TEMPERATURE REGULATION AND RESPIRATION IN THE OSTRICH

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The Ostrich (*Struthio camelus*), the largest living bird, is an inhabitant of semi-arid and desert areas of Africa and, until exterminated, the Near East and the Arabian Peninsula. When exposed to the heat stress of a hot desert, it must use water for evaporation in order to avoid overheating. While its size prevents it from taking advantage of microclimates to the extent that small desert birds and mammals can, its large size is an advantage in its water economy, as has been discussed previously (Schmidt-Nielsen 1964).

Birds have no sweat glands, and under heat stress they rely upon increased evaporation from the respiratory system as a major avenue for heat dissipation. We were interested in the role of the respiratory system in evaporation, and particularly in the sites of evaporation. Furthermore, while in mammals an increased ventilation causes alkalosis, in birds the presence of large air sacs connected to the respiratory system may have radically different effects on the gas exchange in the lung. Finally, the fact that the ventilation of the respiratory system can be modified by heat stress without change in the rate of oxygen consumption may provide an avenue for investigation of the poorly understood air-sac system of birds.

The Ostrich, although a non-flying bird, has a well developed air-sac system, and its large size and slow breathing rate provide an opportunity to undertake experimental procedures which in smaller birds result in great technical difficulties or seem impossible.

[1] Deceased 7 April 1967.

MATERIALS AND METHODS

Birds

Twenty semi-domesticated adult Ostriches weighing 63–104 kg (12 males and 8 females) were purchased from commercial sources near Oudtshoorn in South Africa and transported by rail to Onderstepoort Veterinary Research Institute near Pretoria. They were permitted to graze freely in a 30-acre enclosure and were fed daily with fresh alfalfa and dry corn (maize). Water was provided at all times, except when it was removed as part of the experimental procedure. Handling facilities permitted the separation of smaller or larger numbers of birds as well as the isolation and/or capture of a given individual.

Ostriches are very powerful birds and difficult as well as dangerous to handle. For all experimental procedures that required a close approach, the desired bird was driven into a chute, provided with a hood, and transferred to a horizontal V-shaped restraining device, the design of which was based on the restraining procedures used for the commercial plucking of Ostrich feathers from living birds. Once the bird was completely restrained, the hood could be removed.

Most experimental procedures did not require the use of tranquilizers or general anesthesia. However, where catheterization of blood vessels or other cutting procedures were involved, local anesthesia was achieved with xylocaine. During measurements of surface temperatures in the trachea and the air sacs, the birds were tranquilized with M 99 (etorphine hydrochloride, Reckitt & Sons, Ltd.).

Weighing. Body weights of individual birds were determined with the animal in a portable restraining device placed on a platform scale (precision about 0.1 kg). Accurate changes in body weight used for the determination of evaporative water loss were determined by suspending the bird in its restraining device from the arm of a beam balance (designed according to Krogh and Trolle 1936, and modified with magnetic damping). This weighing did not provide the absolute weight of the animal, but gave weight changes with a precision better than 5 g. Since the evaporation might reach 10 g/min, the

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accuracy of the determinations of evaporation by weighing was more than adequate. Correction for metabolic loss of carbon is unnecessary at such high rates of water loss and was not employed.

Temperature-controlled room. All experiments which involved exposure to high temperatures were carried out in a room about $2.3 \times 3.5 \times 2.3$ m high. The temperature in this room was controlled to about ± 1°C. The humidity in the room was not under control, but high humidities were avoided by introducing outside air at a high rate.

Temperature measurements. Cloacal temperatures were usually obtained by thermistor measurements (Yellow Springs Instrument Co.) and occasionally by mercury thermometers. During measurements of tracheal temperatures the cloacal temperature was monitored with thermocouples made from 30-gauge copper-constantan wire.

Temperatures in the respiratory system (surface as well as air) and skin temperatures were measured with 36-gauge copper-constantan thermocouples and recorded on an Esterline Angus Speed Servo AZAS Recorder. The accuracy of these measurements was about 0.5°C. Since the cloacal temperature was an important reference point in all these measurements, it was monitored simultaneously with the same recorder.

Cloacal temperature during exercise was measured with a temperature telemetering transmitter (range in excess of 2 km, accuracy about ± 0.2°C).

Respiration. Respiratory rates (frequency) were determined either by counting and using a stopwatch, or by recording temperature oscillations at the nares or in the trachea.

Respiratory volumes were obtained by fitting a mask on the animal and collecting the expired air. The mask was constructed from a plastic bottle of suitable shape, fitted to the head, and provided with a sleeve of soft rubber dam which was kept closely assembled around the neck with a series of rubber bands. Pressure changes in the mask, and therefore leakage, were minimized by the use of a high flow, six-element MacGregor valve. Expired air was collected in large meteorological balloons and the volume immediately measured with a dry gas meter (± 1 per cent). When desired, air samples were withdrawn from the respiratory system (air sacs and trachea) with 5-ml glass syringes provided with three-way metal valves and no. 16 needles of appropriate length. For continuous recording of the oxygen tension in different air sacs, a no. 16 needle was inserted into the appropriate air sac and the air drawn continuously over a quick-responding oxygen electrode by means of an aquarium pump.

Gas analysis. Air samples taken with glass syringes were analyzed on a Scholander 0.5 ml Gas Analyzer (Scholander 1947). Continuous monitoring of oxygen tension was done with an oxygen electrode according to Kanwisher (1959), using a 12-μ teflon membrane in order to obtain rapid response. The system of the oxygen electrode with the sampling needle attached responded to changes in gas composition within 0.5 sec, while the recording of the full magnitude of a response required several seconds.

Blood. The oxygen content of blood samples was measured with the oxygen electrode by recording the change in oxygen tension when the oxygen was released from combination with hemoglobin with ferricyanide (Kanwisher and Carey, unpublished). The oxygen capacity was determined with the same method after equilibration with oxygen. The oxygen tension of arterial and venous blood samples was also determined directly with the oxygen electrode.

The carbon dioxide tension of blood was determined by the Astrup method using Radiometer tonometer, microelectrode, and PHM-4 *p*H meter. For unexplained reasons the *p*H values of the Ostrich blood did not consistently remain stable, although the same method has previously been used by us for blood of other birds without encountering this difficulty. However, by bracketing samples between suitable gas mixtures it was possible to obtain reliable determinations of the CO_2 tension in the blood samples.

Pressures in the airways. Air pressures were determined by attaching a sensitive pressure transducer (Computer Instruments Corp., Type 6000, range -0.3 to 0.3 psi) to a needle inserted into the appropriate place, and the output was recorded on the same Esterline-Angus Recorder used for thermocouples (see above). Differential pressures within the airways were recorded with the same transducer.

Cutaneous water loss. Cutaneous water loss was determined by the weight increase of silica gel (Randall and McClure 1949). About 30 g silica gel was placed in a cylindrical aluminum container and kept in place by a press-fitted piece of wire mesh. The opening of the container covered a skin area of 31.2 cm^2.

Volumes of respiratory system. Tracheal volume was determined by filling excised tracheas with water and measuring the volume in a graduated cylinder. This method, because of expansion of the trachea under pressure, will yield values somewhat too high, but because of the exceptional rigidity of the Ostrich trachea the error is not likely to be great. No attempt was made to correct for this error.

Air sac volumes were determined either by weighing gelatin casts after filling the entire respiratory system with gelatin and dissecting out the casts, or by a dilution technique which employed the quick injection into an air sac of 100 ml of oxygen (containing 2.2 per cent CO_2). Continuous recording of the change in oxygen concentration permitted an approximate determination of dilution volumes as well as the washout time of the individual air sacs in normal respiration at rest. During panting this approach could not be used because of the relatively slow response time of the oxygen electrode (a few seconds).

RESULTS

BODY TEMPERATURE AND TOTAL EVAPORATION

The Ostriches could maintain their body temperature at a stable level during prolonged exposure to a range of ambient temperatures of 15–50°C (fig. 1). At the highest temperatures they became slightly hyperthermic, but many could still maintain their body temperature at a stable level below 40°C for periods as long as 8 hr at 50°C ambient. In fact, if the initial cloacal temperature were high (e.g., due to struggling), some Ostriches were able to lower their cloacal temperature at any ambient temperature. These observations suggest that the body temperatures could have been maintained for longer periods if the exposure had been continued. The variability at

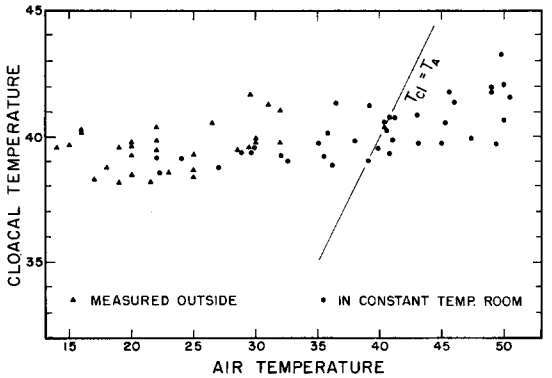

FIGURE 1. Cloacal temperatures (°C) of 15 restrained Ostriches at various ambient temperatures. Values were selected from individuals that maintained stable cloacal temperature for 0.5–8 hr.

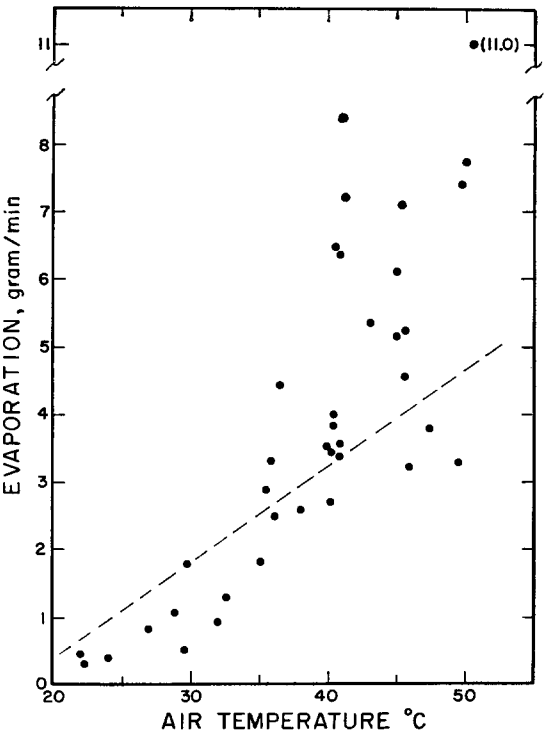

FIGURE 2. Evaporative water loss of Ostriches at various ambient temperatures determined by direct weighing. All values are from restrained birds and represent rates sustained for 20 min or more. The dashed line indicates the mean evaporation from the respiratory tract of the Ostrich as previously reported by Crawford and Schmidt-Nielsen (1967).

a given ambient temperature, in addition to individual differences, undoubtedly is due to the fact that the birds were restrained and showed various degrees of nervousness or excitement.

The maintenance of a stable body temperature below ambient temperature can only be achieved by evaporation of water. The evaporative water loss in Ostriches increased with increasing heat load (fig. 2). There is considerable variation at any given temperature, particularly at higher temperatures. The lowest values we recorded at any ambient temperature are similar to those previously recorded for Ostriches (Crawford and Schmidt-Nielsen 1967). The highest rate of evaporation we measured, 11 g/min, was maintained for 40 min, and is about twice the maximum rate of 4.5 g/min obtained by Crawford and Schmidt-Nielsen (1967). Eleven g/min from an 88-kg bird represents 0.75 per cent of the body weight per hour. In man evaporation rates frequently are twice as high (1.5 per cent of body weight, or 1 liter/hr).

SITES OF EVAPORATION

The skin plays a minor role in evaporative water loss. Determinations of water loss from bare skin areas of the upper leg showed evaporation of the magnitude of 0.05 g per m^2/min at an ambient temperature of 40°C. This loss from the skin is less than 2 per cent of the total water loss from the bird measured at the same ambient temperature. Furthermore, skin surface temperatures during heat stress were no lower than cloacal temperatures. When the skin is at the same temperature as the body core, heat cannot flow from core to skin, and consequently the skin cannot serve in heat dissipation.

In contrast, the respiratory volumes during heat load (see below) were of a magnitude sufficient for evaporation of the observed water losses, provided the expired air is exhaled saturated at body temperature. Furthermore, the estimates of evaporation based on tidal volumes do not include exaporation from the gular area, where temperature measurements revealed an important site of evaporation.

Ambient temperature 40°C. Surface temperatures within the respiratory system give a great deal of information about the site of evaporation. Figure 3 presents a diagrammatic representation of a typical situation when an Ostrich was exposed to an ambient temperature equal to body temperature (40°C). In this situation no heat exchange can occur through conduction or radiation, and the entire metabolic heat production must be dissipated by evaporation of water.

The surface temperatures recorded within the respiratory system did not fluctuate appreciably during the respiratory cycle, although in any particular experiment they might deviate appreciably from the figures in

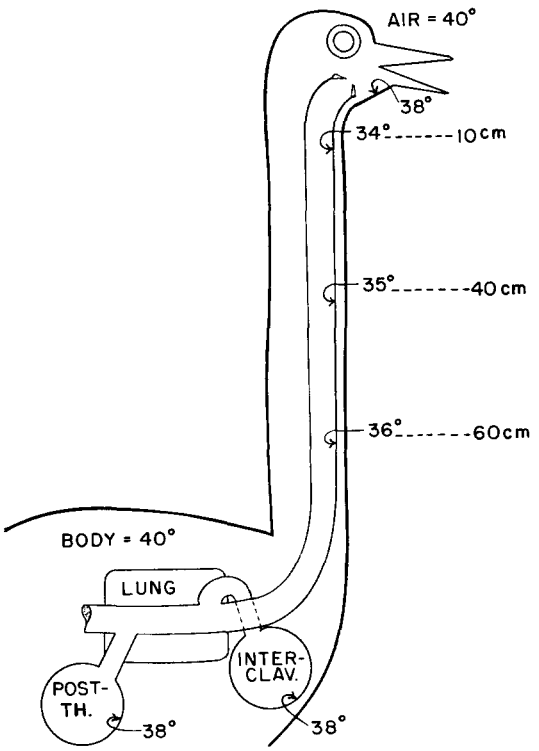

FIGURE 3. Representative surface temperatures in the respiratory tract of an Ostrich kept at an air temperature (40°C) equal to the body temperature. The tracheal locations marked 10 cm, 40 cm, and 60 cm refer to the distance from the glottis.

the diagrammatic representation of figure 3. The surface temperatures describe the possibilities for heat exchange between circulating blood and the cooling surface, and it can be seen that the blood can lose heat in the gular area, throughout most of the trachea, and in the walls of the air sacs.

Although temperatures lower than ambient and body indicate sites of evaporation, they do not indicate the amount of heat transfer in any given place, for the amount of heat transfer also depends on surface area, rate of blood flow through this area, and the temperature of the blood. Surface temperatures within the airways were quite variable, particularly in the region of the trachea. In the Ostrich the tracheal wall is highly vascularized and the blood flow changes visibly with heat exposure. The surface temperature is lowered by increased evaporation and raised by increased blood flow; a low temperature is therefore not a measure of the amount of cooling taking place. Under the conditions represented in figure 3, surface temperatures as low as 31.9°C have been recorded, both in the upper part of the trachea (20 cm below glottis) as well as lower down (60 cm below glottis). These low temperatures give excellent conditions for transfer of heat from blood to surface, but as stated above, low temperatures may indicate either a relatively low blood flow at the moment of measurement or a high rate of evaporation.

The temperature of the air stream may be quite different from that of the adjacent surface and fluctuate greatly with the respiratory cycle. The mean air velocity in the trachea can be calculated from the tidal volume, the duration of the respiratory cycle, and the cross-sectional area of the trachea. Such estimates show that the air velocity may reach values as high as 20 m/sec. Temperature equilibration between tracheal wall and the core of the air stream cannot be expected under these conditions, and we had many measurements of air temperatures in the tracheal air stream far higher than the surface temperature.

In the air sacs of panting Ostriches we recorded surface temperature (post-thoracic and interclavicular sacs) as much as 2°C below body temperature. These low surface temperatures implicate the air sacs as possible sites of heat transfer and/or evaporation, but their role relative to the trachea cannot be evaluated in the absence of information on blood flow. Although the surface area of the air sacs is large, they appear to be poorly vascularized.

Ambient temperature 50°C. At an ambient temperature of 50°C the tracheal wall might still be several degrees below body temperature (about 40–42°C) at all levels measured. Under these hot conditions the core of the inspired air steam might be several degrees hotter than the tracheal surface and thus also above body temperature. The hot ambient air could thus penetrate to more than 60 cm below the glottis (which was the lowest point in the trachea where it was practical for us to make measurements). The presence of a hot core of air at this level suggests that additional evaporation could take place lower down, presumably in the air sacs.

When Ostriches were panting at 50°C ambient temperature, the temperature in the post-thoracic sac oscillated as much as 5° with each breath, and in the interclavicular sac as much as 1°. From this we conclude that a hot core of air from the tracheal air stream may penetrate directly all the way to the post-thoracic sac, bypassing the lung surfaces. It is less certain whether the oscillations in the interclavicular sac are due to the same hot air entering directly into this sac.

The surface temperature of the gular area

is surprisingly low, and this area must also be important in heat dissipation. We recorded gular temperatures more than 3° below body temperature when ambient temperature was 54°C (gular surface 38°C, cloacal 41.3°C). The gular area is heavily vascularized, which permits the cooling of large quantities of blood.

The movements of the gular area are synchronized with the respiratory cycle. At the very end of each inspiration the gular membrane and associated structures suddenly drop, bringing into the oral cavity an additional volume of air, over and above the tidal volume. At the beginning of expiration, the entire gular structure is again raised. The quantitative importance of this mechanism (henceforth designated "gular pumping") is difficult to estimate, but the low surface temperatures, even at 54°C ambient, clearly show that the gular area must be a significant site of evaporation.

RESPIRATORY RATES AND VOLUMES

The majority of respiratory rates observed in our Ostriches fell within two ranges, either a low rate of about 6–12 cycles/min or a high rate of 40–60 cycles/min. These rates were very easily disturbed by experimental procedures such as covering the bird with a hood or the use of the respiratory mask, and sometimes even by activities of the experimenter which did not directly involve the bird. Intermediate rates were observed quite frequently, and many (but not all) of these were in connection with the use of the hood or the respiratory mask.

It is worth noting that the high respiratory rates during heat load remained quite stable, and for any given individual did not seem to change with increasing heat load. In one particular case a bird exposed to an ambient temperature rising from 39.2 to 56°C over 3 hr kept its respiration quite constant at 58 cycles/min with a total variation of only ± 1 cycle/min (table 1). The tidal volume of resting birds not exposed to heat load was about 1.2 to 1.5 liters. During panting at moderate heat load the tidal volume was less, but it increased during more severe heat loads. The largest tidal volume we measured in a bird during heat stress was 2.6 liters, but it seems unlikely that this represents the maximal tidal volume for birds that weigh 70–100 kg and have a total volume of the respiratory system (lungs and air sacs) of some 15 liters. We had a strong subjective impression that the use of a mask for measuring tidal volumes interfered with the mechanics of breathing. It also seems unlikely that tidal volumes during exercise or heat stress should not increase more than two-fold. Nevertheless, if the observed tidal volumes and respiratory rates are used to estimate the rates of evaporation (assuming that expired air is saturated at body temperature) the results correspond to the measured water losses.

TABLE 1. Respiration rates of an Ostrich exposed for 3 hr to a series of air temperatures (T_A) at or above cloacal temperature (T_{Cl}).

T_A °C	T_{Cl} °C	Resp. rate cycles/min
39.2	39.9	58
39.2	39.9	59
39.8	39.8	57
45.0	39.6	59
49.6	39.7	58
56.0	40.2	58

AIR SAC AND LUNG FUNCTION

Anatomy of air-sac system. The Ostrich has a well developed air-sac system which is diagrammatically presented in figure 4. The trachea branches into two primary bronchi, one to each lung. These primary bronchi continue directly through the lungs (where they are called mesobronchi) and connect to the most posterior air sacs (abdominal and posthoracic sacs). The connection from the main mesobronchi to the more anterior sacs (the interclavicular, lateral clavicular, and prethoracic sacs) is via secondary branches (at times called ventrobronchi).

Volumes of the air sacs. The total volume of the respiratory system in a 100-kg Ostrich is about 15 liters, as determined by the volume of liquefied gelatin that would fill the system in dead birds. The largest sacs are the posthoracic; the others, in order of decreasing size, are the interclavicular (which is unpaired), abdominal, prethoracic, and lateral clavicular sacs. The volumes of the major air sacs were determined by weighing gelatin casts made by filling the entire respiratory system with liquefied gelatin.

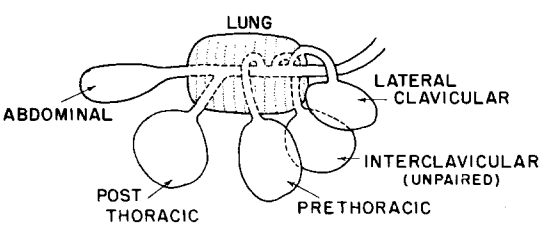

FIGURE 4. Diagrammatic location of the air sacs of the Ostrich.

TABLE 2. Approximate air-sac volumes of Ostriches, determined from gelatin casts, or as dilution volumes derived from oxygen injection into the sacs.

		Gelatin vol, ml	Dilution vol, ml		Approx. vol, liters[a]	
			Bird A	Bird B	One side	Both sides
Interclavicular	unpaired	470	1200	870	1.0	1
Lateral clavicular	paired	450	630		0.5	1
Prethoracic	paired	530	1340	1960	0.5	1
Post-thoracic	paired	2400	2660	2900	2.5	5
Abdominal	paired	1020	1500	910	1.0	2
Lung					1.5	3
Total: major air sacs + lungs						13

[a] These two columns represent compromise values given as rounded-off magnitudes to reflect the uncertainty of the estimates.

Air sac volumes were also determined as the dilution volume obtained from the injection of 100 ml O_2 into a sac, and the results yielded volumes similar to those obtained from gelatin casts (table 2). These determinations are less accurate than gelatin casts since they assume instantaneous mixing in a fixed volume, which is incorrect because respiration and air exchange continue during the measurements. Any loss of oxygen from the sacs would lead to an increase in the calculated dilution volume, and we believe that the large dilution volume obtained for the prethoracic sac may be due to an immediate oxygen loss through the air sac connection.

The volumes given in table 2 do not represent the total volume of the respiratory system, for they do not include the many small diverticuli from the air sacs, the spaces in pneumatized bones, or the volumes of the trachea and lungs. The volume of gelatin (about 15 liter) used for the casts is probably larger than the actual volume of the living system due to expansion caused by the weight of the gelatin mass.

Gas concentrations in the air sacs. Gas concentrations in the air sacs during quiet breathing at rest tended to fall into groups. The most anterior sacs (interclavicular, lateral clavicular, and prethoracic) had lower O_2 concentrations and higher CO_2 concentrations than the posterior sacs (post-thoracic and abdominal). Typical values are seen at the right side of figure 5. The magnitude of these values is substantiated by several hundred measurements of the various air sacs on Ostriches at rest, but as explained below, we consider reported means and standard deviations as arbitrary and misleading.

Information about O_2 concentration alone was also obtained with the oxygen electrode. On the whole this method confirmed the information obtained by analysis of withdrawn samples, but on occasion it showed that there can be considerable oscillation in the O_2 concentration in a given air sac, a fact not revealed in series of single samples which are withdrawn and analyzed. These oscillations may be related to the location of the sampling needle (whether or not it is near the incoming air stream) although the oscillations were not consistently related to the respiratory cycle. Whatever the reasons for the oscillations in O_2 concentration, their existence points to two dangers: (1) the use of concentrations obtained by spot sampling as representative of the gas composition in a given sac, and (2) the use of observed differences between the various sacs for the interpretation of function.

Arrival of inspired gas at the air sacs. The arrival times of oxygen at different air sacs, obtained when Ostriches inhaled a single breath of oxygen, are given in figure 5. Some of the inhaled oxygen went directly to the abdominal and post-thoracic sacs, and appeared by the end of the first inspiration. The rise in oxygen concentration continued through the expiratory phase of this first cycle, but there was no further increase during the second cycle. This confirms that the inhaled air, which during the second cycle again is atmospheric air, arrives directly at the posterior air sacs.

There was a delay of more than one full respiratory cycle before the inhaled oxygen caused any increase in oxygen tension in the anterior sacs. Since only one single breath of oxygen was inhaled, the oxygen which appeared in the anterior sacs during the second and third respiratory cycle must have been located elsewhere during the first cycle. Presumably the air entering the anterior sacs is derived from air which has passed through posterior sacs and lungs.

These arrival times of the inhaled gas, taken in conjunction with the normal concentration of oxygen and carbon dioxide in the air sacs, suggest that the following sequence of

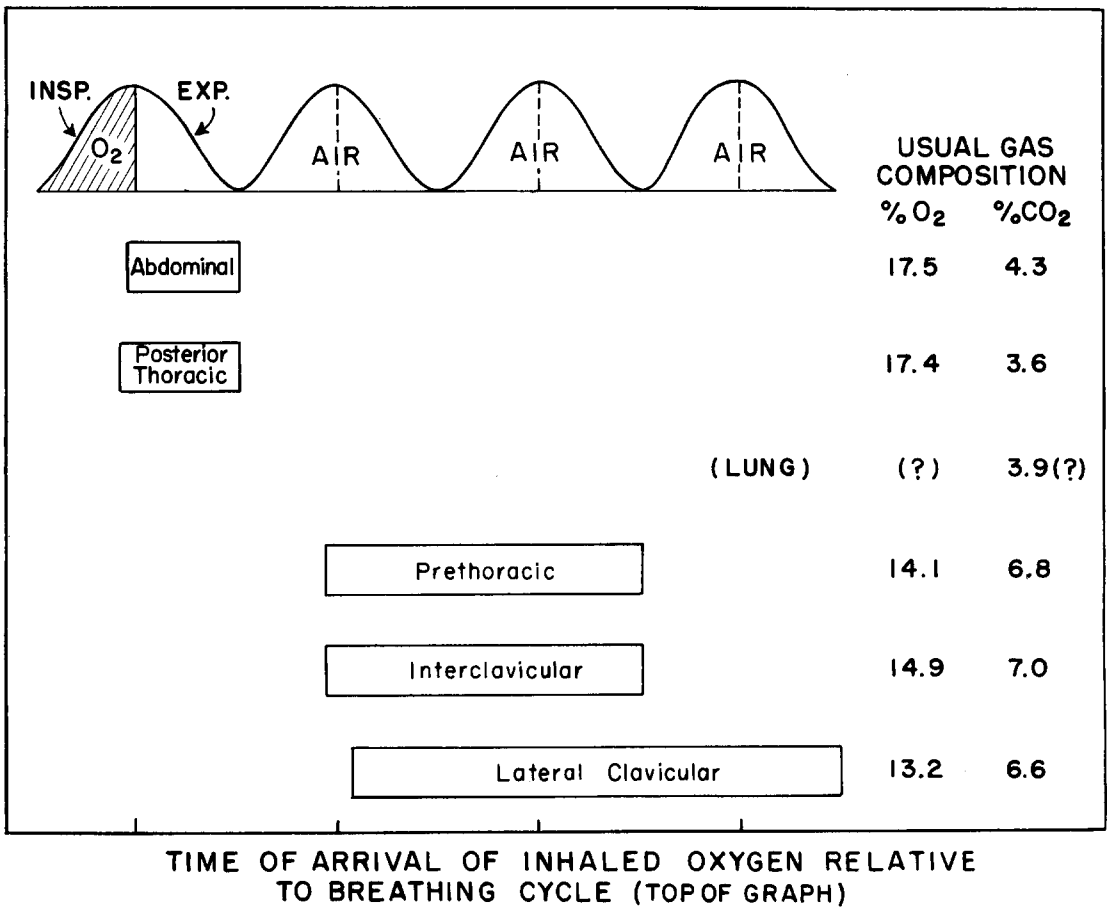

FIGURE 5. Summary of times of arrival in the various air sacs of inhaled O_2 in relation to the breathing cycle. After one single inhalation of O_2 the arrival of this gas in the air sac was recorded with an oxygen electrode. The left end of each horizontal bar indicates the earliest observed initial arrival of the O_2 in that particular sac. The right end of the bar indicates the latest time at which the O_2 concentration in the sac was observed to increase. The respiratory cycle is indicated at the top of the graph; the shaded portion of the first cycle denotes a single inspiration of O_2. Respiratory rate about 6 cycle/min, i.e., each cycle about 10 sec.

air flow may occur: inhaled air arrives first at the posterior sacs (although some may enter the lung directly); then, during expiration, much of the air from the posterior sacs enters the lung, and the anterior sacs receive air that has passed across the respiratory surface of the lung.

All air sacs in the resting Ostrich are highly ventilated, as shown by the time required for return to normal gas composition after injection of 100 ml O_2. The time required to reduce to one-half the originally achieved increase in O_2 concentration varied from less than two to about four respiratory cycles. This rapid washout shows that none of the air sacs contains an inert air mass. The longest time for the washout was observed in the post-thoracic sac where its duration was the equivalent of about four respiratory cycles, as opposed to between one and one-half and two and one-half respiratory cycles in all the other sacs. The post-thoracic sac is the largest of the air sacs, and the long washout time suggests that it is not ventilated in proportion to its volume.

The relatively short washout time of the anterior sacs provides evidence that these sacs do not receive outside atmospheric air during normal respiration at rest. The high renewal rate of air in conjunction with the observed gas composition (relatively high CO_2 and low O_2) can best be explained by postulating that the air entering these sacs has passed across the gas exchange surfaces of the lung.

Pressures in the airways. The pressures within the respiratory system were below atmospheric during inspiration, above during expiration. All pressure differences (ΔP) were relatively small; in quiet breathing, ΔP between air sacs and outside reached about

0.3×10^{-3} atm, and during maximal ventilation (heat stress) ΔP rose to 5×10^{-3} atm. The pressure differences between anterior sacs (interclavicular) and posterior sacs (post-thoracic) were very small, in the magnitude of 0.1 of the inhalation or exhalation pressures.

The small pressure differences within the respiratory system during quiet breathing do not suggest the movement of air from one sac system to another within any given moment of the respiratory cycle, but since resistance is unknown, the possibility cannot be eliminated. The Ostrich respiratory system is a high velocity-low pressure system. Aerodynamic flow patterns therefore become more important than changes in resistance (valving) in directing flow. Anatomically, valves are not evident; functionally, they seem unlikely, and in fact unnecessary.

Ventilation during panting. The increased ventilation volume during panting resulted in decreased CO_2 concentrations and increased O_2 concentrations in all air sacs. After several hours of heat exposure and panting the CO_2 concentration in the post-thoracic sac reached values between 0.5 and 1 per cent, with correspondingly high O_2 concentrations (20–20.4 per cent). In the interclavicular sac the CO_2 concentration was also low, up to 1.5 per cent after long exposures, and far below the concentration at rest (6–7 per cent).

These results show that air sac ventilation is greatly increased in panting, and that the interclavicular sac participates in the increased air renewal. However, the somewhat higher CO_2 concentration in the interclavicular sac than in the post-thoracic suggests that the former still may receive some air from the lung.

Apparently the ventilation of the lung itself is not increased during heat stress in spite of the great increase in total ventilation. We observed no decrease in arterial P_{CO_2} during heat stress, even when Ostriches panted heavily for periods up to 8 hr. If the gas exchange surfaces of the lung were ventilated in proportion to the increased respiratory minute volumes, the P_{CO_2} in the blood should decrease drastically and alkalosis should occur. The absence of alkalosis after long periods of heavy panting in the Ostrich contrasts sharply with the situation observed in other birds (Calder and Schmidt-Nielsen 1966, 1968) which showed extreme alkalosis after several hours of heat stress. We conclude that, although large air volumes flow through the respiratory system of the heat-stressed Ostrich, the air flow over the gas exchange surfaces of the lung is not increased. This indicates the presence of a functional shunting system which by-passes the lungs of the Ostrich. The pathway of the shunt is obviously the mesobronchus, but the anatomical basis for directing the air flow one way or the other is obscure.

Metabolic rate and exercise. Our determinations of oxygen consumption in Ostriches cannot be considered as standard resting values. The birds were semi-domesticated but remained somewhat apprehensive under all experimental procedures. They were restrained, remained standing, and were not postabsorptive. The lowest values we observed under these conditions was 415 ml O_2/min in a bird weighing 88 kg.

Although not measured during exercise, oxygen consumption was determined immediately after the termination of running 11 km at moderate speed (17km/hr). Within 2 min of the termination of the run, the oxygen consumption was 3,260 ml O_2/min in a bird that weighed 104 kg.

After exercise the CO_2 concentrations were reduced in the air sacs and the O_2 concentrations were increased, corresponding to an increased ventilation of the air sacs. The CO_2 concentration in the arterial blood did not decrease after exercise, which again suggests an accurate control of pulmonary ventilation independent of any increased air sac ventilation.

Respiratory rates immediately after exercise varied between 38 and 60 cycles/min. These rates are similar to those obtained by heat stress alone. The maximum heart rate observed immediately after exercise was 176 beats/min, representing a five-fold increase over resting heart rates (36–40 beats/min were common in quiescent birds).

DISCUSSION

Ostriches are quite tolerant of high temperatures, both under natural conditions and in the laboratory. When exposed to high ambient temperatures they increase evaporation by increasing the rate and amplitude of respiration. The flightless Ostrich has a well-developed and extensive air-sac system, and its size and low respiratory rate make it particularly well suited for studies of avian respiratory physiology.

The body temperature of Ostriches can be maintained below 40°C even when the birds are exposed to ambient temperatures as high as 56°C for more than 6 hr. Dehydrated Ostriches expend less water for evaporation than do hydrated ones, and are more likely

to permit their body temperature to rise to hyperthermic levels (Crawford and Schmidt-Nielsen 1967). In this respect Ostriches are similar to camels. A temperature rise of 4°C over "normal" levels in a 100-kg ostrich constitutes a storage of 320 kcal of heat (sp heat = 0.8), which represents a saving of 550 ml of water. Furthermore, an elevated body temperature diminishes the gradients between the body and a hot environment, thereby reducing heat gain from the environment. It is probable that the reduced gradients are quantitatively far more important for water economy than is heat storage. In camels this was found to be the case (Schmidt-Nielsen 1964).

The lowest oxygen consumption we measured (415 ml O_2/min) in an 88-kg bird falls within the values obtained by Crawford and Schmidt-Nielsen (1967) on a tame 100-kg Ostrich. The relationship between avian standard metabolic rates and body weight has recently been reviewed by Lasiewski and Dawson (1967). They presented an equation for the metabolic rate of birds in relation to body weight, based on data from 72 non-passerine birds ranging from hummingbirds to the Ostrich: $M = 78.3\ W^{0.723}$, where M is standard metabolism in kcal/day, and W is body weight in kg. This equation is statistically indistinguishable from similar equations for mammals (Brody 1945; Kleiber 1947, 1961).

The equation predicts an oxygen consumption of 290 ml O_2/min for an 88-kg bird, and the value we obtained in the present study is 43 per cent higher. The discrepancy between predicted and measured rates can be ascribed to the fact that the birds were standing up, apprehensive and restless, and that they were not postabsorptive.

The oxygen consumption measured at the end of running (3260 ml O_2/min) was approximately 10 times the standard metabolism predicted for a bird of this size (104 kg). It should be noted that this rate was not obtained during activity but during the initial recovery period. Nevertheless, the level is consistent with measurements of metabolism during flight in small birds, which are 8–13 times higher than standard metabolism (Lasiewski 1963; LeFebvre 1964; Tucker 1968).

The amount of water evaporated by Ostriches at high temperature is moderate when compared to man, who is similar in weight. The highest rate we observed, 11 ml H_2O/min at 50.5°C, is similar to that in non-acclimatized man (Ladell et al. 1944a, 1944b). Acclimatized man may sweat as much as 40–50 ml/min (Eichna et al. 1945), a rate which almost certainly exceeds that of which an Ostrich is capable.

The rate of evaporation in the Ostrich can be accounted for totally on the basis of measured respiratory volumes and frequencies, provided air is exhaled saturated at body temperature. Modulation of the amount of water evaporated during varying heat stress must be achieved by varying tidal volume, for panting frequencies do not change with changes in heat stress. Panting rates are relatively constant (40–60 cycles/min) and several times higher than resting rates (6–12 cycles/min). Intermediate rates were observed, but these appeared mostly during use of a respiratory mask or a "hood." Whether Ostriches use intermediate respiratory frequencies during moderate exercise is not known.

The two distinct levels of respiratory frequencies in the Ostrich are reminiscent of the situation in dogs, which pant at frequencies determined by the resonant characteristics of their thoracic cavity (Crawford 1962). Subjectively, Ostriches do not appear to use the elastic components of the respiratory system to the same degree as dogs, and it appears as if both inspiration and expiration are achieved by the muscles driving the thoracic cage. There is no support for the suggestion that Ostriches pant at the natural resonant frequency of their thoracic cavity.

Evaporation in the panting Ostrich occurs mainly in the trachea, gular region, and probably in the air sacs. The amount of water lost through the skin constitutes less than 2 per cent of water evaporated from the respiratory surfaces. Temperature measurements indicate that the trachea is a major site of evaporative water loss.

At the very end of inspiration in the panting Ostrich, the gular membrane and associated structures suddenly drop, to be raised again at the beginning of expiration. This "gular pumping" is timed so that additional ambient, non-saturated air is brought into contact with the moist oral surfaces at the end of inspiration. This should result in higher rates of evaporation than would otherwise be obtained. The gular pumping is similar to gular fluttering in many smaller birds (Dawson and Schmidt-Nielsen 1964; Lasiewski and Bartholomew 1966). The value of evaporation from the oral surfaces can be inferred from the observation that air could be cooled by 10–15°C by the time it reached the glottis during inspiration, and from the low temperatures of the gular surface. Lasiewski and Bartholomew

(1966) measured gular temperatures as much as 3° below body temperature in the Poorwill (*Phalaenoptilus nuttallii*), demonstrating the importance of this area as a site of heat loss in small birds that employ gular flutter.

The relative roles of oral surfaces, trachea, and air sacs in heat dissipation remain uncertain. The fact that air-sac temperatures are low could be interpreted either as local evaporation, or as due to the arrival of cool air from the trachea. Subjectively, the air-sac wall looks poorly vascularized, while the tracheal wall is extremely well vascularized and hyperemic during heat stress. On the other hand, the total area of the air sacs is much greater than that of the trachea.

The extent to which the inhaled air is cooled during its passage through the trachea depends on whether the flow is laminar or turbulent. In normal breathing with a tidal volume of 1.2–1.5 liters at a rate of 6–12 cycles/min, the flow rate in a tube of 1 cm radius gives Reynolds numbers between 450 and 1100, and flow should still be laminar. If air velocity increases considerably, as it does in panting, the Reynolds number will be some 10,000 and the flow must be turbulent. If the air flow in the trachea is laminar, heat transfer between the air stream and the wall is by conduction, a very slow process. For rapid heat transfer in the trachea the air flow must be turbulent, but it must not be too turbulent or the work of breathing will increase too much. It seems that the dimensions of the trachea of the Ostrich are such that they permit laminar flow and low work of breathing at rest, but that the flow changes to turbulence during panting.

It was mentioned above that modulation of evaporation in the panting Ostrich must be achieved by changes in tidal volume, for respiratory frequency remains constant. However, such variations in tidal volume may also have an indirect effect through the changes in turbulence which result from changes in linear velocity. Thus, not only does the volume of tidal air change, but the heat exchange between the tracheal air and the wall is influenced as well. This suggests a modulation of heat transfer greater than that resulting merely from the change in tidal volume.

Our results on the Ostrich permit some conclusions about the patterns of air flow in the air-sac system. Numerous previous studies employing a variety of birds and techniques have led to several conflicting theories and much controversy. Many extensive reviews have been published. (For a brief and elegant presentation, see King and Farner 1964.) Three main patterns for air movement in the lung have been suggested: 1) back-and-forth tidal flow (e.g., Zeuthen 1942); 2) outside → lung → air sacs → outside (e.g., Shepard et al. 1959); and 3) outside → air sacs → lung → outside (e.g., Donoso and Cohn 1962; Cohn et al. 1963).

The relatively small pressure differences between air sacs in the Ostrich at rest and the outside suggest that all air sacs may be filling and emptying at the same time. Synchronous pressure changes in air sacs of other species have been found by Baer (1896), Soum (1896, as quoted from Zeuthen 1942), Francois-Franck (1906), Victorow (1909), Sturkie (1954), Donoso and Cohn (1962), and Cohn et al. (1963).

The experiments on inhalation of pure oxygen in the Ostrich suggest that inhaled air passes through the trachea and mesobronchus directly to the abdominal and post-thoracic sacs (and perhaps to the lungs). The concentration of gas normally found in these sacs could be obtained by mixing approximately equal volumes of dead-space air and outside air. No detectable amounts of inspired air seem to go directly to the anterior sacs (prethoracic, cervical, and interclavicular). From the abdominal and post-thoracic sacs the air supposedly passes across the respiratory surfaces of the lungs, probably via the dorsobronchi-parabronchi-ventrobronchi system proposed by Hazelhoff (1951), to the prethoracic, cervical, and interclavicular sacs. In spite of the high CO_2 and low O_2 in the anterior sacs, these must be well ventilated (low wash-out time), which agrees with the observations of Graham (1939), Sturkie (1954), Donoso and Cohn (1962), and Cohn et al. (1963), but not with Zeuthen (1942).

The complex pattern of air flow operates under high velocity and low pressure, and we found no evidence of anatomical valves. The direction of air flow seems to be controlled by aerodynamic forces and the spatial orientation of the openings and passages. The patterns of flow which we have suggested in the Ostrich are similar to those proposed by Dotterweich (1936) and Hazelhoff (1951), although contrary to the much-quoted theory of Zeuthen (1942).

The anterior sacs have a higher CO_2 concentration (about 6–7 per cent) than the posterior sacs (about 4 per cent), a situation previously noted by several investigators. The arterial blood appears to be in equilibrium with air similar to that in the posterior sacs

(fig. 5). Presumably the high CO_2 concentration in the anterior sacs can be achieved only by air reaching these sacs from the lung, without admixture of air from other sources. If so, gas exchange between blood and air in the lung can hardly take place in the same way as in the mammalian lung. On the other hand, a higher P_{CO_2} in air coming from the lung than in arterial blood could be achieved by a counter-current flow pattern. One condition for counter-current flow, a unidirectional movement of the air, is possible because the bird lung parenchyma does not have alveoli but rather air capillaries which permit a through-flow of air. The air passing out of the lung could thus be in equilibrium with the high P_{CO_2} of incoming venous blood. Similar counter-current exchange has been described for gas exchange in the placenta of certain mammals and in the fish gill (Scholander 1958).

During heat stress the air sacs were ventilated more vigorously than at rest, and the gas concentrations of all sacs approached those of outside air. The CO_2 concentrations remained slightly higher in the anterior than in the posterior sacs. A similar pattern has been found in heat-stressed pigeons (Scharnke 1938). The distribution of O_2 and CO_2 concentrations in heat-stressed Ostriches suggests that at least some of the air reaching the anterior sacs first passes through the lungs.

The complete absence of alkalosis in Ostriches after panting for up to 8 hr suggests that during panting the lungs are bypassed by much of the ventilation volume, and that the air flow across the gas exchange surfaces remains precisely adjusted to the metabolic need for oxygen. In contrast, all other birds examined (nine species) exhibit marked alkalosis after heat stress (Calder and Schmidt-Nielsen 1966, 1968). The regulation of air flow to the lung could be achieved by aerodynamic changes in flow patterns, or by changes in resistance to air flow through the lungs as suggested by Zeuthen (1942). The parabronchial muscles discussed by Brandes (1924) could achieve the necessary resistance changes.

The striking fact that the heat-stressed Ostrich does not develop alkalosis, while all other birds examined do so, seems paradoxical. It is therefore tempting to speculate and suggest that severe heat stress in the Ostrich usually occurs when the bird is at rest, while in flying birds the greatest need for heat dissipation occurs during flight (i.e., severe exercise). Teleologically, it would therefore be advantageous for the Ostrich to separate the need for increased ventilation due to heat stress from the need for increased oxygen uptake. In the flying bird, on the other hand, the demand for oxygen and for heat dissipation are frequently concurrent, and a disassociation of the two may be less imperative.

SUMMARY

The role of the avian respiratory system in temperature regulation and the air flow in the air-sac system were studied in the Ostrich (*Struthio camelus*). The Ostrich can maintain its body temperature below 40°C during 8 hr at ambient temperatures as high as 50°C. This is achieved by increased evaporation from the respiratory tract (panting). Evaporation increased with heat load to a maximum of about 0.75 per cent of the body weight per hour at 50°C ambient temperature. In comparison, a man under hot desert conditions may lose water (sweat) at twice this rate. Respiratory rates rose from 6–12 cycle/min at rest to about 40–60 cycle/min during heat load. The amount of water evaporated could be accounted for on the basis of respiratory volumes, and skin loss was apparently insignificant.

All air sacs are highly ventilated during both rest and panting. Experimental inhalation of pure O_2 indicates that during inspiration outside air passes directly to the posterior sacs, while the anterior sacs receive air that has already passed over the respiratory surfaces of the lung. Gas composition in the anterior sacs suggests a counter-current flow of air and blood in the lung. Sustained panting did not cause alkalosis (decrease in arterial blood P_{CO_2}), although air sac P_{CO_2} fell markedly. This suggests a functional shunt system which permits a regulated by-pass of the lungs.

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