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VENTILATORY AND CIRCULATORY RESPONSES TO HYPERTHERMIA IN THE MUTE SWAN (*CYGNUS OLOR*)

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SUMMARY

Ventilatory parameters of mute swans were measured at thermoneutral conditions and during heat stress. Deep body temperature increased from 39·5 to 41·1 °C. Breathing frequency increased 29 times, compared to the thermoneutral condition. Tidal volume decreased to 18% of the pre-panting value, and the total ventilatory volume increased by 5·4 times. End-tidal P_{CO_2} and P_{O_2} values decreased and increased, respectively.

The swans developed a slight respiratory alkalosis; arterial P_{CO_2} decreased from an average of 27·1 to 25·7 mmHg and arterial pH increased from 7·501 to 7·559.

Cardiac output, heart rate and stroke volume were 106%, 154%, and 70%, respectively, of the values at thermoneutrality. Mean arterial blood pressure and total peripheral resistance were slightly reduced.

It is concluded that the increased ventilation during panting mainly constitutes dead space ventilation resulting from the great reduction in tidal volume. Parabronchial ventilation remains nearly unchanged, resulting in only a slight hypocapnic alkalosis.

INTRODUCTION

Most birds respond to heat stress by panting and gular fluttering, which are mechanisms of heat dissipation. Panting typically involves a 5- to 6-fold increase in ventilation (Richards, 1970; Calder & King, 1974) and appears to cause a respiratory alkalosis in some species (Calder & Schmidt-Nielsen, 1968), whereas others either maintain blood acid–base balance during panting or become only slightly alkalotic (Schmidt-Nielsen *et al.* 1969; Bouverot, Hildwein & LeGoff, 1974).

In the service of increasing evaporative heat loss without disturbing pulmonary gas exchange, the ventilation increase in the panting bird should mainly involve the dead space of the airways and not the parabronchial space. Very few studies have, however, been directed to a detailed analysis of ventilation on a breath-to-breath basis in birds during panting (Van Salfeld, 1936; Frankel, Hollands & Weiss, 1962; Smith, 1972; Bouverot *et al.* 1974; Ramirez & Bernstein, 1976; Bech, Johansen & Maloiy, 1979). An earlier study has described the ventilatory and circulatory patterns in undisturbed mute swans at thermoneutral conditions (Bech & Johansen, 1980). In the present study, similar techniques have been employed to study ventilation, circulation and blood acid–base status in the mute swan during panting at high ambient temperatures.

MATERIALS AND METHODS

Four birds were used in this study. Their capture and care during captivity have been described earlier (Bech & Johansen, 1980). All experiments were conducted during the period from September through November 1978.

Ventilation

Ventilation was measured using a laboratory-made Fleisch tube attached to a mask, fitted and fastened to the upper beak. The Fleisch tube was connected to a Statham-Godart pneumotachograph for continuous recording of tidal volume (V_T), breathing rate (f), air velocity, and total ventilation (MV). A Searle Medspect mass spectrometer was used for recordings of expired gas tensions (P_{ET}). For a complete description of the making and application of the mask and the use of the pneumotachographic technique for measuring ventilation see Glass, Wood & Johansen (1978), and Bech, Johansen & Maloiy (1979).

Cannulation and blood analysis

Cannulations of the brachial artery and vein were done during general anaesthesia (chloral hydrate). The venous catheter was advanced and positioned centrally in the right atrium: this was verified by pressure measurements and post-mortem examination of catheter position. Arterial and mixed venous blood samples were obtained anaerobically into pre-heparinized 1 ml syringes and stored in iced water.

Arterial blood pressure and heart rate were monitored via the brachial artery catheter using a Statham strain gauge transducer (model Pb 23 d).

Analysis of blood gas tensions and pH were done using Radiometer P_{O_2} and P_{CO_2} equipment (PHM 72 K). O_2 capacity was measured on blood tonometered against 50% O_2 and 5% CO_2 in nitrogen (Radiometer BM 2) and read on a LexO_2con O_2 content analyser. Blood O_2 content was also measured using the LexO_2con analyser. All blood analyses were done within 30 min from sampling time.

A thermocouple was inserted 5–10 cm into the cloaca and connected to an Ellab potentiometer recorder for monitoring the cloacal temperature. This temperature will be referred to as the body temperature (T_B).

Experimental procedures

During experimentation the birds were confined to a box, which allowed normal postures. The experimental chamber was placed in a climatic room where the temperature and humidity could be controlled. All recording equipment was placed outside the climatic room to minimize disturbance of the birds. Blood sampling via the indwelling catheters was similarly done, without the bird noticing, by guiding the catheters through portholes in the experimental chamber.

Following a period of rest and conditioning to the experimental arrangement, the birds were studied for 2–3 h at thermoneutral temperatures (15–20 °C) before the ambient temperature was raised. The room temperature, when set to 35 °C, took about 60–70 min to reach the set temperature. The birds typically started panting when

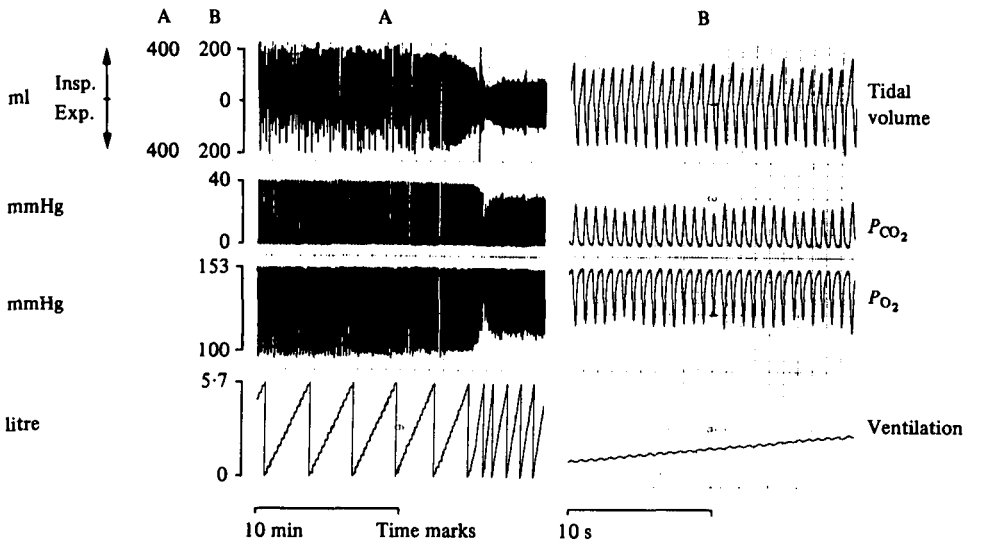

Fig. 1. Tracings depicting the transition from normal respiration to panting (A), and the panting pattern after ½ h panting (B). Note the difference in the calibration of tidal volume between A and B.

(ambient) was 32–34 °C and cloacal temperature between 40·5 and 41·5 °C, and continued panting as long as the ambient temperature remained at the high level. All measurements and samples were obtained after 1 h continued panting at steady-state conditions.

RESULTS

Fig. 1 shows the ventilatory pattern changing from normal breathing to the panting condition. The transition, which in this experiment took place when the ambient and cloacal temperatures were 33° and 41·7 °C, respectively, was rapid. A steady-state panting rhythm was established within 2–3 min. In other experiments the transition could be more gradual.

Initially, when the tidal volume was first reduced a marked increase in end-tidal P_{O_2} and decrease in P_{CO_2} were observed. Subsequently, within the next few minutes these changes were somewhat reversed and stable values established. If small changes in tidal volume occurred during the continued panting, accompanying changes in end-expired gas composition occurred.

The swans typically displayed a regular panting rhythm (Fig. 1 B) with no intermittent large variations in tidal volumes such as described for the greater flamingo (Bech *et al.* 1979).

Table 1 shows mean values of respiratory parameters for the mute swan after 1 h panting at an ambient temperature of 35 °C. For comparison corresponding values during thermoneutrality are shown.

Compared to conditions at thermoneutrality, the body temperature has increased 1·6 °C. If the swans were exposed for a longer time to the experimental temperature, body temperature increased still further. The highest body temperature recorded in a

Table 1. *Respiratory values in the mute swan obtained after 1 h of continued panting at an ambient temperature of 35 °C and compared with the normal respiratory values at ambient temperature of 15–20 °C*

		Panting (P)			
	Normal (N)*	n	Range	x ± 2 S.E.	P/N
W (kg)	9·77	10	9·1 – 11·3	10·0 ± 0·38	
T_B (°C)	39·5	6	40·8 – 41·7	41·1 ± 0·3	
f (min^{-1})	3·1	10	75·8 – 105·0	89·5 ± 4·9	28·87
V_T (ml kg^{-1})	55·0	10	6·8 – 12·9	9·9 ± 1·1	0·18
MV (ml kg^{-1} min^{-1})	162·8	10	629·0 – 1033·9	878·4 ± 79·2	5·40
$P_{ET}CO_2$ (mmHg)	42·3	7	15·8 – 31·2	23·5 ± 3·2	
$P_{ET}O_2$ (mmHg)	95·1	7	109·2 – 124·7	117·4 ± 3·5	

* After Bech & Johansen (1980).

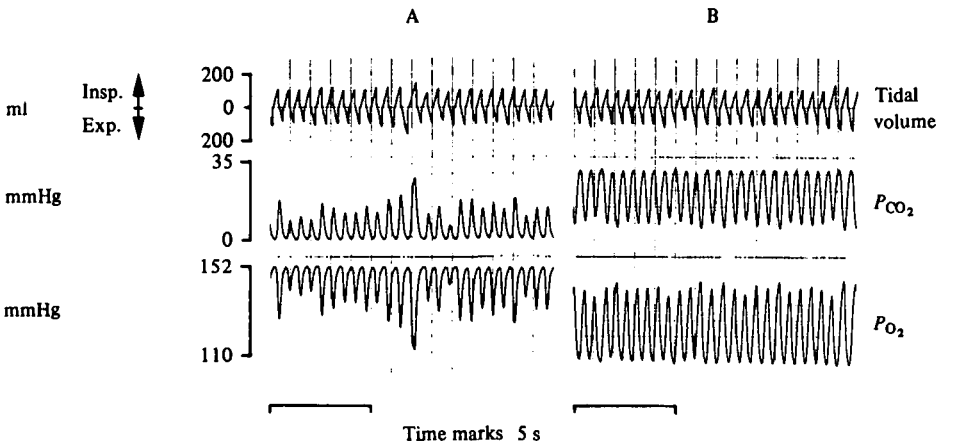

Fig. 2. Tracings showing the tidal volume (A and B, top) and the gas tensions monitored at the opening of the nostrils (A) and at a position just above the syrinx (B). The tracings were obtained during sustained panting at an ambient temperature of 35 °C.

mute swan was 43·15 °C. This bird was not severely stressed, and recovered without ill effects.

During steady-state panting, breathing frequency, tidal volume and total ventilation showed changes typical of birds during heat stress, with a marked increase in breathing rate, a reduced tidal volume, and an increase in total ventilation. The factor P/N in Table 1 denotes the relative changes.

Based on an inspiratory P_{O_2} of 149 mmHg, values of end-tidal gas tensions yield a respiratory exchange ratio (R_E) of 0·78 at thermoneutrality against 0·74 during panting.

To further elucidate the pattern of gas exchange during panting, we implanted a catheter (PE 50) into the trachea approximately 15 cm below the glottis. The catheter was advanced into a position just above the bifurcation of the trachea at the syrinx. Catheter placement was verified post-mortem. The catheter was connected to the mass-spectrometer for continuous monitoring of the gas tensions. Fig. 2 shows a comparison between gas analysis from the mask (A) and from the trachea at the position above the syrinx (B).

Table 2. *Blood and circulatory parameters in the mute swan after 1 h panting compared with thermoneutral conditions*

	Thermoneutral (15–20 °C)*	Panting (35 °C)
pH_a	7·501	7·559
pH_v	7·456	7·525
Pa_{CO_2}, *a*	27·1	25·7
Pv_{CO_2}, *v* (mmHg)	32·5	30·8
Pa_{O_2}, *a*	91·3	90·9
Pv_{O_2}, *v* (mmHg)	34·2	32·4
O_2 saturation$_a$ (%)	92·9	93·2
O_2 saturation$_v$ (%)	45·9	43·7
A–V difference (vol. %)	7·80	9·14
O_2 uptake (ml O_2 min^{-1})	109·6	148·3
Cardiac output (ml min^{-1} kg^{-1})	153·3	161·9
Heart rate (min^{-1})	113·8	174·8
Mean arterial blood pressure (mmHg)	115·5	107·6
Stroke volume (ml)	13·2	9·3
Total peripheral resistance (PRU)	0·75	0·66
Ventilation/perfusion (ml ml^{-1})	1·06	5·43
Blood convection requirement (ml ml^{-1})	12·82	10·94
Air convection requirement (ml ml^{-1})	13·61	59·30

* Values from Bech & Johansen (1980).

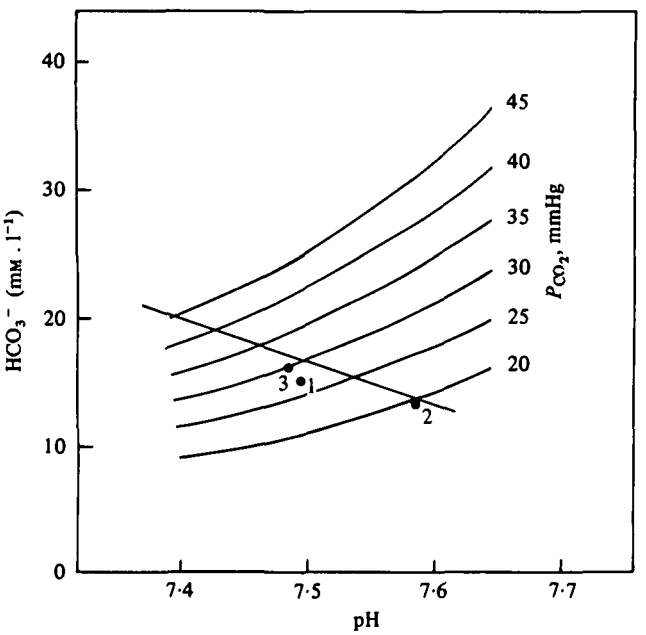

Fig. 3. Diagram showing the relationship between HCO_3^-, pH and P_{CO_2}. The normal buffer line for the mute swan obtained at thermoneutrality is shown. The points 1, 2 and 3 depict the acid–base relationship in a swan at pre-panting conditions, after 5 min panting and after 45 min panting, respectively.

Table 2 summarizes data and calculations concerning blood gases and circulatory parameters, again based on samples and measurements taken after 1 h of panting. Information pertaining to thermoneutrality is listed for comparison. It is evident from Table 2 that the mute swan develops a slight respiratory alkalosis during panting. The average arterial pH and P_{CO2} changes from 7·501 to 7·559 and from 27·1 to 25·7 mmHg, respectively. Note, however, that the gradients in P_{O2} and P_{CO2} between arterial blood and end-tidal gas (Table 1) change dramatically, in particular for CO_2, for which the gradient (average) may actually reverse.

Fig. 3 shows one example of the time course of acid–base changes before and during a panting episode in the mute swan. The normal buffer line represents a buffer capacity of 33 mM $HCO_3^-/\Delta pH$. Pre-panting values of pH and P_{a,CO_2} were 7·492 and 27·0 mmHg, respectively (point 1). Five minutes after onset of panting, $P_{a,CO2}$ had dropped to 19·8 mmHg and pH had increased to 7·575 (point 2). As panting continued, P_{CO2} again rose and, after 45 minutes of continuous panting, $P_{a,CO2}$ was 30 mmHg and pH 7·487 (point 3). Experimental runs were variable between individuals, but the general trend of the illustrated experiment was common.

The oxygen uptake increased during panting (35%—Table 2). However, the cardiac output increased less than the O_2 uptake judged from an increased arteriovenous O_2 content difference. This implies that the perfusion requirement ($\dot{Q}/\dot{V}_{O2}$) actually declined during panting. The increase in cardiac output (6%) was caused by an appreciable increase in heart rate, changing on the average from 114 to 175 beats per min associated with a reduction in stroke volume. Total peripheral vascular resistance was likewise slightly reduced, as was the mean arterial blood pressure.

DISCUSSION

Typically, panting in birds involves an increased breathing frequency and a much reduced tidal volume (Richards, 1970). In a comparison of panting patterns in birds, Calder & King (1974) reported the relative increase in breathing rate during panting to be nearly independent of body size, averaging 15·7 times the resting frequency. Their comparison included, however, data from only nine species, and evidence from recent studies document a larger variation ranging from a ninefold increase in breathing rate in the ostrich (Crawford & Schmidt-Nielsen, 1967) to a 35-fold increase in the rock partridge (Krausz, Bernstein & Marder, 1977). This variability appears to refute the often-made claim that breathing frequency during panting becomes adjusted to the resonant frequency of the lungs and airways (Crawford & Kampe, 1971).

It has also been reported that tidal volume may increase during panting (Salt, 1964; Lasiewski & Bartholomew, 1966; Crawford & Schmidt-Nielsen, 1967). This is probably atypical of normal panting (Richards, 1970) and should be classified as type II panting, reflecting an abnormal stress response, in distinction to the very shallow breathing characteristic of normal panting (type I). A bird subjected to heat stress in the laboratory will always show type I panting first, and heavy laboured panting will only set in when homeostasis breaks down at very high body temperatures. In nature, birds will probably only practise the rapid shallow panting classified as type I.

Very few studies of panting birds have involved direct measurements of the tidal

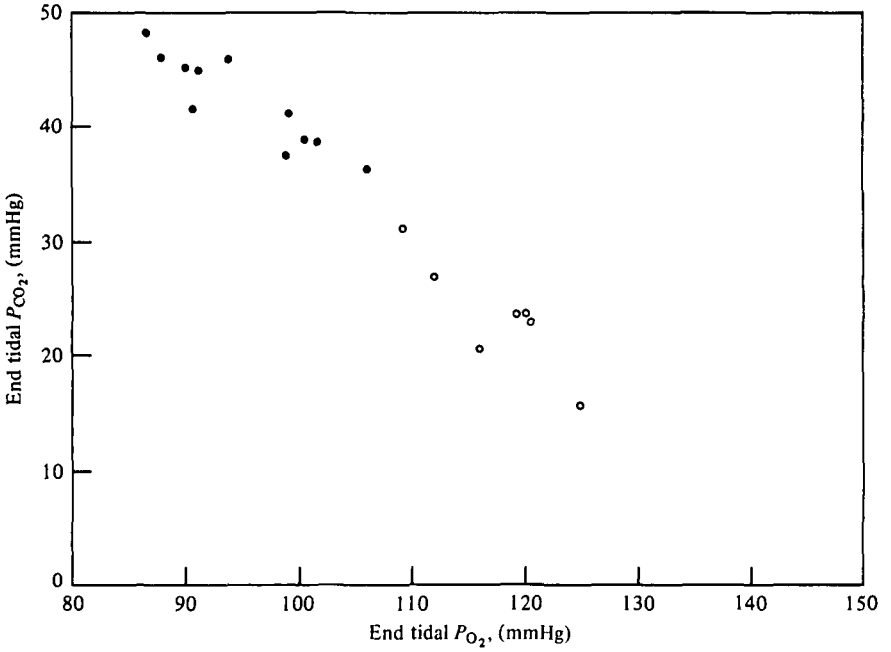

Fig. 4. P_{CO_2}–P_{O_2} diagram based on corresponding values for end-tidal gas compositions at normal respiration (●) and during panting (○). Each point represents the mean value of several measurements obtained during one experiment.

volume and breathing rate, both of which are needed for the classification of panting. The idea that natural panting of the type I involves a breathing rate at the resonant frequency of the lungs and airways may thus still prove valid.

The 29-fold increase in breathing rate recorded here for the mute swan during panting compares well with a 26-fold increase in the duck (Bouverot *et al.* 1974), 23-fold in the greater flamingo (Bech *et al.* 1979) and 22-fold for the pigeon (Calder & Schmidt-Nielsen, 1966).

Our swan data show that tidal volumes during panting are 18% of the resting value. When using the allometric equations from Calder & King (1974) relating breathing rate to total ventilation both at normal breathing and panting, we calculate the following relationship between tidal volumes at the two states: V_T panting/V_T rest = 0·27 $W^{0.1}$ (W, body mass in kilograms). It is apparent that the mute swan reduces its tidal volume more than predicted. The total ventilation, however, comes out at 5·4 times the resting value (Table 1), a value corresponding well with the Calder–King predictions.

The long neck of the swan is of obvious consequence for the breathing pattern. Bech & Johansen (1980) demonstrated that the mute swan has an unusually low breathing rate at resting conditions and a far higher O_2 extraction from the ventilated air than is typical for birds. Hinds & Calder (1971) measured tracheal dead space in an 8·57 kg mute swan to be 77 ml. A 9·0 kg mute swan measured in the present study by post-mortem volumetric filling of the trachea from the syrinx to glottis gave 84 ml. If this figure is used to calculate parabronchial ventilation using the directly measured values for tidal volume and breathing rate, we arrive at a value of 144·5 ml min^{-1} kg^{-1}

at normal breathing during rest and 134·3 ml min^{-1} kg^{-1} during panting. These calculations suggest that there is no increased parabronchial ventilation associated with panting in the mute swan. That conclusion is untenable when viewed in the context of the alterations of end-tidal gas composition associated with panting.

In the above calculations the anatomical dead space was used, and not the physiological dead space, which has been found to decrease during panting, at least in the ox (Hales & Findley, 1968). If this is true for the swans also, it might explain the altered end-tidal gas tensions during panting.

Referring to Fig. 2, it is apparent that while the CO_2 and O_2 tensions at the mask are reaching atmospheric conditions at each inspiration, this is not the case deep in the trachea. Obviously, fresh air is not filling this region. However, large fluctuations in both CO_2 and O_2 tensions indicate that a great deal of mixing occurs with each breath cycle and suggest that pulmonary gas exchange may continue rather effectively at the panting levels of tidal volume. Fig. 4 brings additional evidence for this, by showing that gas exchange during panting occurs more or less along an extension of the line representing the gas-exchange ratio characteristic of normal breathing.

The arterial pH and P_{CO_2} measured in the swan at thermoneutrality were close to values reported for other birds (Bech & Johansen, 1980). Calder & Schmidt-Nielsen (1968) gave average values for eight species of 7·52 and 28·2 mmHg, corresponding to 7·501 and 27·1 mmHg measured for the mute swan (Table 1). While the species quoted by Calder & Schmidt-Nielsen (1968) all developed a rather pronounced respiratory alkalosis with panting, the mute swan developed only a slight alkalosis at steady-state panting (Table 2). The example provided by Fig. 3 of the time course of acid–base changes shows the changes to occur nearly parallel to the normal buffer line, thus expressing a reversible respiratory alkalosis.

One reason for the much greater respiratory alkalosis reported by other authors (Calder & Schmidt-Nielsen, 1968) is probably related to their employment of much higher ambient temperatures (43–50 °C) resulting in heavy laboured panting (type II) involving an increased or maintained tidal volume as part of the ventilatory response (Linsley & Burger, 1964). By contrast, when moderate thermal stress is employed and ambient temperatures are kept between 35 and 40 °C, shallow panting of type I results and no respiratory alkalosis occurs during sustained panting. The transition between type I and II panting may, however, depend on species and habitat characteristics, since desert-dwelling species like the rock partridge (*Alectoris chukar*) and Abdims stork (*Sphenorhynchus abdimii*) showed only small changes in arterial pH after continued panting at high ambient temperatures (45 °C) (Marder & Arad, 1975; Krausz *et al.* 1977). No measurements of tidal volume were done in these studies hence no classification of the panting patterns could be made. Similarly in the ostrich (*Struthio camelus*) no alkalosis occurred even after continued panting for 8 h at an ambient temperature of 50 °C (Schmidt-Nielsen *et al.* 1969).

The absence of a hypocapnic response during panting in the rock partridge, Abdims stork, and domestic fowl (Marder, Arad & Gafni, 1974; Marder & Arad, 1975; Krausz, *et al.* 1977) led these authors to suggest that there must be a shunt mechanism operating during panting to prevent these birds from getting alkalotic. Since the ventilation volumes were not directly measured in their studies, it is not conclusive that the actual parabronchial ventilation was increased during panting. In

the present study it has clearly been demonstrated that the mute swan does not increase its parabronchial ventilation appreciably, although the total ventilation is more than 5 times higher during panting. As demonstrated, this can be the result of a reduced tidal volume, and no shunt mechanism need be postulated.

Three different panting responses have been described in birds, all resulting in a reduced parabronchial ventilation during the overall ventilation increase associated with panting. Many species, including the swan as presently demonstrated, limit parabronchial ventilation by decreasing the tidal volume to a value near the dead space volume. Another pattern, described for the pigeon and referred to as compound ventilation (Ramirez & Bernstein, 1976), involves a biphasic breathing, including a very fast and shallow component superimposed on a much slower and deeper breathing rhythm. The rapid shallow rhythm allegedly causes the ventilation increase needed for evaporative heat loss without disturbing the parabronchial ventilation satisfied by the slower and deeper breathing.

A third panting pattern, recently described for the greater flamingo (Bech, *et al.* 1979), involves shallow breathing at tidal volumes less than the dead space. At regular intervals this rhythm is interrupted by a short sequence of deeper breaths, referred to as 'flushouts'. The shallow rapid breathing serves in evaporative heat loss while the flushouts maintain the needed parabronchial gas-exchange ventilation.

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