or 34°C (triangles). Open symbols represent normal (control) ventilatory variables at each T_a and closed symbols represent the ventilatory variables after 4 min of spinal cord cooling. Dashed lines link variables at the same T_a . In (B) ventilatory variables are shown from measurements made in the 4th, 9th and 14th minute of exercise. The small numbers alongside each symbol represent the time of measurements, in minutes, after the onset of exercise. The spinal cord was cooled during minutes 5–10 of the exercise period. Bars represent $\pm \text{s.e.}$ Data from five birds. \dot{V}_E , minute volume; V_T , tidal volume; T , respiratory period; f , respiratory frequency. Spinal cord cooling measurements made at rest (in the same birds) are from Barnas, Gleeson & Rautenberg (1984).

the 14th minute of exercise compared with the 4th minute of exercise at 0.5 m s^{-1} (Figs 3B, 4), although \dot{V}_{O_2} , \dot{V}_{CO_2} and R remained unchanged (Fig. 2).

Spinal cord cooling during running exercise at thermoneutral T_a caused no significant changes in \dot{V}_{O_2} , \dot{V}_{CO_2} , R or \dot{V}_E (Fig. 2). However, f was lower and V_T higher than end-exercise values (Figs 3B, 4).

Effects of exercise and spinal cord cooling at T_a of 9°C

Resting cockerels at 9°C exhibited similar T_{re} (Fig. 1), \dot{V}_{O_2} and \dot{V}_E (Fig. 2) compared to resting controls at 23°C T_a . However, at 9°C f (Fig. 3A) was lower, while \dot{V}_{CO_2} and R (Fig. 2) and V_T (Fig. 3A) were higher.

Exercise at 0.5 m s^{-1} at 9°C only slightly increased T_{re} (Fig. 1). \dot{V}_{O_2} increased by 2.0 times compared to the resting values and this increase appears to be less than that produced by the same intensity of exercise at 23°C (Fig. 2). However, these differences were not significant when values from the same cockerels were compared using a paired t -test. \dot{V}_E was similar during exercise at 9°C to that measured at 23°C (Fig. 2). However, during exercise at 9°C , f was lower and V_T higher than at 23°C (Figs 3B, 4).

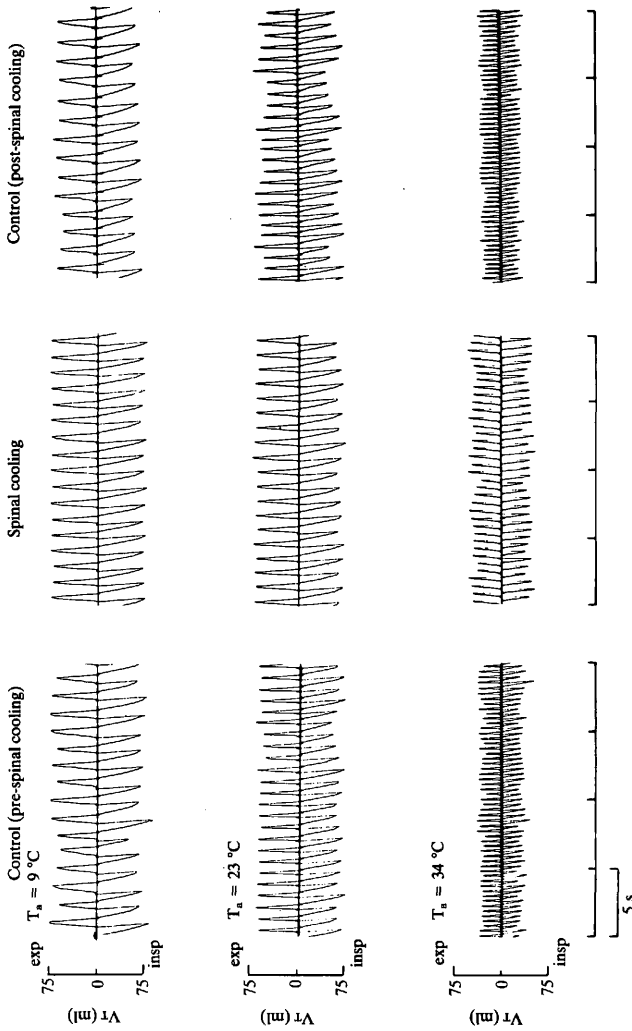


Fig. 4. Recording of the ventilatory pattern of a cockerel running at 0.5 m s^{-1} at 9°C , 23°C or 34°C , showing the effect of cooling the spinal cord. Recordings are from the 4th (control = pre-spinal cooling), 9th (spinal cooling) and 14th (control = post-spinal cooling) minute of exercise. V_t , tidal volume; exp, expiration; insp, inspiration.

Exercising control values of T_{re} , \dot{V}_{O_2} , \dot{V}_{CO_2} , R , \dot{V}_E , f and V_T measured during the 14th minute of exercise were not significantly different from those observed during the 4th minute of exercise.

Spinal cord cooling during exercise at 0.5 ms^{-1} at 9°C caused immediate increases in \dot{V}_{O_2} (Figs 2, 5), \dot{V}_{CO_2} and \dot{V}_E (Fig. 2). The increased \dot{V}_E was achieved by an increased f and V_T (Figs 3B, 4). When spinal cord cooling was stopped, \dot{V}_{O_2} (Fig. 5) and other respiratory variables returned to pre-cooling values within 2 min.

Effects of exercise and spinal cord cooling at T_a of 34°C

In resting cockerels at 34°C , T_{re} was significantly higher than at either of the lower T_a (Fig. 1). At 34°C the resting birds exhibited varying degrees of thermal panting. Thus \dot{V}_E (Fig. 2) and f were increased and V_T decreased (Fig. 3A) compared to both thermoneutral and low T_a controls. In similar comparisons, no change in \dot{V}_{O_2} was evident but \dot{V}_{CO_2} and R were decreased at the high T_a .

Exercise at 0.5 ms^{-1} at 34°C progressively increased T_{re} (Fig. 1). \dot{V}_{O_2} increased by 2.4 times compared to resting controls, a similar increase to that produced by the same intensity of exercise at the lower T_a (Fig. 2). However, as exercise progressed there was a small but significant increase in \dot{V}_{O_2} at 34°C . After the onset of exercise R increased to a value similar to that in exercising birds at the lower T_a (Fig. 2). During exercise at 34°C , \dot{V}_E was significantly higher than at 9 or 23°C (Fig. 2) and the exercising birds exhibited a faster and shallower breathing pattern than at either of the lower T_a (Figs 3B, 4).

Control birds measured during the 14th minute of exercise had a higher T_{re}

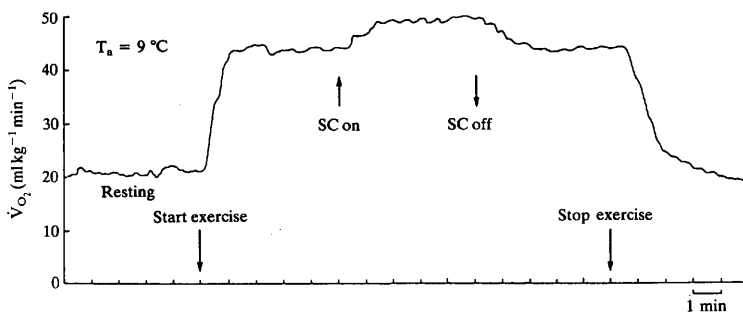


Fig. 5. The effect of spinal cord cooling (SC) in a cockerel on oxygen consumption (\dot{V}_{O_2}) during exercise at 0.5 ms^{-1} at an ambient temperature (T_a) of 9°C .

(Fig. 1), \dot{V}_{O_2} , \dot{V}_E (Fig. 2) and f , together with a lower \dot{V}_T (Figs 3B, 4) than control birds measured at the 4th minute of exercise. \dot{V}_{CO_2} and R were not significantly different.

Spinal cord cooling during exercise at 34°C caused immediate decreases in \dot{V}_E (Fig. 2) and f with an increase in \dot{V}_T (Figs 3B, 4). \dot{V}_{O_2} was significantly higher during spinal cord cooling than during the 4th minute of exercise (Fig. 2), but remained elevated after the spinal cord cooling was stopped.

Effects of spinal cord cooling during exercise at 0.8 m s⁻¹ at T_a of 9°C and 23°C

Exercise at 0.8 m s⁻¹ at 9°C produced significantly larger changes in \dot{V}_{O_2} , \dot{V}_{CO_2} , R and \dot{V}_E than at 0.5 m s⁻¹ at 9°C (Table 1). Both f and \dot{V}_T were further increased at the higher running speed. T_{re} was 0.4°C lower during running at 0.8 m s⁻¹ than at 0.5 m s⁻¹ at 9°C.

Spinal cord cooling during exercise at 0.8 m s⁻¹ caused smaller increases in \dot{V}_{O_2} , \dot{V}_{CO_2} and \dot{V}_E than at 0.5 m s⁻¹ (Table 1). Responses to spinal cord cooling during both exercise intensities were less than those previously observed in the same cockerels at rest (Table 1; data on resting birds from Barnas *et al.* 1984). The effects of spinal cord cooling at 0.5 m s⁻¹ appear equivalent to an increase in the exercise intensity since \dot{V}_{O_2} , \dot{V}_{CO_2} , \dot{V}_E , f and \dot{V}_T were increased to values similar to those observed during exercise at 0.8 m s⁻¹ (Table 1). Exercise at 0.8 m s⁻¹ at 23°C also produced significantly larger changes in \dot{V}_{O_2} , \dot{V}_{CO_2} , \dot{V}_E , f and \dot{V}_T than at 0.5 m s⁻¹ at 23°C. However, spinal cord cooling during exercise at 0.8 m s⁻¹ at 23°C did not produce any significant changes in these measured variables.

DISCUSSION

Critique of tidal volume measurement

Tidal volume and ventilation in exercising birds have been measured by a number of techniques that have included flow transducers attached to a tracheal cannula or mouthpiece (Kiley *et al.* 1979; Hudson & Bernstein, 1981) and tight-fitting facial masks containing resistance screens (Brackenbury *et al.* 1982b). The use of a pneumotachograph attached to a tracheal cannula undoubtedly alters the normal humidifying and filtering of inspired air, respiratory deadspace volume and airway resistance, all of which are factors that could influence the breathing pattern. Moreover, the use of a tracheal cannula eliminates a section of the respiratory tract that has been shown (Menuam & Richards, 1974) to be the main contributor to respiratory evaporative cooling. This would lead to less heat loss than would otherwise be expected at any given ambient temperature.

The air-perfused facial mask described by Brackenbury *et al.* (1982b) proved unsuitable for use with our Leghorn cockerels, since their large combs and wattles made it almost impossible to achieve a hermetically sealed facial mask without obstructing the birds' vision. However, the cockerels would accept wearing a helmet made of light, clear but rigid Perspex, and an air-tight seal could be achieved around the neck. The helmet was designed to allow full opening of the beak since

Table 1. The effects of spinal cord cooling (SC) on respiratory variables at rest or during exercise at 0.5 m s^{-1} or 0.8 m s^{-1} at T_a of 9°C

	Resting		Exercise (0.5 m s^{-1})		Exercise (0.8 m s^{-1})	
	Control	SC	Control	SC	Control	SC
\dot{V} (min^{-1})	5 21.6 \pm 2.3	5 26.8 \pm 1.6*	5 40.8 \pm 2.1	5 43.1 \pm 1.9*	5 44.4 \pm 1.9	4 45.3 \pm 3.4*
\dot{V}_T (ml BTPS)	35.8 \pm 2.8	47.2 \pm 2.1*	51.6 \pm 1.2	54.9 \pm 1.4*	56.9 \pm 1.7	61.3 \pm 1.8*
\dot{V}_E (ml BTPS min^{-1})	759 \pm 51	1257 \pm 62*	2107 \pm 29	2367 \pm 113*	2541 \pm 183	2828 \pm 254*
\dot{V}_{O_2} (ml STPD $\text{kg}^{-1} \text{min}^{-1}$)	21.6 \pm 1.0	29.9 \pm 1.8*	42.6 \pm 2.4	47.9 \pm 0.9*	47.2 \pm 2.8	49.2 \pm 3.7*
\dot{V}_{CO_2} (ml STPD $\text{kg}^{-1} \text{min}^{-1}$)	20.3 \pm 0.8	28.4 \pm 2.1*	39.0 \pm 2.1	44.5 \pm 1.8*	46.6 \pm 2.9	49.8 \pm 4.2*
\dot{V}	0.94 \pm 0.02	0.95 \pm 0.02	0.92 \pm 0.03	0.93 \pm 0.03	0.99 \pm 0.01	1.01 \pm 0.01

Mean values \pm s.e. Data from N birds.

*Significantly different from control ($P < 0.05$).

Testing values are from Barnas, Gleeson & Rautenberg (1984).

this was the attitude normally adopted by the running birds. The constant flow of air through the helmet virtually eliminated any dead space and also allowed measurement of \dot{V}_{O_2} and \dot{V}_{CO_2} by sampling the dried effluent air from the helmet and constantly monitoring the air flow rate. The effects of air flow resistance of the pneumotachograph (attached *via* a 25 cm length of tube to the helmet) were assumed to be small. The maximum pressure changes occurring in the mask were approximately ± 10 Pa compared to measured changes in air-sac pressure in exercising cockerels of ± 500 Pa (Brackenbury & Avery, 1980).

Spinal thermosensitivity in exercising fowl

The data presented in this paper clearly show that the exercising domestic fowl has some sensitivity to spinal cord cooling as has previously been found in the resting bird (Barnas *et al.* 1984). However, the increases in \dot{V}_{O_2} , \dot{V}_{CO_2} and \dot{V}_E caused by cooling the spinal cord were evident only at the lower T_a . Decreased external temperature clearly potentiates the effects of spinal cord cooling. The respiratory responses to spinal cord cooling at 9°C are probably a secondary result of the increase in metabolic rate, but it is also possible that spinal cord cooling may directly affect respiratory responses. The increased metabolic rate caused by spinal cord cooling during exercise at 0.5 m s⁻¹ at 9°C (Figs 2, 5) suggests that the spinal cord cooling at the low T_a caused shivering during exercise. Spinal cord cooling in resting cockerels produces shivering at both low and thermoneutral T_a (Barnas *et al.* 1984). The increase in \dot{V}_E resulting from the spinal cord cooling during exercise was achieved by an increase in both f and V_T (qualitatively similar, although smaller in magnitude to the effect of spinal cord cooling at rest at 9°C – see Table 1). Thus the responses of the increased metabolic rate caused by spinal cord cooling during exercise at 9°C were equivalent to an increase in the exercise intensity. Furthermore, the responses to spinal cord cooling were further reduced during exercise at 0.8 m s⁻¹ compared to 0.5 m s⁻¹ (Table 1). This may have been because muscles involved in the locomotor movement are incapable of also participating in shivering or that the metabolic demands override the thermoregulatory effector responses. Brackenbury *et al.* (1982a) have previously suggested that non-thermal factors assume a more dominant role in respiratory control at higher exercising work loads. Furthermore, increased contractile activity of muscles during exercise also produces heat which would, at least in part, offset the stimulus for elevated shivering metabolism.

Spinal cord cooling during exercise at 23°C caused no changes in \dot{V}_{O_2} , \dot{V}_{CO_2} or \dot{V}_E , although V_T was increased and f decreased compared to end-exercise controls. This suggests a direct effect of spinal thermal stimulation on the thermoregulatory respiratory response. This contrasts with the cardiovascular responses reported in the previous paper (Barnas *et al.* 1985): all cardiovascular responses to spinal cord cooling were indirect, that is, proportional to the change in \dot{V}_{O_2} . This finding is of interest since it shows that respiratory changes have a direct thermoregulatory function, whereas the observed cardiovascular changes do not.

Cockerels exercising at 34°C exhibited a faster and shallower breathing pattern than at either of the lower T_a values. Ventilation was also markedly increased at

34°C compared to 23 or 9°C. The blood gas data (Barnas *et al.* 1985), which show larger decreases in P_{aCO_2} and P_{vCO_2} and increases in pH_a and P_{aO_2} at the high T_a compared with the lower T_a , suggest hyperventilation of active exchange tissue, similar to that previously reported by Gleeson & Brackenbury (1984).

The respiratory responses to spinal cord cooling were reversed at the high T_a . Barnas *et al.* (1984) also observed in resting cockerels that \dot{V}_E and f were reduced by spinal cord cooling at high T_a . This response suggests a direct effect of the thermosensory neurones in the spinal cord on motor output from the respiratory centre; spinal cord cooling inhibits the thermal drive emanating from the spinal cord thermosensory neurones and the linkage between thermoregulation and respiration is broken. Cooling the spinal cord during exercise at 34°C increased V_T and decreased f but the effects were less than those previously observed at rest (Fig. 3). Body (rectal) temperature was increased markedly by exercise at 34°C and the reduced effects of spinal cooling during exercise compared to rest indicate that extraspinal sensory inputs also influence the hyperthermic thermoregulatory respiratory response (panting). This conclusion is supported by experiments involving spinal cord heating: in ducks, at thermoneutral T_a , panting can be induced by heating the spinal cord, but the degree of response is variable and breathing rate (f) rarely reaches the level attained during normally (high external T_a) induced panting (Bech, Rautenberg, May & Johansen, 1980). Similarly in the chicken, heating the spinal cord only increases the breathing frequency to approx. 100 min^{-1} (Richards & Avery, 1978).

Rate and depth of breathing in exercising birds

The data from this study on the effects of external temperature on breathing pattern in exercising cockerels confirm the findings of Brackenbury *et al.* (1982a) and Gleeson & Brackenbury (1984) who investigated the responses of exercising female domestic fowl. At thermoneutral and low ambient temperatures exercise causes an increase in f and V_T . At higher ambient temperatures (when the resting bird is moderately panting) exercise causes an increased V_T with a reduced or only slightly changed f . Since these quoted studies each used different methods to quantify V_T and \dot{V}_E it appears not unreasonable to assume that the measured responses approximate closely to those of the normal running fowl.

Hart & Roy (1966) measured ventilation in walking, unrestrained pigeons at an environmental temperature of 25°C. They observed a moderate increase in f and a two-fold increase in V_T which markedly increased total \dot{V}_E . Walking and running ducks at 25°C exhibited a three-fold increase in f and a significant decrease in V_T (Kiley *et al.* 1979). When ducks were made to run at low ambient temperature (-5°C), f and \dot{V}_E increased to a smaller extent but V_T still decreased (Kiley, Kuhlmann & Fedde, 1982). Clearly the ventilatory pattern response to exercise in running ducks appears to be different from that in fowl. However, the duck is not a particularly good runner – probably a reflection of the fact that running is not the physiologically natural mode of locomotion in these birds – and the technique used to measure ventilation involved tracheal cannulation immediately prior to the experiment, factors which might be expected to influence the breathing pattern. In

view of this, present data on running ducks should be viewed with some caution.

Some data on exercising ventilatory pattern are also available for flying birds: white-necked ravens showed an increase in f with increasing colonic temperature during flight in a wind tunnel at 10 m s^{-1} . Both V_T and \dot{V}_E increased linearly with colonic temperature over the environmental temperature range of $22\text{--}34^\circ\text{C}$ (Hudson & Bernstein, 1981). In contrast, the pigeon exhibited large increases in respiratory frequency (up to twenty times resting values) with little change in tidal volume (Hart & Roy, 1966; Butler, West & Jones, 1977). In agreement with our own findings in the running fowl, coupled increases in tidal volume and respiratory frequency have been reported in the starling (Torre-Bueno, 1978) and fish-crow (Bernstein, 1976) during flight in a wind-tunnel. Some of these differences in respiratory pattern response to exercise may simply reflect interspecies differences in ventilatory requirement or may be related to wingbeat frequency. However, such comparative measurements may also be complicated by differences in the degree of thermal influence on ventilation, governed by exercise intensity and duration and by environmental temperature.

Control of rate and depth of breathing in fowl compared with mammals

At 9°C the pattern of respiratory response (changes in V_T and f) to spinal cooling at rest, to exercise, and to spinal cooling during exercise (see Fig. 6) is markedly similar to that previously reported (in female domestic fowl) in response to isothermic exercise at graded running speeds (Brackenbury & Gleeson, 1983). Increases in ventilation are brought about by coupled increases in f and V_T . The respiratory pattern response is described by an inverse hyperbolic relationship between V_T and T (respiratory period) (Fig. 6). Brackenbury & Gleeson (1983) also found that when normal intrapulmonary P_{CO_2} was held constant during hyperthermic exercise, as a result of the administration of CO_2 -enriched air, polypnea was suppressed, and the V_T - T relationship became identical to that observed during graded isothermic exercise. Furthermore, maintenance of normal P_{CO_2} in resting birds subjected to a gradual increase in environmental temperature also resulted in changes in respiratory pattern identical to those observed during graded isothermic or eucapnic exercise.

During exercise and/or spinal cooling at 9°C , PaCO_2 remains unchanged, or falls only slightly (Barnas *et al.* 1985). Thus there is an apparent inherent relationship between V_T and T when intrapulmonary CO_2 or temperature is held constant. Miller & Kunz (1977) have reported a similar finding from their work on the pacing of respiration in fowl by an oscillating CO_2 signal administered in the inspired air: there appeared to be an inherent relationship between V_T and f when mean CO_2 , O_2 and temperature were held constant.

Of particular interest is the fact that a qualitatively similar inverse hyperbolic relationship between V_T and T has also been described in anaesthetized cats (Clark & Von Euler, 1972; Grunstein, Younes & Milic-Emili, 1973) and awake humans (Hey *et al.* 1966). Furthermore, in human subjects the pattern of respiratory (f and V_T) changes in a given individual were the same whatever the nature of the respiratory drive. Hence, these findings tentatively suggest that there may be

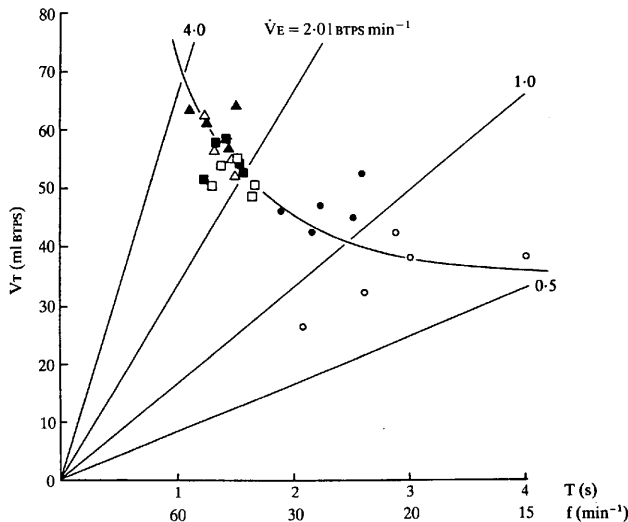


Fig. 6. Ventilatory variables of individual domestic fowl during rest (circles) and exercise at 0.5 m s^{-1} (squares) or 0.8 m s^{-1} (triangles) at T_a of 9°C . Open and closed symbols represent measurements made immediately before spinal cooling and during spinal cord cooling respectively. Resting ventilatory variables of fowl during spinal cord cooling at 9°C are from Barnas, Gleeson & Rautenberg (1984). The curve shows the inverse hyperbolic relationship between tidal volume (V_T) and respiratory period (T) which is discussed in the text. \dot{V}_E , minute volume; f , respiratory frequency.

fundamental similarities in the mechanisms controlling rate and depth of breathing in these birds and mammals despite the differences in pulmonary structure and intrapulmonary receptor types.

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