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HYDROGEN SULFIDE: EFFECTS ON AVIAN RESPIRATORY CONTROL AND INTRAPULMONARY CO_2 RECEPTORS

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ABSTRACT

The respiratory response to acute inhalation of hydrogen sulfide (H_2S) and the response of intrapulmonary CO_2 receptors to this gas were studied in male White Leghorn chickens. Inhaling low concentrations of H_2S (0.05%) for 30 minutes had no effect on ventilation; however, during inhalation of 0.2% and 0.3% H_2S for this time period respiratory frequency and tidal volume became irregular and variable. All birds that inhaled 0.4% H_2S died within 15 minutes.

H_2S, presented in the gas stream of unidirectionally ventilated birds, caused an increase in the discharge frequency of intrapulmonary CO_2 receptors and an increase in the amplitude of sternal movements. Because an increase in the discharge of these receptors normally inhibits the central respiratory neurons and may lead to apnea, it is clear that H_2S has additional actions that increase the output from these central neurons. The possibility that H_2S may produce its effects on the intrapulmonary CO_2 receptors by inhibiting carbonic anhydrase in these receptors is discussed.

INTRODUCTION

Hydrogen sulfide (H_2S) is a noxious, toxic gas produced by organic decomposition and by many industrial processes (cf. Yant and Sayers, 1927). Inhalation by dogs and men of only one or two breaths of high concentrations of H_2S (0.18% and more) causes immediate cessation of breathing and death, and lower concentrations (0.05 - 0.15%) may produce death due to respiratory failure after longer exposure (Haggard, 1925; O'Donoghue, 1961; Kleinfeld et al., 1964). In non-lethal cases the effects of H_2S are reversible and noncumulative. Toxicity depends on the capacity of the blood to oxidize H_2S to nontoxic forms (Haggard, 1921; Evans, 1967). At levels above this capacity, the active form of this compound, the hydrosulfide ion HS^-, is present and inhibits many enzyme systems including catalases, peroxidases, dopa oxidase, succinic dehydrogenase, carbonic anhydrase, dipeptidases, and benzamidase (Smith and Gosselin, 1966; Evans, 1967).

The systemic action of H_2S in mammals appears to be not only on the nervous system (Haggard, 1925), but also on peripheral chemoreceptors in the cardioaortic region and in the carotid bodies (Winder and Winder, 1933). With the recent discovery in the lungs of birds of intrapulmonary CO_2-sensitive receptors (Peterson and Fedde, 1968; Fedde and Peterson, 1970; Peterson and Fedde, 1971) and their possible importance in the control of breathing, it became apparent that there might be an additional site of action of H_2S - one that could be readily studied. Because of the paucity of information on the effect of H_2S on birds, its effects on the spontaneous breathing pattern and on intrapulmonary CO_2 receptors in the chicken have been studied.

METHODS

SPONTANEOUSLY BREATHING BIRDS

Animal preparation

Male, White Leghorn chickens, Gallus domesticus, (Babcock strain, mean body weight 2.1 kg) were anesthetized to a light plane (slight response to comb pinch) with sodium phenobarbital (150 mg/kg), administered intravenously via a cannulated cutaneous ulnar vein. Thirty minutes after anesthetization, a tracheostomy was performed approximately 4 cm cranial to the syrinx, and the femoral artery was cannulated for monitoring blood pressure and heart rate. The bird was positioned upright, to simulate natural posture, in a specially designed frame (Fig. 1). A nonrebreathing valve (6 ml dead space; 1.9 cm H_2O/l/sec inspiratory resistance and 2.4 cm H_2O/l/sec expiratory resistance at 1.2 l/min flow) was attached to the trachea by pulling the trachea into a side arm of the valve. In that way, the tracheal diameter was not decreased and mucous formation due to tracheal irritation was minimized.

A "bag in a box" ventilation system was used (Fig. 1). The system consisted of a 53.2 liter carboy fitted inside with a large, collapsed air tight plastic bag. The bird inhaled from the carboy and exhaled into the bag, thus establishing a closed ventilatory system. A sensitive pressure transducer (Statham P23BB, with its dome removed) was placed through a rubber stopper in the mouth of the carboy to monitor pressure changes as the bird breathed.

Pressure changes within the carboy were recorded on a multichannel pen recorder (Beckman, type S). The system was calibrated to obtain tidal volume (V_T) by recording the pressure changes when various volumes of air were injected and withdrawn from the carboy. Respiratory frequency (f) was also obtained from these records. Minute ventilation ($\dot{V}$) was computed as the product of V_T and f.

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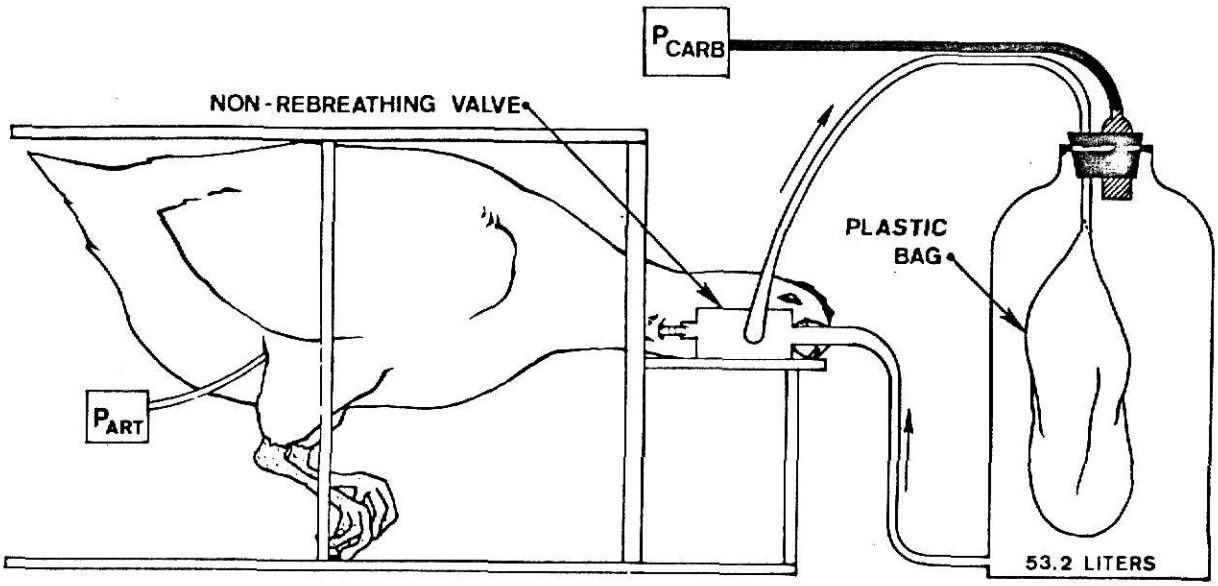

Fig. 1. Experimental arrangement for studying the effects of hydrogen sulfide (H_2S) on the breathing pattern of chickens. P_{art}, arterial blood pressure; P_{carb}, pressure within the carboy.

(2) Experimental protocol

Experiments were conducted in three tandem 30-minute parts. Each bird breathed from a carboy containing air during part 1 (pretreatment), another carboy containing air plus H_2S during part 2 (treatment), and a carboy containing air only during part 3 (post-treatment).

One hundred percent H_2S was obtained in a tank from a commercial supplier (Matheson Scientific). A calculated amount of H_2S gas at ambient temperature and pressure was injected into the treatment carboy to obtain the desired H_2S concentration in air. The H_2S concentration in the carboy was measured (Bendix Unico 400 Gas Detector, accuracy $\pm$ 10%) just before and just after part 2. At the end of each part, the inspiratory gas supply was tested for CO_2 with an infrared analyzer (Beckman, LB-1) to insure that diffusion of CO_2 out of the bag had not occurred.

Five groups of birds were tested, each of which inhaled a different H_2S concentration during the treatment period. Ten birds each were exposed to 0.0%, 0.05%, and 0.2% H_2S; five birds each to 0.3% and 0.4% H_2S. Although each individual bird served as its own control, the group receiving 0.0% H_2S served as a control group for all other treatments in that data from this group reflected the effects of anesthesia, time, and experimental procedures.

(3) Data analysis

V_T (ml), f (breaths$\cdot$min^{-1}), and $\dot{V}$ (ml$\cdot$min^{-1}) were obtained during designated sampling minutes (1, 5, 10, 15, 20, 25, and 30) of each 30 minute part. V_T was the average tidal volume during a given sampling minute; f was the number of breaths during each of these minutes; and $\dot{V}$ was the minute volume computed from product of V_T and f for each of these minutes.

The influence of inhaling H_2S on ventilation in each bird was determined by obtaining the difference between mean values of V_T, f and $\dot{V}$ for all

minutes of part 1 (air breathing only) and V_T, f and $\dot{V}$ at each sampling during parts 2 and 3 (H_2S treatment and post-treatment, respectively). These differences were tested for significance ($P < 0.05$) using a paired comparison Student's t-test (Snedecor and Cochran, 1967). At each sampling, H_2S treated groups were tested against the control group (0.0% H_2S) using Student's t-test for analysis of independent samples with unequal variance.

To identify any changes in variability of respiration caused by H_2S inhalation, variances of data taken at each sampling minute and variances of calculated differences for all groups were obtained. Variances of H_2S-treated groups were tested for significance ($P < 0.05$) against respective control group variances using a test of equality of two variances (Snedecor and Cochran, 1967).

UNIDIRECTIONALLY VENTILATED BIRDS

Animal preparation

Figure 2 illustrates the experimental arrangement. Adult, Single Comb White Leghorn roosters were anesthetized as before and secured in dorsal recumbancy. Body temperature was monitored by a thermistor placed in the rectum and maintained at 40 $\pm$ 1°C with a hot water heating pad. In a manner previously described (Burger and Lorenz, 1960; Fedde and Burger, 1962; Fedde et al., 1969; Fedde and Peterson, 1970) birds were unidirectionally, artificially ventilated by flowing gas (4 liters/min) into the trachea, through the lungs and out incised thoracic and abdominal air sacs. Carbon dioxide concentration in the ventilating gas was monitored with an infrared CO_2 analyzer (Beckman, LB-1).

The left vagus nerve was isolated at a midcervical location, and a mineral oil pool was formed with skin of the neck. The nerve, with its

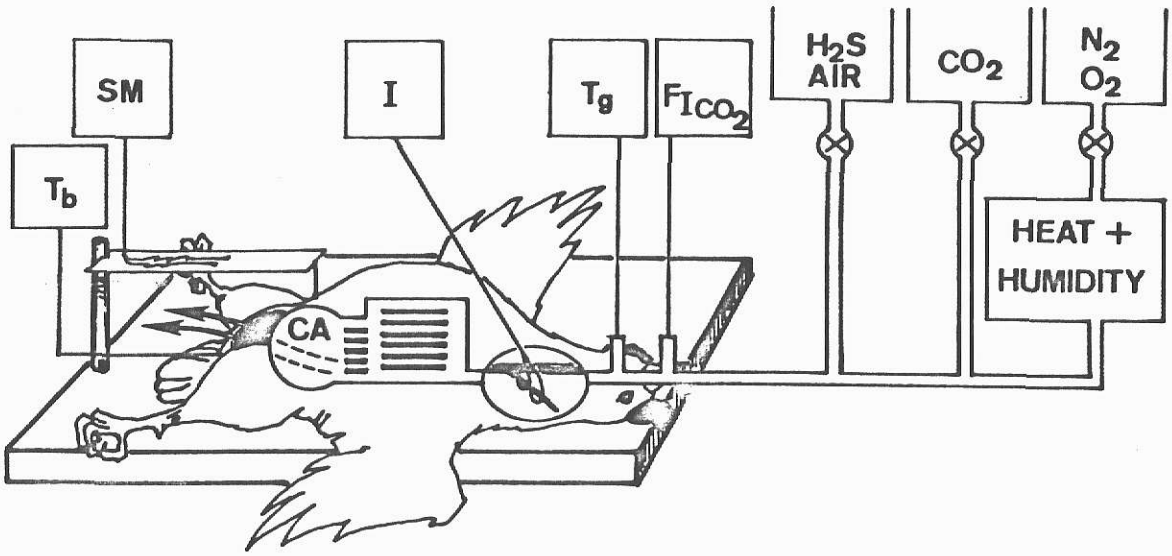

Fig. 2. Diagrammatic representation of the experimental arrangement. Gas was passed unidirectionally through trachea and lungs and out incised caudal (abdominal and thoracic) air sacs (CA). SM, strain gauge for measuring vertical sternal movement; I, electrodes for measuring intrapulmonary CO_2-sensitive receptor discharge; T_g, ventilatory gas temperature; T_b, body temperature; $F_{I_{CO_2}}$, port for measuring % CO_2 in ventilating gas; H_2S-Air, CO_2, and N_2-O_2, reservoirs or tanks of these gases supplied to the bird via flowmeters and metering valves. N_2 and O_2 were heated and humidified before entering the bird.

connective tissue sheath removed, was placed on a mirror support. Small fasciculi of the vagus nerve were progressively divided until a single receptor could be identified.

Recordings

Vertical sternal movement was monitored with a strain gauge attached to the tip of the sternum. The strain gauge was activated by a Tektronix Q unit whose output was displayed on an oscilloscope (Tektronix, type 565) and recorded on an FM tape recorder (Hewlett-Packard, 3960).

Afferent activity from intrapulmonary CO_2-sensitive receptors was monitored using bipolar hook electrodes (90% platinum - 10% iridium), an amplifier (Grass Model P-5), and an oscilloscope, and it was also recorded on a second channel of the tape recorder. Receptors were characterized by their dynamic response to a rapid change in airway CO_2 concentration and by their discharge frequency during delivery of static concentrations of airway CO_2. The dynamic response was tested by ventilating the bird at a CO_2 concentration greater than 5% and then by closing a solenoid valve eliminating CO_2 from the gas stream. To characterize receptor sensitivity to static CO_2 concentration discharge frequency was recorded while flowing gas with various constant concentrations of CO_2 through the birds lungs.

H_2S administration

H_2S (100%) was added by syringe at ambient temperature and pressure to a 53 liter carboy to produce a desired H_2S concentration. The carboy contained a large evacuated plastic bag which could be filled with air at a controlled rate to put the H_2S-air mixture in the carboy under pressure. The pressurized H_2S-air mixture was metered into the ventilating gas stream so as to produce the desired H_2S concentration to be delivered to the bird. At the end of the

experiment, the concentration of H_2S delivered to the bird was tested using an H_2S detector (Bendex Unico 400 Gas Detector, accuracy $\pm$ 10%).

Experimental protocol

Prior to and during H_2S treatment CO_2 was maintained at a static level (about 5%) that produced ventilatory movements. Receptor response to CO_2 was tested in three birds after approximately five minutes of H_2S treatment. Sternal movement and intrapulmonary CO_2 sensitive receptor discharge were monitored continuously.

Data analysis

The data recorded on tape were replayed at 1/8 real time and recorded on a multichannel pen recorder (Brush, Model 481) at fast paper speed in order to distinguish the discharge from the CO_2 receptor based on shape and characteristics of the impulse waveform. The effects of acute H_2S exposure on ventilation and receptor discharge were studied in all six birds by comparison of immediate pre-exposure data to acute exposure data. In three birds it was possible to compare receptor sensitivity to CO_2 before and during H_2S exposure.

RESULTS

RESPONSE TO H_2S INHALATION

Table 1 contains the pretreatment group means for f, V_T and $\dot{V}$ with their standard errors.

Changes in ventilation due to inhaling H_2S are shown in figure 3. Birds inhaling no H_2S exhibited only a small insignificant fall in f and a small rise in V_T over the entire experiment. A slight change was seen in this group when carboys were switched between parts 2 and 3 of the experiment. Similarly, inhalation of 0.05% H_2S for 30 minutes produced no significant effect on respiration. However, inhaling the three higher H_2S concentrations produced what appeared to be concentration related alterations in respiration. At those concentrations respiratory variables in most birds increased within one minute. Thereafter, although the variables tended to oscillate somewhat, the values tended to approach those of the pretreatment period, although the birds were still inhaling H_2S. All birds exposed to 0.4% H_2S exhibited struggling, gasping, apnea and intermittant bursts of irregular breaths at various times during the exposure, and they died within 15 minutes of exposure. Cardiac arrest was taken as the indicator of death in that cardiac function continued beyond the final apneic period.

Within the first five minutes of the post-treatment period, the 0.2% and 0.3% groups responded with increased ventilation, which tended to return to normal during the remainder of the period.

One primary effect of H_2S inhalation was an increase in variability of both V_T and f (exemplified in figure 4 by the positive standard errors of the calculated mean differences in f, V_T and $\dot{V}$). As concentration of inhaled H_2S increased, so did within group variability of respiratory response. That relationship was seen during both treatment and post-treatment periods, though

TABLE 1

Pretreatment means (± SE) of respiratory variables for each of the H_2S treatment groups

H_2S treatment (%)	n	Mean Body wt. (kg)	f (breaths·min^{-1})	V_T (ml)	$\dot{V}$ (ml·min^{-1})
0.0	10	2.13	22.0 ± 1.4	25.4 ± 1.4	561 ± 35
0.05	10	2.04	18.6 ± 2.0	20.5 ± 2.6	541 ± 54
0.2	10	2.34	21.8 ± 2.9	25.0 ± 2.3	516 ± 67
0.3	5	1.97	24.9 ± 3.6	18.4 ± 3.4	411 ± 25
0.4	5	2.08	28.5 ± 4.4	18.6 ± 2.7	490 ± 54

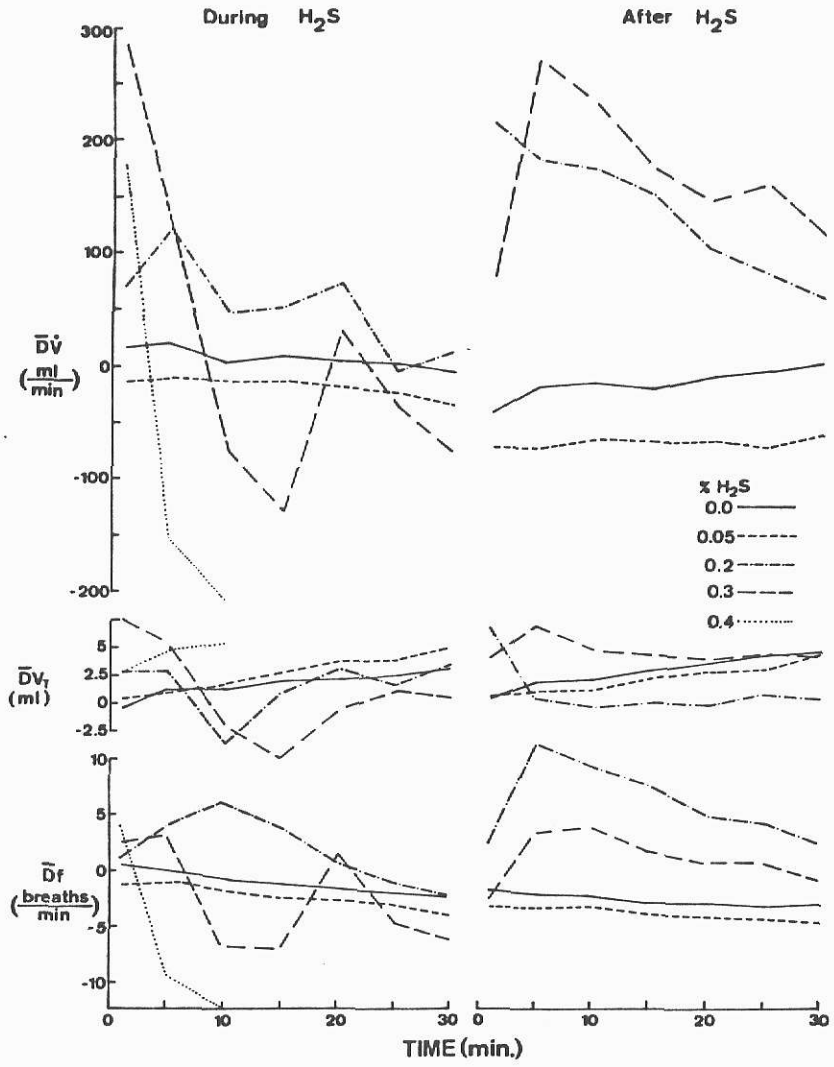

Fig. 3. Mean differences ($\bar{D}$) of pretreatment values (when birds breathed air before H_2S) and values during or after inhaling various concentrations of H_2S.

D = (treatment or post-treatment value) - (individual bird pretreatment mean).

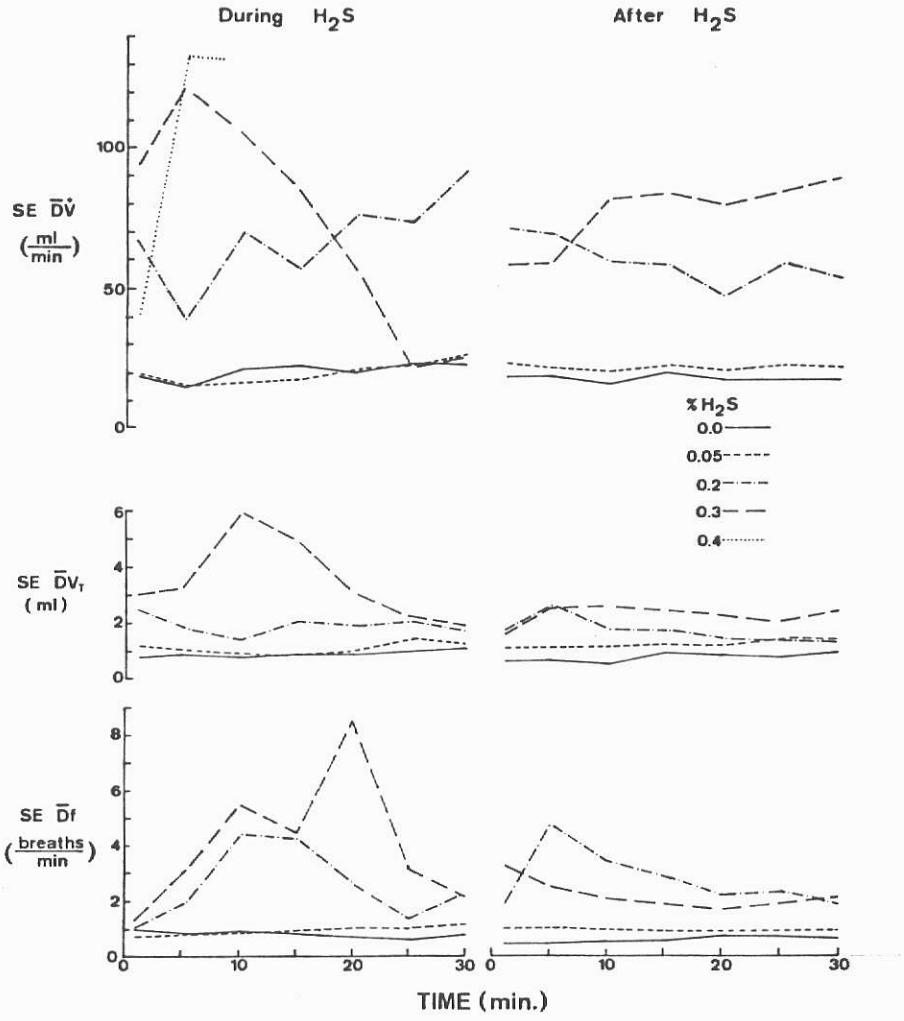

Fig. 4. The positive standard error of the mean differences of pretreatment control values (air breathing before H_2S) and values obtained during or after H_2S inhalation.
D = (treatment or post-treatment value) - (individual bird pretreatment mean).

it was most pronounced during H_2S inhalation. No significant difference in variability was found between the 0.05% group and control group. However, at the 0.2%, 0.3% and 0.4% H_2S levels, nearly all variances were significantly different from those of the control group.

RESPONSE OF INTRAPULMONARY CO_2 RECEPTORS TO H_2S

Identification of intrapulmonary CO_2 receptors

Identification of an intrapulmonary CO_2 receptor was based on its response to rapid changes in airway CO_2 concentration. Figure 5 is a recording from a CO_2-sensitive receptor depicting a typical response to a rapid change in intrapulmonary CO_2 concentration. When CO_2 was suddenly eliminated from the ventilating gas by a solenoid valve (first arrow), the discharge frequency rapidly increased to a peak and then slowly decreased to a stable frequency. The receptor quickly stopped discharging when CO_2 was suddenly added to the air stream (second arrow), and after a short silent period regained a discharge typical for the static CO_2 concentration. Apnea occurred quickly when CO_2 was eliminated from the gas stream.

The sensitivity of a CO_2-sensitive receptor was characterized by its discharge frequency at various static airway CO_2 concentrations (figure 6). As airway CO_2 concentration decreased, receptor discharge frequency increased.

Response to H_2S

Each of five birds received one of the following H_2S concentrations: 0.035%, 0.045%, 0.050%, 0.052%, or 0.055%. Two birds (four receptors) received 0.10% H_2S. The birds receiving 0.1% H_2S died within five minutes of exposure; all others survived 30 minutes.

Figure 7 is a recording of CO_2 receptor discharge and vertical sternal movement from a bird that received 0.05% H_2S. The first record was made

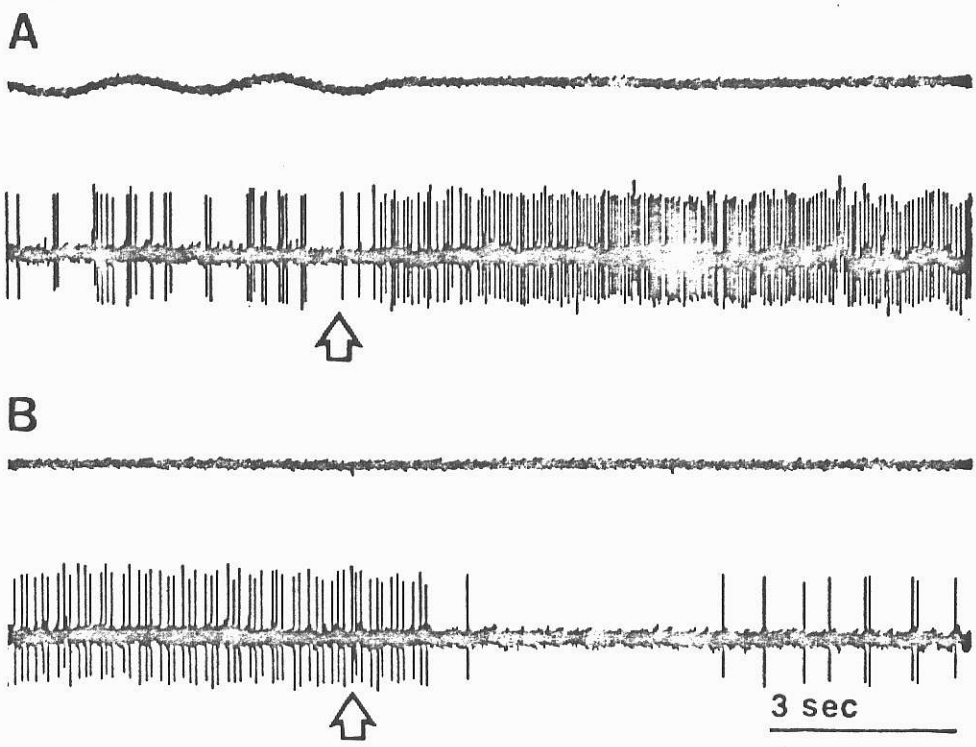

Fig. 5. Response of an intrapulmonary CO_2 receptor to a sudden change in airway CO_2 concentration. A. Bird ventilated with 9.2% CO_2 until arrow when a solenoid valve halted CO_2 delivery. B. After adaptation to 0.0% CO_2 in ventilating gas, CO_2 was added to gas by use of solenoid valve (at arrow). Note response of receptor discharge (lower tracings) and ventilating movements (upper tracings).

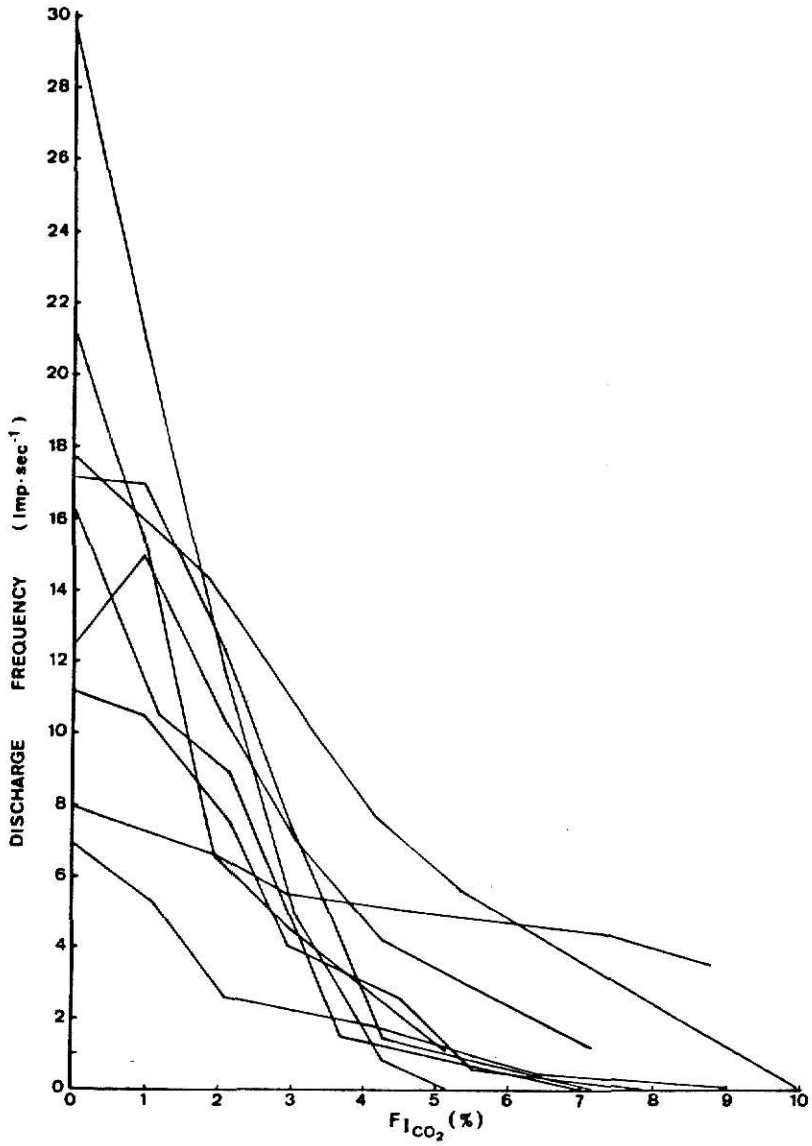

Fig. 6. Static sensitivity curves of nine intrapulmonary CO_2 sensitive receptors. Discharge frequency increased as airway CO_2 concentration decreased.

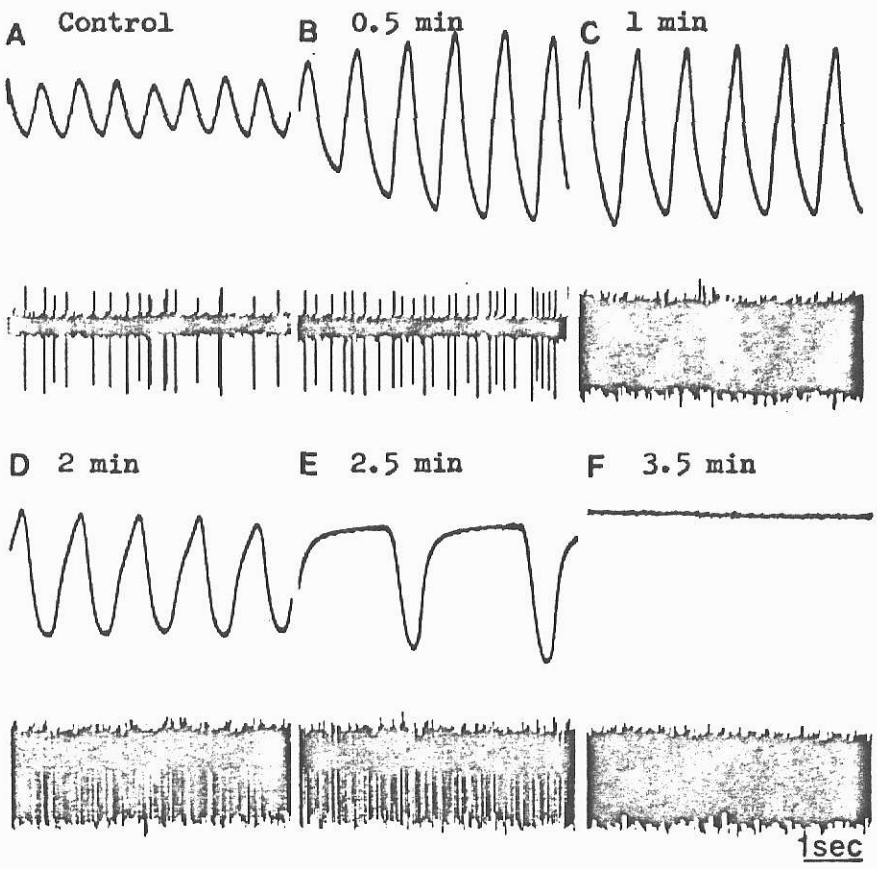

Fig. 7. Response to H_2S exposure. Upper tracings are vertical sternal movement (inspiration down); lower tracings, receptor discharge. Segment A was immediately prior to H_2S exposure. Time above each figure represents length of time after H_2S administration began.

immediately before H_2S exposure, and subsequent records were taken at indicated times during H_2S exposure. The bird responded within 30 seconds of H_2S exposure with increased amplitude of sternal movement and decreased respiratory frequency. Respiratory change was maximal after 90 seconds of exposure and respiration ceased after 200 seconds. Receptor discharge frequency began to increase within 30 seconds of exposure, with peak discharge frequency occurring at approximately 70 seconds.

The results presented in figure 7 were typical for the majority of the birds studied. All birds responded to H_2S with increased sternal movement approximately 30 seconds after exposure began. Sternal movements ceased within four minutes in all but one bird (0.04% H_2S), in which they continued for ten minutes. The increase in discharge frequency was most pronounced between 20 and 60 seconds of exposure, with peak discharge after 40 seconds in eight units (Table 2).

Figure 8 compares static sensitivity curves of three CO_2-sensitive receptors before and during H_2S exposure. After five minutes of H_2S exposure, two of the units (b and c) discharged less frequently at given CO_2 concentrations. The third unit, after ten minutes of H_2S exposure, discharged more slowly at 0.0% CO_2 but faster at other CO_2 concentrations than before H_2S.

TABLE 2

Effect of H_2S treatment on discharge frequencies of CO_2 receptors in unidirectionally ventilated chickens.

Unit (No.)	CO_2[a] (%)	H_2S[b] (%)	Discharge frequency (imp·sec^{-1}) at various times from beginning of H_2S delivery (sec.)							
			0[c]	10	20	40	60	80	100	120
1	4.5	0.035	0.6	2.5	2.0	7.0	5.5	8.4	14.0	0.0
2	5.2	0.045	7.5	8.5	9.0	7.8	5.1	sporadic bursts		
3	4.2	0.05	7.5	3.0	4.1	8.7	44.0	38.0	32.2	29.7
4	4.7	0.055	11.5	8.5	7.0	4.5	12.5	14.0	16.5	36.0
5	3.6	0.052	0.0	1.6	2.3	11.9	2.9	9.0	0.0	3.5
6	4.9	0.1	2.7	2.7	4.4	13.5	14.9	16.0	0.0	0.0
7	4.9	0.1	4.5	4.0	5.5	15.7	18.2	8.5	15.7	----
8	4.9	0.1	6.5	4.5	6.6	7.3	7.9	4.5	2.0	0.0

[a]Static concentration of CO_2 in ventilating gas stream.

[b]Concentration of H_2S in ventilating gas.

[c]Time 0 is the pretreatment discharge frequency at the indicated CO_2 concentration.

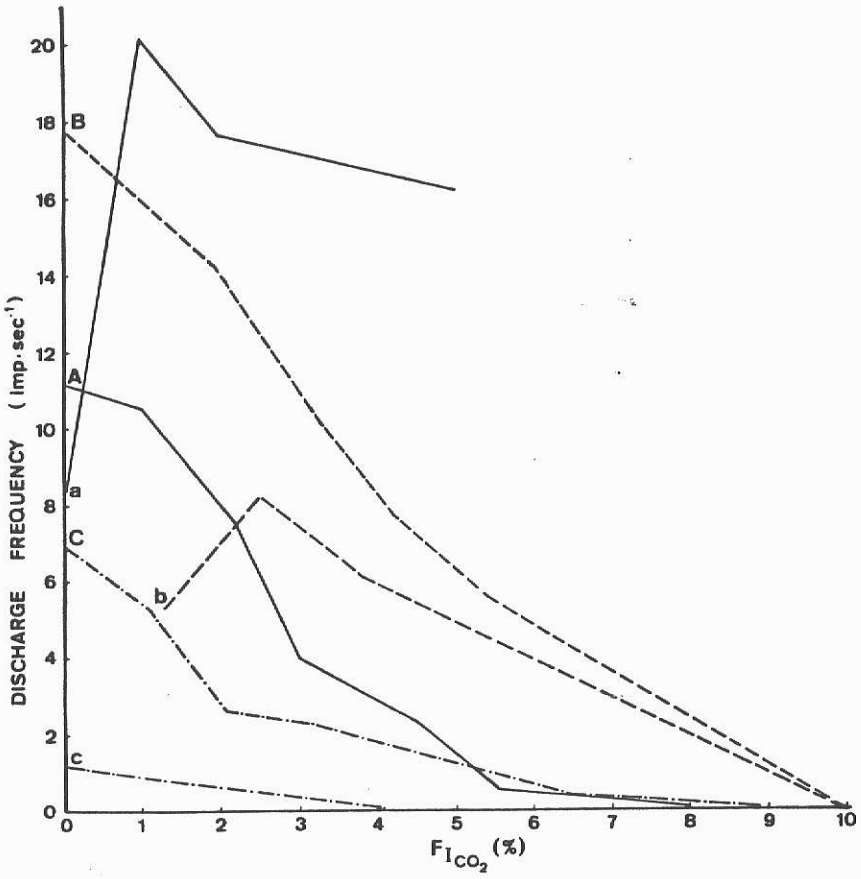

Fig. 8. Comparison of static CO_2 sensitivity curves before and during H_2S treatment. A, B and C curves were produced before H_2S treatment; a, b and c during H_2S exposure. Aa bird received 0.05% H_2S, and tracing a was produced after ten minutes of exposure. Bb bird received 0.045% H_2S, and tracing b was produced after five minutes of exposure. Cc bird received 0.035% H_2S, and tracing c was produced after five minutes of exposure.

DISCUSSION

CRITIQUE OF METHODS

Though the birds were lightly anesthetized, the tendency for f to fall and V_T to rise over time (in the pretreatment period and control group) may have been anesthetic related. Upright posture allowed a more normal V_T than occurs in supine posture (King and Payne, 1964), and use of a nonrebreathing valve prevented CO_2 contamination of inspired gas. Group means of V_T, f and $\dot{V}$ during the pretreatment period (Table 1) corresponded well with expected values (Frankel et al., 1962).

The procedures used to isolate and identify intrapulmonary CO_2 receptors in the chicken have been previously described and discussed (Fedde and Peterson, 1970; Fedde et al., 1974).

Although we used lower H_2S concentrations during unidirectional ventilation (0.035% to 0.1%) than during spontaneous breathing (0.05% to 0.4%), the flow of gas presented was approximately six times more than the average $\dot{V}$ of the spontaneously breathing birds. Thus, the ventilated birds were subjected to somewhat more H_2S than was a spontaneously breathing bird at the same H_2S concentration. It could be expected that birds receiving a given level of H_2S during spontaneous breathing could survive longer than birds ventilated unidirectionally with a similar H_2S level. That expectation was borne out.

VENTILATORY RESPONSE TO H_2S

Hydrogen sulfide produced similar ventilatory responses in the chicken as in other animals studied, (Haggard and Henderson, 1922; Haggard, 1925). The response is immediate and proportional to the inhaled concentration. Low concentrations had little or no influence on breathing but higher concentrations led to hyperpnea, which could terminate in respiratory failure.

However, our results suggested that the chicken is somewhat less sensitive to H_2S than are mammals since chickens inhaling 0.4% H_2S did not die immediately. Inhaled concentrations of 0.2% H_2S paralyze breathing in the dog after only one or two breaths (Haggard, 1925) and pigs die within about 40 minutes after inhaling 0.12% H_2S (O'Donoghue, 1961).

RESPONSE OF INTRAPULMONARY CO_2 RECEPTORS TO H_2S

The discharge patterns of the CO_2 receptors herein studied were typical of those previously studied in chickens and ducks (Fedde and Peterson, 1970; Fedde et al., 1974; Osborne and Burger, 1974). Discharge frequency increased as intrapulmonary CO_2 concentration was decreased, and some receptors ceased discharging when $F_{I_{CO_2}}$ was elevated to slightly more than 5%. In addition, some receptors decreased their discharge frequency when $F_{I_{CO_2}}$ was 0%.

Most CO_2 receptors were clearly stimulated by H_2S. Their discharge frequency increased dramatically in some cases but to a lesser degree in others. That response sharply contrasted with the lack of response of the receptors to carbon monoxide (Tschorn and Fedde, 1974) and to the reduction in discharge produced by sulfur dioxide (Chiang and Kunz, 1976).

EFFECT OF CO_2 RECEPTOR DISCHARGE ON BREATHING

If intrapulmonary CO_2 concentration is suddenly decreased to low values, receptor discharge increases and output from the respiratory neuronal pool decreases, quickly leading to apnea (Fedde and Peterson, 1970). The same response occurs whether or not blood flows through the lungs, suggesting that other receptors receiving a blood-borne change in CO_2 as a stimulus are not needed for the response (Peterson and Fedde, 1968; Burger et al., 1974). The intrapulmonary receptors thus appear to have a powerful central inhibitory influence on breathing. It has been clearly shown by Kunz and Miller (1974)

that breathing in nonanesthetized chickens can be paced by cyclic oscillations in intrapulmonary CO_2 concentration, further amplifying the importance of these receptors on the control of breathing.

ACTION OF H_2S

It is paradoxical that both the discharge of intrapulmonary CO_2 receptors and the respiratory movements increased when H_2S was given in the unidirectional gas stream. Normally those two events are inversely related. Because the CO_2 receptor discharge is strongly inhibitory to central respiratory neurons (Fedde and Peterson, 1970), it is probable that H_2S also acts centrally in an apparent antagonistic manner either by blocking the peripheral inhibitory influences and/or stimulating the respiratory neuronal pool.

The first dissociation constant of H_2S in water is 0.87×10^{-7} (Loy and Himmelblau, 1961). Thus at body pH nearly equal quantities of H_2S and HS^- would exist. HS^- appears to bind strongly with the zinc of carbonic anhydrase and, thus, acts as an inhibitor of this enzyme (Coleman, 1967; Lindskog, 1972). Carbonic anhydrase is widely distributed in the body and has been demonstrated in mammalian carotid bodies (Laurent et al., 1969), the central nervous system (Giacobini, 1962), in various avian tissues (Gay and Mueller, 1973), and in amphibian and reptilian lung (Fain and Rosen, 1973). It has recently been shown that the carbonic anhydrase inhibitor, acetazolamide, causes an increase in the discharge frequency from intrapulmonary CO_2 receptors in the Tegu lizard (Scheid et al., 1977) and in ducks (M. R. Fedde and P. Scheid, unpublished observations). Furthermore, the lizard and duck CO_2 receptors became relatively insensitive to CO_2 following injection of the drug. These observations suggest that intrapulmonary CO_2 receptors contain carbonic anhydrase and that its inhibition markedly influences the discharge of the receptors. The response

of CO_2 receptors to inhalation of H_2S is consistent with the hypothesis that HS^- acts to inhibit carbonic anhydrase in these receptors and thus causes their discharge frequency to increase.

It is more difficult to explain the increased output of central respiratory neurons while the birds inhaled H_2S. Possibly HS^- or H_2S directly stimulated central neurons, either by an effect of HS^- on carbonic anhydrase in those cells, or by other means to cause an increase in their output. It is also possible that these central neurons may be stimulated by a secondary effect of HS^- on carbonic anhydrase in the red blood cells. The inhibition of carbonic anhydrase by acetazolamide has been shown to produce severe acidosis in ducks (Anderson and Hustvedt, 1967). The acidosis may have an excitatory effect on the central respiratory neurons which overrides the inhibitory effect from the intrapulmonary CO_2 receptors to produce the ensuing increase in neural output to respiratory muscles.

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APPENDIX TABLE 1

RESPIRATORY FREQUENCY (BREATHS·MIN^{-1})

BEFORE 0.0% H_2S TREATMENT

WITH MEANS ($\bar{X}$), AND STANDARD ERROR (SE)

BIRD No.	TIME (MIN) 1	5	10	15	20	25	30	$\bar{X}$
1	21.6	22.6	23.4	21.8	22.0	22.2	22.8	22.3
2	24.2	25.6	25.8	25.0	24.2	24.4	24.1	24.8
3	18.4	18.0	18.1	18.3	18.0	17.7	17.4	18.0
4	24.8	24.3	23.6	24.2	25.6	24.6	23.5	24.4
5	29.2	29.5	28.6	28.2	28.7	29.3	27.2	28.7
6	32.0	31.7	29.1	25.8	24.0	24.2	22.7	27.1
7	21.7	22.0	22.4	22.2	21.2	21.2	21.0	21.7
8	24.1	21.2	20.1	19.7	19.6	18.6	18.8	20.3
9	14.1	18.5	18.3	19.0	19.0	18.9	18.2	18.0
10	14.6	15.0	15.2	15.4	15.2	15.0	14.5	15.0
$\bar{X}$	22.5	22.8	22.5	22.0	21.8	21.6	21.0	22.0
SE	1.8	1.6	1.4	1.2	1.3	1.3	1.2	1.4

APPENDIX TABLE 2

RESPIRATORY FREQUENCY (BREATHS·MIN^{-1})

DURING 0.0% H_2S TREATMENT

WITH MEANS ($\bar{X}$), AND STANDARD ERROR (SE)

BIRD No.	TIME (MIN) 1	5	10	15	20	25	30
1	23.3	24.0	24.0	22.0	21.8	20.8	20.6
	1.0*	1.7	1.7	-0.3	-0.5	-1.5	-1.7
2	26.5	23.6	21.7	23.9	23.3	22.8	22.7
	1.7	-1.2	-3.1	-0.9	-1.5	-2.0	-2.1
3	17.0	16.9	16.7	15.3	17.5	17.5	17.0
	-1.0	-1.1	-1.3	-2.7	-0.5	-0.5	-1.0
4	24.8	24.6	23.0	22.8	22.8	22.5	21.9
	0.4	0.2	-1.4	-1.6	-1.6	-1.9	-2.5
5	36.6	35.1	34.2	32.8	29.0	28.2	27.0
	7.9	6.4	5.5	4.1	0.3	-0.5	-1.7
6	24.0	23.4	23.1	22.8	21.2	21.7	20.0
	-3.1	-3.7	-4.0	-4.3	-5.9	-5.4	-7.1
7	21.0	21.4	20.4	19.9	20.0	20.1	19.5
	-0.7	-0.3	-1.3	-1.8	-1.7	-1.6	-2.2
8	19.8	18.3	16.4	15.6	15.0	15.1	14.3
	-0.5	-2.0	-3.9	-4.7	-5.3	-5.2	-6.0
9	17.3	17.0	17.2	17.0	17.5	16.8	16.2
	-0.7	-1.0	-0.8	-1.0	-0.5	-1.2	-1.8
10	16.1	15.9	16.0	16.3	15.6	14.5	14.2
	1.1	0.9	1.0	1.3	0.6	-0.5	-0.8
$\bar{X}$	22.6	22.0	21.3	20.8	20.4	20.0	19.3
*	0.3	0.0	-0.8	-1.2	-1.7	-2.0	-2.5
SE	1.9	1.8	1.7	1.7	1.3	1.3	1.3
*	0.9	0.9	0.9	0.8	0.7	0.6	0.8

*Change in frequency obtained by subtracting individual bird mean frequency during pretreatment period from frequency at times 1,5,...30. Mean change and standard error of mean change shown with $\bar{X}$ and SE.

APPENDIX TABLE 3

RESPIRATORY FREQUENCY (BREATHS·MIN^{-1})

AFTER 0.0% H_2S TREATMENT

WITH MEANS ($\bar{X}$), AND STANDARD ERROR (SE)

BIRD No.	TIME (MIN) 1	5	10	15	20	25	30
1	21.0	20.1	19.6	19.3	19.0	19.6	18.9
	-1.3*	-2.2	-2.7	-3.0	-3.3	-2.7	-3.4
2	21.5	22.2	24.2	23.1	23.6	22.0	23.5
	-3.3	-2.6	-0.6	-1.7	-1.2	-2.8	-1.3
3	17.8	18.0	18.2	18.0	17.8	18.6	18.6
	-0.2	0.0	0.2	0.0	-0.2	0.6	0.6
4	24.0	22.8	23.4	22.2	24.6	23.6	22.7
	-0.4	-1.6	-1.0	-2.2	0.2	-0.8	-1.7
5	28.8	27.3	26.5	25.4	26.0	24.9	24.0
	0.1	-1.4	-2.2	-3.3	-2.7	-3.8	-4.7
6	23.1	21.9	21.1	19.9	19.3	18.6	19.7
	-4.0	-5.2	-6.0	-7.2	-7.8	-8.5	-7.4
7	19.8	19.2	19.4	18.7	18.8	18.2	18.3
	-1.9	-2.5	-2.3	-3.0	-2.9	-3.5	-3.4
8	17.4	18.2	17.9	17.6	16.2	17.2	17.1
	-2.9	-2.1	-2.4	-2.7	-4.1	-3.1	-3.2
9	15.1	15.7	15.6	15.5	15.1	14.9	15.0
	-2.9	-2.3	-2.4	-2.5	-2.9	-3.1	-3.0
10	14.6	14.0	12.2	12.6	11.3	11.2	11.7
	-0.4	-1.0	-2.8	-2.4	-3.7	-3.8	-3.3
$\bar{X}$	20.3	19.9	19.8	19.2	19.2	18.9	19.0
*	-1.7	-2.1	-2.2	-2.8	-2.9	-3.2	-3.1
SE	1.4	1.2	1.3	1.2	1.4	1.3	1.2
*	0.5	0.4	0.5	0.6	0.7	0.7	0.7

*Change in frequency obtained by subtracting individual bird mean frequency during pretreatment period from frequency at times 1,5,...30. Mean change and standard error of mean change shown with $\bar{X}$ and SE.

APPENDIX TABLE 4

RESPIRATORY FREQUENCY (BREATHS·MIN^{-1})

BEFORE 0.05% H_2S TREATMENT

WITH MEANS ($\bar{X}$), AND STANDARD ERROR (SE)

BIRD No.	TIME (MIN) 1	5	10	15	20	25	30	$\bar{X}$
1	20.1	21.0	21.1	21.2	21.1	21.1	21.4	21.0
2	20.9	20.0	19.0	18.1	16.0	12.2	11.4	16.8
3	18.5	18.4	18.4	17.9	18.2	16.9	16.3	17.8
4	7.4	8.3	8.0	7.4	9.1	8.3	7.8	8.0
5	14.0	13.3	12.8	14.0	13.3	12.0	12.0	13.1
6	34.2	31.0	28.2	27.1	26.2	25.3	23.7	28.0
7	29.0	29.0	27.2	26.8	27.0	27.0	27.0	27.6
8	20.0	19.0	18.4	18.0	17.9	17.4	16.6	18.2
9	10.9	11.2	13.0	15.7	16.4	16.0	16.2	14.2
10	22.5	23.0	21.8	21.1	20.9	19.5	20.0	21.3
$\bar{X}$	19.8	19.4	18.7	18.7	18.6	17.6	17.2	18.6
SE	2.5	2.3	2.0	1.8	1.7	1.9	1.9	2.0

APPENDIX TABLE 5

RESPIRATORY FREQUENCY (BREATHS·MIN^{-1})

DURING 0.05% H_2S TREATMENT

WITH MEANS ($\bar{X}$), AND STANDARD ERROR (SE)

BIRD No.	TIME (MIN) 1	5	10	15	20	25	30
1	20.0	20.1	19.0	19.0	17.7	17.7	17.1
	-1.0*	-0.9	-2.0	-2.0	-3.3	-3.3	-3.9
2	17.0	16.2	15.4	13.6	12.2	12.3	11.5
	0.2	-0.6	-1.4	-3.2	-4.6	-4.5	-5.3
3	15.8	25.5	14.3	13.6	12.7	10.8	9.7
	-2.0	-2.3	-3.5	-4.2	-5.1	-7.0	-8.1
4	9.0	8.1	8.3	9.2	9.1	9.3	11.0
	1.0	0.1	0.3	1.2	1.1	1.3	3.0
5	9.9	8.8	8.3	7.9	7.4	7.2	6.6
	-3.2	-4.3	-4.8	-5.2	-5.7	-5.9	-6.5
6	23.2	23.2	21.3	20.9	20.0	20.2	18.7
	-4.8	-4.8	-6.7	-7.1	-8.0	-7.8	-9.3
7	28.8	30.7	30.4	30.6	30.8	27.7	23.8
	1.2	3.1	2.8	3.0	3.2	0.1	-3.8
8	15.4	16.6	16.6	17.0	17.8	17.8	17.5
	-2.8	-1.6	-1.6	-1.2	-0.4	-0.4	-0.7
9	15.8	16.0	15.2	14.2	13.1	14.1	13.4
	1.6	1.8	1.0	0.0	-1.1	-0.1	-0.8
10	18.8	18.9	19.1	18.0	18.0	17.6	17.6
	-2.5	-2.4	-2.2	-3.3	-3.3	-3.7	-3.7
$\bar{X}$	17.4	17.4	16.8	16.4	15.9	15.5	14.7
*	-1.2	-1.2	-1.8	-2.2	-2.7	-3.1	-3.9
SE	1.8	2.1	2.0	2.0	2.1	1.9	1.6
*	0.7	0.8	0.9	1.0	1.0	1.0	1.2

*Change in frequency obtained by subtracting individual bird mean frequency during pretreatment period from frequency at times 1,5,...30. Mean change and standard error of the mean change shown with $\bar{X}$ and SE.

APPENDIX TABLE 6

RESPIRATORY FREQUENCY (BREATHS·MIN^{-1})

AFTER 0.05% H_2S TREATMENT

WITH MEANS ($\bar{X}$), AND STANDARD ERROR (SE)

BIRD No.	TIME (MIN) 1	5	10	15	20	25	30
1	16.7	16.9	16.2	15.7	15.2	14.8	14.3
	-4.3*	-4.1	-4.8	-5.3	-5.8	-6.2	-6.7
2	12.9	12.7	13.9	12.1	13.2	12.5	12.7
	-3.9	-4.1	-2.9	-4.7	-3.6	-4.3	-4.1
3	10.2	9.9	10.4	9.9	10.1	9.5	10.0
	-7.6	-7.9	-7.4	-7.9	-7.7	-8.3	-7.8
4	8.5	8.6	7.8	8.8	8.3	9.0	8.7
	0.5	0.6	-0.2	0.8	0.3	1.0	0.7
5	6.7	6.6	6.8	6.4	6.1	7.0	6.2
	-6.4	-6.5	-6.3	-6.7	-7.0	-6.1	-6.9
6	21.0	20.0	19.6	20.0	19.0	19.4	18.0
	-7.0	-8.0	-8.4	-8.0	-9.0	-8.6	-10.0
7	29.2	28.0	28.4	27.3	26.4	26.0	25.4
	1.6	0.4	0.8	-0.3	-1.2	-1.6	-2.2
8	17.3	18.1	17.0	15.8	14.9	13.2	14.6
	-0.9	-0.1	-1.2	-2.4	-3.4	-5.0	-3.6
9	12.9	12.7	12.7	12.7	12.2	12.0	11.4
	-0.9	-0.1	-1.2	-2.4	-3.3	-5.0	-3.6
10	18.4	19.0	19.6	18.4	18.8	18.1	17.8
	-2.9	-2.3	-1.7	-2.9	-2.5	-3.2	-3.5
$\bar{X}$	15.4	15.3	15.2	14.7	14.4	14.2	13.9
*	-3.2	-3.3	-3.3	-3.9	-4.2	-4.4	-4.7
SE	2.1	2.0	2.0	2.0	1.9	1.8	1.8
*	1.0	1.0	1.0	0.9	1.0	1.0	1.0

*Change in frequency obtained by subtracting individual bird mean frequency during pretreatment period from frequency at times 1,5,...30. Mean change and standard error of the mean change shown with $\bar{X}$ and SE.

APPENDIX TABLE 7

RESPIRATORY FREQUENCY (BREATHS·MIN^{-1})

BEFORE 0.2% H_2S TREATMENT

WITH MEANS ($\bar{X}$), AND STANDARD ERROR (SE)

BIRD No.	TIME (MIN)							
	1	5	10	15	20	25	30	$\bar{X}$
1	13.4	14.0	15.0	15.6	17.1	16.0	16.1	15.3
2	17.8	14.5	15.1	15.1	15.7	14.6	14.7	15.4
3	31.2	29.0	28.9	25.3	23.5	23.5	24.2	26.5
4	11.6	12.0	13.0	14.0	14.6	15.0	15.0	13.6
5	20.6	18.4	17.7	16.2	16.9	16.9	15.5	17.5
6	23.6	21.6	21.6	21.4	21.2	21.4	20.2	21.6
7	45.0	42.7	47.5	45.3	45.6	43.3	46.9	45.2
8	23.8	23.7	25.5	26.5	27.5	26.6	24.3	25.4
9	22.3	20.2	20.0	20.8	22.0	21.3	20.7	21.0
10	18.4	17.1	16.8	17.4	16.9	16.1	16.2	17.0
$\bar{X}$	23.8	21.3	22.1	21.8	22.1	21.5	21.4	21.8
SE	3.0	2.8	3.2	3.0	2.9	2.1	3.1	2.9

APPENDIX TABLE 8

RESPIRATORY FREQUENCY (BREATHS·MIN^{-1})

DURING 0.2% H_2S TREATMENT

WITH MEANS ($\bar{X}$), AND STANDARD ERROR (SE)

BIRD No.	TIME (MIN) 1	5	10	15	20	25	30
1	18.2	17.6	15.8	15.0	14.0	12.9	15.6
	2.9*	2.3	0.5	-0.3	-1.3	-2.4	0.3
2	16.4	14.2	13.3	17.1	15.6	16.3	18.3
	1.0	-1.2	-2.1	1.7	0.2	0.9	2.9
3	21.3	35.6	31.4	18.9	15.0	15.6	9.0
	-5.2	9.1	4.9	-7.6	-11.5	-10.9	-17.5
4	14.0	16.4	12.0	9.8	19.3	16.2	18.3
	0.4	2.8	-1.6	-3.8	5.7	2.6	4.7
5	15.0	17.1	12.2	17.0	16.2	15.4	17.6
	-2.5	-0.4	-5.3	-0.5	-1.3	-2.1	0.1
6	24.1	20.8	18.4	19.0	20.0	24.3	29.0
	2.5	-0.8	-3.2	-2.6	-1.6	2.7	7.4
7	50.6	60.7	64.8	63.0	62.5	48.4	38.8
	5.4	15.5	19.6	17.8	17.3	3.2	-6.4
8	25.7	35.8	37.5	26.3	18.6	21.2	16.7
	0.3	10.4	12.1	0.9	-6.9	-4.2	-8.7
9	21.2	18.8	18.2	17.7	17.4	17.9	18.2
	0.2	-2.2	-2.8	-3.3	-3.6	-3.1	-2.8
10	22.3	19.5	55.0	54.2	26.2	18.5	15.2
	5.3	2.5	38.0	37.2	9.2	1.5	-1.8
$\bar{X}$	22.9	25.6	26.4	25.8	22.5	20.7	19.7
*	1.0	3.8	6.0	4.0	0.6	-1.2	-2.2
SE	3.3	4.6	6.5	5.7	4.6	3.2	2.6
*	1.0	1.9	4.3	4.3	2.6	1.4	2.3

*Change in frequency obtained by subtracting individual bird mean frequency during pretreatment period from frequency at times 1,5,...30. Mean change and standard error of the mean change are shown with $\bar{X}$ and SE.

APPENDIX TABLE 9

RESPIRATORY FREQUENCY (BREATHS·MIN^{-1})

AFTER 0.2% H_2S TREATMENT

WITH MEANS ($\bar{X}$), AND STANDARD ERROR (SE)

BIRD No.	TIME (MIN) 1	5	10	15	20	25	30
1	18.7	61.0	33.3	30.6	26.4	24.1	20.4
	3.4*	45.7	18.0	15.3	11.1	8.8	5.1
2	13.4	16.0	15.2	14.7	14.2	18.2	17.0
	-2.0	0.6	-0.2	-0.7	-1.2	2.8	1.6
3	21.5	24.1	26.9	26.3	27.1	24.6	23.0
	-5.0	-2.4	0.4	-0.2	0.6	-1.9	-3.5
4	14.2	21.0	21.8	20.0	17.8	17.0	15.9
	0.6	7.4	8.2	6.4	4.2	3.4	2.3
5	17.1	18.0	16.2	16.1	15.0	14.8	14.1
	-0.4	0.5	-1.3	-1.4	-2.5	-2.7	-3.4
6	28.3	27.0	25.7	22.3	21.9	20.4	20.2
	6.7	5.4	4.1	0.7	0.3	-1.2	-1.4
7	61.0	71.5	75.7	68.6	58.8	56.8	51.0
	15.8	26.3	30.5	23.4	13.6	11.6	5.8
8	25.8	37.0	37.0	35.8	33.2	32.5	31.3
	0.4	11.6	11.6	10.4	7.8	7.1	5.9
9	20.0	20.5	21.2	21.1	20.1	17.7	17.0
	-1.0	-0.5	0.2	0.1	-0.9	-3.3	-4.0
10	24.5	35.7	39.0	36.0	34.4	36.3	33.8
	7.5	18.7	22.0	19.0	17.4	19.3	16.8
$\bar{X}$	24.5	33.2	31.2	29.2	26.9	26.2	24.4
*	2.6	11.3	9.4	7.3	5.0	4.4	2.5
SE	4.3	6.0	5.6	4.9	4.2	4.0	3.6
*	1.9	4.8	3.5	2.9	2.2	2.3	2.0

*Change in frequency obtained by subtracting individual bird mean frequency during pretreatment period from frequency at times 1,5,...30. Mean change and standard error of the mean change are shown with $\bar{X}$ and SE.

APPENDIX TABLE 10

RESPIRATORY FREQUENCY (BREATHS·MIN^{-1})

BEFORE 0.3% H_2S TREATMENT

WITH MEANS ($\bar{X}$), AND STANDARD ERROR (SE)

BIRD No.	TIME (MIN) 1	5	10	15	20	25	30	$\bar{X}$
1	19.3	18.7	18.0	17.7	16.0	15.1	15.9	17.2
2	35.0	34.0	26.5	30.6	31.0	25.2	30.2	30.4
3	17.2	13.6	14.5	15.1	15.4	15.6	16.8	15.5
4	28.0	29.0	30.0	29.2	29.4	28.2	27.2	28.7
5	39.0	35.3	33.3	33.0	31.9	29.0	29.0	32.9
$\bar{X}$	27.7	26.1	24.5	25.1	24.7	22.6	23.8	24.9
SE	4.2	4.3	3.6	3.6	3.7	3.0	3.1	3.6

APPENDIX TABLE 11

RESPIRATORY FREQUENCY (BREATHS·MIN^{-1})

DURING 0.3% H_2S TREATMENT

WITH MEANS ($\bar{X}$), AND STANDARD ERROR (SE)

BIRD No.	TIME (MIN) 1	5	10	15	20	25	30
1	17.0	15.5	18.4	17.2	48.4	13.1	11.3
	-0.2*	-1.7	1.2	0.0	31.2	-4.1	-5.9
2	33.8	38.0	33.9	31.2	27.8	25.2	21.7
	3.4	7.6	3.5	0.8	-2.6	-5.2	-8.7
3	22.0	13.3	9.0	10.0	18.8	18.9	15.0
	6.6	-2.2	-6.5	-5.5	3.3	3.4	-0.5
4	32.5	36.0	24.7	22.0	26.7	26.3	26.0
	3.8	7.3	-4.0	-6.7	-2.0	-2.4	-2.7
5	32.0	25.0	5.5	9.0	11.0	17.0	20.0
	-0.9	-7.9	-27.4	-23.9	-21.9	-15.9	-12.9
$\bar{X}$	27.5	25.6	18.3	17.9	26.5	20.1	18.8
*	2.5	0.6	-6.6	-7.1	1.6	-4.8	-6.1
SE	3.4	5.1	5.2	4.1	6.2	2.6	2.6
*	1.4	3.0	5.5	4.4	8.6	3.1	2.2

*Change in frequency obtained by subtracting individual bird mean frequency during pretreatment period from frequency at times 1,5,...30. Mean change and standard error of the mean change are shown with $\bar{X}$ and SE.

APPENDIX TABLE 12

RESPIRATORY FREQUENCY (BREATHS·MIN^{-1})

AFTER 0.3% H_2S TREATMENT

WITH MEANS ($\bar{X}$), AND STANDARD ERROR (SE)

BIRD No.	TIME (MIN) 1	5	10	15	20	25	30
1	16.2	24.7	25.9	23.5	20.7	20.0	18.4
	-1.0*	7.5	8.7	6.3	3.5	2.8	1.2
2	33.9	34.0	31.8	28.0	28.2	26.8	25.5
	3.5	3.6	1.4	-2.4	-2.2	-3.6	-4.9
3	18.1	20.5	22.9	21.4	21.3	21.3	21.7
	2.6	5.0	7.4	5.9	5.8	5.8	6.2
4	27.0	35.9	34.0	30.5	29.8	31.8	29.0
	-1.7	7.2	5.3	1.8	1.1	3.1	0.3
5	18.1	26.7	30.0	30.2	29.5	29.1	27.5
	-14.8	-6.2	-2.9	-2.7	-3.4	-3.8	-5.4
$\bar{X}$	22.7	28.4	28.9	26.7	25.9	25.8	24.4
*	-2.3	3.4	3.9	1.8	1.0	0.9	-0.5
SE	3.4	2.9	2.0	1.8	2.0	2.2	1.9
*	3.3	2.5	2.1	1.9	1.7	1.9	2.1

*Change in frequency obtained by subtracting individual bird mean frequency during pretreatment period from frequency at times 1,5,...30. Mean change and standard error of the mean change are shown with $\bar{X}$ and SE.

APPENDIX TABLE 13

RESPIRATORY FREQUENCY (BREATHS·MIN^{-1})

BEFORE 0.4% H_2S TREATMENT

WITH MEANS ($\bar{X}$), AND STANDARD ERROR (SE)

BIRD No.	TIME (MIN) 1	5	10	15	20	25	30	$\bar{X}$
1	30.5	30.4	32.1	32.3	30.9	29.6	31.0	31.0
2	44.1	43.5	43.3	42.2	41.0	41.9	41.8	42.5
3	20.2	15.7	14.3	14.0	15.4	17.6	16.5	16.2
4	34.3	32.0	32.8	33.0	28.8	26.3	27.0	30.6
5	22.7	20.0	21.2	23.1	23.0	23.3	23.7	22.4
$\bar{X}$	30.4	28.3	28.6	28.9	27.8	27.7	28.0	28.5
SE	4.3	4.9	5.0	4.8	4.2	4.0	4.2	4.4

APPENDIX TABLE 14

RESPIRATORY FREQUENCY (BREATHS·MIN^{-1})

DURING 0.4% H_2S TREATMENT

WITH MEANS ($\bar{X}$), AND STANDARD ERROR (SE)

BIRD No.	TIME (MIN) 1	5	10
1	32.0		
	1.0*		
2	47.0	3.0	
	4.5	-39.5	
3	21.1	11.5	3.0
	4.9	-4.7	-13.2
4	31.2		
	0.6		
5	31.0	38.0	11.0
	8.6	15.6	-11.4
$\bar{X}$	32.5	17.5	7.0
*	3.9	-9.5	-12.3
SE	4.1	8.2	2.5
*	1.5	16.1	0.9

*Change in frequency obtained by subtracting individual bird mean frequency during pretreatment period from frequency at times 1,5,...30. Mean change and standard error of the mean change are shown with $\bar{X}$ and SE.

APPENDIX TABLE 15

RESPIRATORY TIDAL VOLUME (ML)

BEFORE 0.0% H_2S TREATMENT

WITH MEANS ($\bar{X}$), AND STANDARD ERROR (SE)

BIRD No.	TIME (MIN) 1	5	10	15	20	25	30	$\bar{X}$
1	33.8	33.7	33.9	32.3	32.1	32.0	32.4	33.2
2	24.9	25.6	27.1	28.5	28.0	30.4	30.6	27.2
3	29.2	29.2	29.1	31.7	30.5	31.8	32.9	30.2
4	23.0	26.9	23.2	25.6	26.8	26.9	28.2	25.4
5	20.9	20.9	22.3	24.2	23.2	23.3	23.7	22.1
6	14.9	16.5	16.0	21.3	23.7	21.3	22.5	18.6
7	23.4	24.8	25.2	25.0	27.7	26.5	25.2	25.0
8	17.6	21.5	21.8	20.5	23.8	21.8	21.5	20.6
9	21.4	24.2	25.1	25.1	25.5	25.7	26.2	24.4
10	25.7	27.3	28.7	28.8	27.7	27.8	28.9	27.6
$\bar{X}$	23.5	25.1	25.2	26.3	26.9	26.8	27.2	25.4
SE	1.7	1.5	1.6	1.3	0.9	1.2	1.3	1.4

APPENDIX TABLE 16

RESPIRATORY TIDAL VOLUME (ML)

DURING 0.0% H_2S TREATMENT

WITH MEANS ($\bar{X}$), AND STANDARD ERROR (SE)

BIRD No.	TIME (MIN) 1	5	10	15	20	25	30
1	32.5	32.6	32.4	32.8	32.3	32.5	32.5
	-0.7*	-0.6	-0.8	-0.4	-0.9	-0.7	-0.7
2	29.1	30.7	31.0	32.5	31.3	31.4	31.4
	1.9	3.5	3.8	5.3	4.1	4.2	4.2
3	34.5	33.3	34.0	34.7	33.4	34.7	35.6
	4.3	3.1	3.8	4.5	3.2	4.5	5.4
4	24.3	27.7	25.0	27.7	27.2	27.7	30.4
	-1.1	2.3	-0.4	2.3	1.8	2.3	5.0
5	21.7	21.0	23.5	24.9	27.0	28.8	29.2
	-0.4	-1.1	1.4	2.8	4.9	6.7	7.1
6	20.4	22.6	22.7	22.0	23.2	22.9	24.0
	1.8	4.0	4.1	3.4	4.6	4.3	5.4
7	27.4	28.1	27.3	27.5	27.6	27.8	27.8
	2.4	3.1	2.3	2.5	2.6	2.8	2.8
8	19.2	20.0	20.1	21.6	21.7	21.8	23.1
	-1.4	-0.6	-0.5	1.0	1.1	1.2	2.5
9	25.2	26.9	26.1	26.9	27.8	27.7	27.9
	0.8	2.5	1.7	2.5	3.4	3.3	3.5
10	24.3	23.4	24.5	23.4	24.0	23.6	23.5
	-3.3	-4.2	-3.1	-4.2	-3.6	-4.0	-4.1
$\bar{X}$	25.9	26.6	24.4	27.4	27.6	27.9	28.5
*	0.4	1.2	1.2	2.0	2.1	2.5	3.1
SE	1.6	1.5	2.8	1.5	1.2	1.3	1.3
*	0.7	0.8	0.8	0.8	0.8	1.0	1.0

*Change in tidal volume obtained by subtracting individual bird mean tidal volume during pretreatment period from tidal volume at times 1,5,...30. Mean change and standard error of the mean change are shown with $\bar{X}$ and SE.

APPENDIX TABLE 17

RESPIRATORY TIDAL VOLUME (ML)

AFTER 0.0% H_2S TREATMENT

WITH MEANS ($\bar{X}$), AND STANDARD ERROR (SE)

BIRD No.	TIME (MIN) 1	5	10	15	20	25	30
1	28.7	31.8	34.8	35.2	37.0	37.6	38.0
	-4.5*	-1.4	1.6	2.0	3.8	4.4	4.8
2	28.5	28.6	28.5	28.2	28.5	31.2	30.2
	1.3	1.4	1.3	1.0	1.3	4.0	3.0
3	31.0	30.4	31.6	31.4	32.2	32.4	33.2
	0.8	0.2	1.4	1.2	2.0	2.2	3.0
4	25.8	26.6	26.8	25.2	25.4	27.1	25.6
	0.4	1.2	1.4	-0.2	0.0	1.7	0.2
5	25.0	27.8	27.5	28.8	29.6	30.0	32.0
	2.9	5.7	5.4	6.7	7.5	7.9	9.9
6	18.0	19.5	19.6	20.0	23.7	22.5	23.7
	-0.6	0.9	1.0	1.4	5.1	3.9	5.1
7	26.5	27.9	27.3	26.9	27.7	27.9	27.9
	1.5	2.9	2.3	1.9	2.7	2.9	2.9
8	21.7	22.2	21.3	22.6	22.0	22.3	23.1
	1.1	1.6	0.7	2.0	1.4	1.7	2.5
9	25.2	28.3	29.0	29.9	30.5	31.1	30.9
	0.8	3.9	4.6	5.5	6.1	6.7	6.5
10	27.3	30.3	29.2	36.0	34.6	34.9	36.0
	-0.3	2.7	1.6	8.4	7.0	7.3	8.4
$\bar{X}$	25.8	27.3	27.6	28.4	29.1	29.7	30.1
*	0.3	1.9	2.1	3.0	3.7	4.3	4.6
SE	1.2	1.2	1.4	1.6	1.5	1.6	1.6
*	0.6	0.6	0.5	0.9	0.8	0.7	0.9

*Change in tidal volume obtained by subtracting individual bird mean tidal volume after H_2S treatment period from tidal volume at times 1,5,...30. Mean change and standard error of the mean change are shown with $\bar{X}$ and SE.

APPENDIX TABLE 18

RESPIRATORY TIDAL VOLUME (ML)

BEFORE 0.05% H_2S TREATMENT

WITH MEANS ($\bar{X}$), AND STANDARD ERROR (SE)

BIRD No.	TIME (MIN) 1	5	10	15	20	25	30	$\bar{X}$
1	23.8	25.8	26.4	26.3	26.6	27.5	26.7	26.1
2	30.9	33.7	35.8	39.7	48.0	58.2	55.7	43.1
3	35.5	34.6	35.8	35.8	38.4	38.4	39.9	36.9
4	20.5	26.1	28.8	27.5	28.2	27.5	27.5	26.6
5	15.5	17.4	18.8	19.1	19.1	20.8	20.3	18.7
6	22.6	26.4	28.3	27.0	27.9	28.0	28.0	26.9
7	18.8	22.7	21.6	23.8	26.7	23.5	25.7	23.3
8	26.2	28.5	29.3	30.9	30.9	31.8	31.1	29.8
9	47.2	49.9	48.4	43.5	39.7	37.1	37.5	43.3
10	27.2	27.2	29.4	30.8	30.8	31.6	32.4	29.9
$\bar{X}$	26.8	29.2	28.3	30.4	31.6	32.4	35.5	30.5
SE	2.9	2.8	2.5	2.4	2.6	3.4	4.9	2.6

APPENDIX TABLE 19

RESPIRATORY TIDAL VOLUME (ML)

DURING 0.05% H_2S TREATMENT

WITH MEANS ($\bar{X}$), AND STANDARD ERROR (SE)

BIRD No.	TIME (MIN) 1	5	10	15	20	25	30
1	24.7	24.7	26.2	26.3	27.3	27.2	27.6
	-1.4*	-1.4	0.1	0.2	1.2	1.1	1.5
2	37.8	41.5	42.7	47.2	50.2	52.5	55.1
	-5.3	-1.6	-0.4	4.1	7.1	9.4	12.0
3	33.7	36.1	37.9	39.4	41.8	45.0	46.4
	-3.2	-0.8	1.0	2.5	4.9	8.1	9.5
4	32.2	32.4	32.2	29.8	29.7	26.9	26.6
	5.6	5.8	5.6	3.2	3.1	0.3	0.0
5	20.7	21.9	21.0	22.9	24.1	23.9	24.7
	2.0	3.2	2.3	4.2	5.9	5.2	6.0
6	31.5	29.0	30.0	31.7	32.8	33.3	32.3
	4.6	2.1	3.1	4.8	5.9	6.4	5.4
7	22.0	21.4	21.5	21.6	21.6	22.6	25.6
	-1.3	-1.9	-1.8	-1.7	-1.7	-0.7	2.3
8	33.2	34.6	35.5	35.5	35.2	34.8	34.8
	3.4	4.8	5.7	5.7	5.4	5.0	5.0
9	39.3	39.2	40.5	42.1	42.3	39.4	43.8
	-4.0	-4.1	-2.8	-1.2	-1.0	-3.9	0.5
10	32.8	31.4	33.5	35.4	36.7	38.0	37.8
	2.9	1.5	3.6	5.5	6.8	8.1	7.9
$\bar{X}$	30.8	31.2	32.1	33.2	33.2	34.4	35.5
*	0.3	0.8	1.6	2.7	3.7	3.9	5.0
SE	2.0	2.2	2.4	2.6	2.9	3.0	3.2
*	1.2	1.0	0.9	0.9	1.0	1.4	1.3

*Change in tidal volume obtained by subtracting individual bird mean tidal volume during pretreatment period from tidal volume at times 1,5,...30. Mean change and standard error of the mean change are shown with $\bar{X}$ and SE.

APPENDIX TABLE 20

RESPIRATORY TIDAL VOLUME (ML)

AFTER 0.05% H_2S TREATMENT

WITH MEANS ($\bar{X}$), AND STANDARD ERROR (SE)

BIRD No.	TIME (MIN) 1	5	10	15	20	25	30
1	27.8	28.0	29.2	30.8	30.8	29.4	31.8
	1.7*	1.9	3.1	4.7	4.7	3.3	5.7
2	44.0	48.2	46.4	47.9	47.0	50.1	50.1
	0.9	5.1	3.3	4.8	3.9	7.0	7.0
3	41.2	42.8	43.0	43.0	45.0	43.4	44.9
	4.3	5.9	6.1	6.1	8.1	6.5	8.0
4	20.0	21.3	20.8	19.7	20.7	18.8	20.5
	-6.6	-5.3	-5.8	-6.9	-5.9	-7.8	-6.1
5	23.3	22.3	23.3	23.7	23.6	23.9	25.1
	4.6	3.6	4.6	5.0	4.9	5.2	6.4
6	27.8	27.9	29.7	31.6	30.4	30.5	32.6
	0.9	1.0	2.8	4.7	3.5	3.6	5.7
7	23.3	24.1	24.0	24.8	26.2	25.6	27.3
	0.0	0.8	0.7	1.5	2.9	2.3	4.0
8	30.1	26.7	28.1	30.0	33.4	36.7	37.4
	0.3	-3.1	-1.7	0.2	3.6	6.9	7.6
9	40.1	41.7	40.1	42.1	42.2	43.5	44.8
	-3.2	-1.6	-3.2	-1.2	-1.1	0.2	1.5
10	33.4	31.8	32.1	33.3	33.3	34.5	34.6
	3.5	1.9	2.2	3.4	3.4	4.6	4.7
$\bar{X}$	31.1	31.5	31.7	32.7	33.3	33.6	34.9
*	0.6	1.0	1.2	2.2	2.8	3.2	4.4
SE	2.6	3.0	2.7	2.9	2.8	3.1	3.0
*	1.1	1.1	1.2	1.3	1.2	1.4	1.3

*Change in tidal volume obtained by subtracting individual bird mean tidal volume during pretreatment period from tidal volume at times 1,5,...30. Mean change and standard error of the mean change are shown with $\bar{X}$ and SE.

APPENDIX TABLE 21

RESPIRATORY TIDAL VOLUME (ML)

BEFORE 0.2% H_2S TREATMENT

WITH MEANS ($\bar{X}$), AND STANDARD ERROR (SE)

BIRD No.	TIME (MIN) 1	5	10	15	20	25	30	$\bar{X}$
1	25.1	24.9	23.8	24.4	22.4	25.3	26.9	24.7
2	23.8	26.7	27.2	28.2	29.0	29.8	29.1	27.7
3	36.0	37.8	39.4	44.3	44.5	42.5	41.3	41.0
4	29.8	30.9	29.2	29.6	29.6	27.9	33.1	30.0
5	22.8	26.2	26.6	26.6	26.8	26.8	26.8	26.1
6	18.9	19.3	19.0	18.4	19.3	18.4	19.3	18.9
7	15.3	14.9	13.9	13.9	13.8	13.9	13.1	14.0
8	18.5	19.6	19.6	20.8	19.4	20.5	22.0	20.1
9	24.0	24.4	24.4	25.1	23.4	24.5	24.5	24.3
10	21.6	22.0	23.3	24.3	24.0	24.3	24.2	23.4
$\bar{X}$	23.6	24.7	24.6	25.6	25.2	25.4	26.0	25.0
SE	1.9	2.0	2.1	2.6	2.6	2.4	2.4	2.3

APPENDIX TABLE 22

RESPIRATORY TIDAL VOLUME (ML)

DURING 0.2% H_2S TREATMENT

WITH MEANS ($\bar{X}$), AND STANDARD ERROR (SE)

BIRD No.	TIME (MIN) 1	5	10	15	20	25	30
1	31.9	25.7	25.5	25.7	29.0	32.5	36.1
	7.2*	1.0	0.8	1.0	4.3	7.8	11.4
2	27.6	35.8	26.0	31.8	26.5	29.4	31.8
	-0.1	8.1	-1.7	4.1	-1.2	1.7	4.1
3	40.4	32.0	37.7	47.2	46.5	41.8	43.1
	-0.6	-9.0	-3.3	6.2	5.5	0.8	2.1
4	26.6	41.4	21.5	19.5	46.5	42.5	31.7
	-3.4	11.4	-8.5	-10.5	16.5	12.5	1.7
5	19.6	27.6	19.1	28.7	25.0	19.8	21.4
	-6.5	1.5	-7.0	2.6	-1.1	-6.3	-4.7
6	25.5	21.5	17.1	23.0	19.7	18.3	17.6
	6.6	2.6	-1.8	4.1	0.8	-0.6	-1.3
7	9.9	12.0	12.2	12.7	13.9	21.6	27.2
	-4.1	-2.0	-1.8	-1.3	-0.1	7.6	13.2
8	36.0	24.2	25.0	29.2	46.2	18.1	25.4
	15.9	4.1	4.9	9.1	6.1	-2.0	5.3
9	38.3	25.5	24.4	26.8	26.8	27.9	29.4
	14.0	1.2	0.1	2.5	2.5	3.6	5.1
10	22.4	32.6	14.4	14.0	20.1	15.1	21.7
	-1.0	9.2	-9.0	-9.4	-3.3	-8.3	-1.7
$\bar{X}$	27.8	27.8	22.3	25.9	30.0	26.7	28.5
*	2.8	2.8	-2.7	0.8	3.0	1.7	3.5
SE	2.9	2.6	2.3	3.1	3.8	3.1	2.4
*	2.4	1.9	1.4	2.0	1.8	2.0	1.8

*Change in tidal volume obtained by subtracting individual bird mean tidal volume during H_2S treatment period from tidal volume at times 1,5,...30. Mean change and standard error of the mean change are shown with $\bar{X}$ and SE.

APPENDIX TABLE 23

RESPIRATORY TIDAL VOLUME (ML)

AFTER 0.2% H_2S TREATMENT

WITH MEANS ($\bar{X}$), AND STANDARD ERROR (SE)

BIRD No.	TIME (MIN) 1	5	10	15	20	25	30
1	27.8	11.1	17.1	18.9	20.2	22.2	25.1
	3.1*	-13.6	-7.6	-5.8	-4.5	-2.5	0.4
2	31.4	27.5	30.0	31.2	30.2	32.5	29.8
	3.7	-0.2	2.3	3.5	2.5	4.8	2.1
3	49.5	38.0	42.2	42.0	37.8	39.9	36.7
	8.5	-3.0	1.2	1.0	-3.2	-1.1	-4.3
4	25.7	20.3	23.3	23.4	23.4	26.7	27.0
	-4.3	-9.7	-6.7	-6.6	-6.6	-3.3	-3.0
5	35.0	37.1	23.4	20.4	23.6	22.8	22.4
	8.9	11.0	-2.7	-5.7	-2.5	-3.3	-3.7
6	31.2	16.4	18.6	20.3	20.2	21.2	21.4
	12.3	-2.5	-0.3	1.4	1.3	2.3	2.5
7	20.3	14.0	13.0	14.0	15.1	15.1	15.1
	6.3	0.0	-1.0	0.0	1.1	1.1	1.1
8	36.6	30.4	29.5	28.4	25.1	28.1	27.5
	16.5	10.3	9.4	8.3	5.0	8.0	7.4
9	30.9	32.2	31.4	32.4	32.0	30.1	31.0
	6.6	7.9	7.1	8.1	7.7	5.8	6.7
10	29.1	18.9	17.8	19.3	20.2	19.5	18.9
	5.8	-4.4	-5.5	-4.0	-3.1	-3.8	-4.4
$\bar{X}$	31.8	24.6	24.6	25.0	24.8	25.8	25.5
*	6.7	-0.4	-0.4	0.0	-0.2	0.8	0.5
SE	7.8	9.7	8.7	8.4	6.8	7.2	6.3
*	5.6	8.2	5.6	5.5	4.5	4.3	4.4

*Change in tidal volume obtained by subtracting individual bird mean tidal volume after H_2S treatment period from tidal volume at times 1,5,...30. Mean change and standard error of the mean change are shown with $\bar{X}$ and SE.

APPENDIX TABLE 24

RESPIRATORY TIDAL VOLUME (ML)

BEFORE 0.3% H_2S TREATMENT

WITH MEANS ($\bar{X}$), AND STANDARD ERROR (SE)

BIRD No.	TIME (MIN) 1	5	10	15	20	25	30	$\bar{X}$
1	18.5	23.2	24.5	29.3	28.1	27.1	28.1	25.5
2	15.4	14.3	14.6	15.7	16.6	16.0	16.3	15.6
3	29.3	27.3	23.1	25.3	27.3	27.3	29.8	27.1
4	14.5	13.4	13.2	13.4	13.4	15.5	14.7	14.0
5	10.4	8.5	9.6	9.4	10.4	10.2	10.4	9.8
$\bar{X}$	17.6	17.3	17.0	18.6	19.8	19.2	19.9	18.4
SE	3.2	3.4	2.9	3.7	3.6	3.4	3.8	3.4

APPENDIX TABLE 25

RESPIRATORY TIDAL VOLUME (ML)

DURING 0.3% H_2S TREATMENT

WITH MEANS ($\bar{X}$), AND STANDARD ERROR (SE)

BIRD No.	TIME (MIN) 1	5	10	15	20	25	30
1	31.0	27.8	22.5	22.5	12.8	25.0	24.5
	5.5*	2.3	-3.0	-3.0	-12.7	-0.5	-1.0
2	28.6	27.4	19.6	18.1	17.8	18.4	18.4
	13.0	11.8	4.0	2.5	2.2	2.8	2.8
3	25.0	41.2	2.5	3.0	28.2	22.8	22.8
	-2.1	14.1	-24.6	-24.1	1.1	-4.3	-4.3
4	28.7	16.2	19.6	16.2	15.1	13.0	12.3
	14.7	2.2	5.6	2.2	1.1	-1.0	-1.7
5	15.6	6.5	18.2	7.8	14.8	18.5	16.4
	5.8	-3.3	8.4	-2.0	5.0	8.7	6.6
$\bar{X}$	25.8	23.8	16.5	13.5	17.7	19.5	18.9
*	7.4	5.4	-1.9	-4.9	-0.7	1.1	0.5
SE	2.7	5.9	3.6	3.5	2.7	2.1	2.2
*	3.0	3.3	6.0	4.9	3.1	2.2	1.9

*Change in tidal volume obtained by subtracting individual bird mean tidal volume during H_2S treatment period from tidal volume at times 1,5,...30. Mean change and standard error of the mean change are shown with $\bar{X}$ and SE.

APPENDIX TABLE 26

RESPIRATORY TIDAL VOLUME (ML)

AFTER 0.3% H_2S TREATMENT

WITH MEANS ($\bar{X}$), AND STANDARD ERROR (SE)

BIRD No.	TIME (MIN) 1	5	10	15	20	25	30
1	31.7	27.1	23.7	25.4	26.8	29.0	31.2
	6.2*	1.6	-1.8	-0.1	1.3	3.5	5.7
2	17.2	16.0	14.4	14.7	13.5	14.4	12.0
	1.6	0.4	-1.2	-0.9	-2.1	-1.2	-3.6
3	29.8	37.4	37.4	34.7	33.5	32.2	31.5
	2.7	10.3	10.3	7.6	6.4	5.1	4.4
4	23.4	22.9	23.4	26.3	25.5	25.5	25.5
	9.4	8.9	9.4	12.3	11.5	11.5	11.5
5	10.8	23.1	16.6	12.7	12.7	12.9	12.5
	1.0	13.3	6.8	2.9	2.9	3.1	2.7
$\bar{X}$	22.6	25.3	23.1	22.8	22.4	22.8	22.5
*	4.2	6.9	4.7	4.4	4.0	4.4	4.1
SE	3.9	3.5	4.0	4.0	4.0	3.9	4.3
*	1.6	2.5	2.6	2.5	2.3	2.1	2.4

*Change in tidal volume obtained by subtracting individual bird mean tidal volume after H_2S treatment period from tidal volume at times 1,5,...30. Mean change and standard error of the mean change are shown with $\bar{X}$ and SE.

APPENDIX TABLE 27

RESPIRATORY TIDAL VOLUME (ML)

BEFORE 0.4% H_2S TREATMENT

WITH MEANS ($\bar{X}$), AND STANDARD ERROR (SE)

BIRD No.	TIME (MIN) 1	5	10	15	20	25	30	$\bar{X}$
1	20.6	21.3	23.7	23.2	23.0	23.5	24.2	22.8
2	10.4	9.2	11.6	10.2	10.9	9.9	11.6	10.5
3	23.2	25.4	29.5	27.1	24.4	23.7	23.7	25.3
4	14.8	14.0	14.3	14.3	14.3	14.5	16.0	14.6
5	17.4	21.0	21.3	19.8	19.8	20.1	19.1	19.8
$\bar{X}$	17.3	18.2	20.1	18.9	18.5	18.3	18.9	18.6
XE	2.2	2.8	3.2	3.0	2.6	2.7	2.4	2.7

APPENDIX TABLE 28

RESPIRATORY TIDAL VOLUME (ML)

DURING 0.4% H_2S TREATMENT

WITH MEANS ($\bar{X}$), AND STANDARD ERROR (SE)

BIRD No.	TIME (MIN) 1	5	10
1	30.9		
	8.1*		
2	14.8	40.5	
	4.3	30.0	
3	26.2	14.3	22.6
	0.9	-11.0	-2.7
4	19.0		
	4.4		
5	15.9	14.5	33.3
	-3.9	-5.3	13.5
$\bar{X}$	21.4	23.1	28.0
*	2.8	4.6	5.4
SE	3.1	6.7	3.4
*	2.0	12.8	8.1

*Change in tidal volume obtained by subtracting individual bird mean tidal volume after H_2S treatment period from tidal volume at times 1,5,...30. Mean change and standard error of the mean change are shown with $\bar{X}$ and SE. All birds died during H_2S exposure.

APPENDIX TABLE 29

RESPIRATORY MINUTE VOLUME ($ML \cdot MIN^{-1}$)

BEFORE 0.0% H_2S TREATMENT

WITH MEANS ($\bar{X}$), AND STANDARD ERROR (SE)

BIRD No.	TIME (MIN) 1	5	10	15	20	25	30	$\bar{X}$
1	730.1	761.6	793.3	704.1	706.2	710.4	738.7	734.9
2	602.6	655.4	699.2	712.5	677.6	741.8	737.5	689.5
3	537.3	525.6	526.7	580.1	549.0	562.9	572.5	550.6
4	570.4	525.6	526.7	580.1	549.0	562.9	572.5	550.6
5	610.3	616.6	637.8	682.4	655.8	682.7	644.6	648.6
6	476.8	523.0	465.6	549.5	568.8	515.5	510.8	517.7
7	507.8	545.6	564.5	555.0	587.2	561.8	529.2	550.2
8	424.2	455.8	438.2	403.8	466.5	405.5	404.2	428.3
9	301.7	488.7	459.3	476.9	484.5	485.7	476.8	447.5
10	375.2	351.0	404.0	419.8	409.5	436.2	443.5	421.0
$\bar{X}$	513.6	559.7	556.8	572.7	581.3	574.5	569.6	561.2
SE	39.7	35.2	38.1	34.4	32.1	38.2	38.7	35.4

APPENDIX TABLE 30

RESPIRATORY MINUTE VOLUME ($ML \cdot MIN^{-1}$)

DURING 0.0% H_2S TREATMENT

WITH MEANS ($\bar{X}$), AND STANDARD ERROR (SE)

BIRD No.	TIME (MIN) 1	5	10	15	20	25	30
1	757.2	782.4	777.6	721.6	704.1	676.0	669.5
	22.3*	47.5	42.7	-13.3	-30.8	-58.9	-65.4
2	771.2	724.5	672.7	776.8	729.3	715.9	712.8
	81.7	35.0	-16.8	87.3	39.8	26.4	23.3
3	586.5	562.8	567.8	530.9	584.5	607.2	605.2
	35.9	12.2	17.2	-19.7	33.9	56.6	54.6
4	602.6	681.4	575.0	631.6	620.2	623.2	665.8
	-26.6	52.2	-54.2	2.4	-9.0	-6.0	36.6
5	794.2	737.1	803.7	816.7	783.0	812.2	788.4
	145.6	88.5	155.1	168.1	134.4	163.6	138.8
6	489.6	528.8	524.4	501.6	491.8	496.8	480.0
	-26.1	13.1	8.7	-14.1	-23.9	-18.8	-35.7
7	575.4	601.3	556.9	547.2	522.0	558.8	542.1
	25.2	51.1	6.7	-3.0	1.8	8.6	-8.1
8	380.2	366.0	329.6	337.0	325.5	329.2	330.3
	-48.1	-62.3	-98.7	-91.3	-102.8	-99.1	-98.0
9	435.0	457.3	448.9	457.3	486.5	565.4	452.0
	-12.5	9.8	1.4	9.8	39.0	17.9	4.5
10	391.2	372.1	393.0	381.4	374.4	342.2	333.7
	-26.1	-45.2	-35.3	-35.9	-42.9	-75.1	-83.6
$\bar{X}$	578.3	581.4	564.4	570.2	566.9	562.7	558.0
*	17.3	20.2	3.7	9.0	4.0	1.5	-3.2
SE	49.4	47.7	48.8	51.6	48.1	49.6	49.8
*	18.8	14.5	21.0	22.5	20.1	23.7	22.8

*Change in minute ventilation obtained by subtracting individual bird mean minute ventilation during pretreatment period from minute volume at times 1,5,...30. Mean change and standard error of the mean change are shown with $\bar{X}$ and SE.

APPENDIX TABLE 31

RESPIRATORY MINUTE VOLUME ($ML \cdot MIN^{-1}$)

AFTER 0.0% H_2S TREATMENT

WITH MEANS ($\bar{X}$), AND STANDARD ERROR (SE)

BIRD No.	TIME (MIN) 1	5	10	15	20	25	30
1	602.7	639.2	682.1	679.4	703.0	737.0	718.2
	-132.2*	-95.7	-52.8	-55.5	-31.9	2.1	-16.7
2	612.8	634.9	686.8	651.4	672.6	686.4	709.7
	-76.7	-54.6	-2.7	-38.1	-16.9	-3.1	20.2
3	551.8	547.2	575.1	565.2	573.2	602.6	617.5
	1.2	-3.4	24.5	14.6	2.6	52.0	66.9
4	619.2	606.5	627.1	559.4	624.8	639.5	581.1
	-10.0	-22.7	-2.1	-69.8	-8.4	10.3	-48.1
5	720.0	758.9	728.8	745.9	769.6	747.0	768.0
	71.4	110.3	80.2	97.3	121.0	98.4	118.4
6	415.8	427.0	413.6	389.0	457.5	418.5	466.9
	-99.9	-88.7	-102.2	-117.7	-58.3	-97.2	-48.8
7	524.7	535.7	529.6	503.0	520.8	507.8	510.6
	-25.5	-14.5	-20.6	-47.2	-29.4	-42.4	-39.6
8	377.6	404.0	381.3	397.8	356.4	383.6	395.0
	-59.7	-24.3	-47.0	-30.5	-71.9	-44.7	-33.3
9	380.5	444.3	452.5	463.4	460.6	463.4	463.5
	-67.0	-3.2	4.9	15.9	13.1	15.9	16.0
10	398.6	424.2	393.1	453.6	391.0	390.9	421.2
	-18.7	6.9	-34.2	36.3	-26.3	-26.4	3.9
$\bar{X}$	520.4	542.2	546.0	541.7	553.0	557.7	571.2
*	-40.8	-19.0	-15.2	-19.5	-8.2	-3.5	4.0
SE	38.3	37.3	42.1	38.1	43.9	45.0	41.9
*	18.2	18.3	15.6	19.4	17.0	17.2	17.3

*Change in minute volume obtained by subtracting individual bird mean minute volume during pretreatment period from minute volume at times 1,5,...30. Mean change and standard error of the mean change are shown with $\bar{X}$ and SE.

APPENDIX TABLE 32

RESPIRATORY MINUTE VOLUME ($ML \cdot MIN^{-1}$)

BEFORE 0.05% H_2S TREATMENT

WITH MEANS ($\bar{X}$), AND STANDARD ERROR (SE)

BIRD No.	TIME (MIN) 1	5	10	15	20	25	30	$\bar{X}$
1	478.4	541.8	557.0	557.6	561.3	580.2	571.4	552.5
2	645.8	674.0	680.2	718.6	704.0	710.0	635.0	681.1
3	656.8	636.6	658.7	640.8	698.9	649.0	650.4	655.9
4	151.7	216.6	230.4	203.5	256.6	228.2	214.5	214.5
5	217.0	231.4	240.6	267.4	254.0	249.6	243.6	243.4
6	772.9	818.4	798.1	731.7	731.0	708.4	663.6	646.3
7	545.2	658.3	587.5	637.8	720.9	634.5	693.9	639.7
8	524.0	541.5	539.1	556.2	553.1	553.3	516.3	540.5
9	514.5	558.9	629.2	683.0	651.1	607.5	593.6	605.4
10	612.0	625.0	640.9	649.9	643.7	616.2	648.0	633.8
$\bar{X}$	511.8	550.3	556.2	564.6	577.5	552.3	544.4	541.3
SE	61.2	60.2	58.2	58.1	57.1	54.7	54.9	54.0

APPENDIX TABLE 33

RESPIRATORY MINUTE VOLUME ($ML \cdot MIN^{-1}$)

DURING 0.05% H_2S TREATMENT

WITH MEANS ($\bar{X}$), AND STANDARD ERROR (SE)

BIRD No.	TIME (MIN) 1	5	10	15	20	25	30
1	494.0	496.5	497.8	499.7	483.2	481.4	472.0
	-58.5*	-56.0	-54.7	-52.8	-69.3	-71.1	-80.5
2	642.6	672.3	659.6	641.9	612.4	645.8	633.6
	-38.5	-8.8	-23.5	-39.2	-68.7	-35.3	-47.5
3	532.5	599.6	542.0	535.8	530.9	486.0	450.1
	-123.4	-97.3	-113.9	-120.1	-125.0	-169.9	-205.8
4	289.8	262.4	267.3	274.2	270.3	250.2	292.6
	75.3	47.9	52.8	59.7	55.8	35.7	78.1
5	204.9	192.7	174.3	180.9	178.3	172.1	163.0
	-38.5	-50.7	-69.1	-62.5	-65.1	-71.3	-80.4
6	730.8	672.8	639.0	662.5	656.0	672.7	604.0
	84.5	26.6	-7.3	16.2	9.7	26.4	-42.3
7	633.6	657.0	653.6	661.0	665.3	626.0	609.3
	-6.1	17.3	13.9	21.3	25.6	-13.7	-30.4
8	511.3	574.4	589.3	603.5	626.6	619.4	609.0
	-29.2	33.9	48.8	63.0	86.1	78.9	68.5
9	620.9	627.2	615.6	597.8	554.1	555.5	586.9
	15.5	21.8	10.2	-7.6	-51.3	-49.9	-18.5
10	616.6	593.5	639.8	637.2	660.6	668.8	661.5
	-17.2	-40.3	6.0	3.4	26.8	35.0	27.7
$\bar{X}$	527.7	530.8	527.6	529.4	523.8	517.8	508.2
*	-13.6	-10.5	-13.7	-11.9	-7.5	-23.5	-33.1
SE	52.2	53.6	54.1	53.5	53.9	55.8	52.2
*	19.4	15.1	16.7	18.1	21.3	22.8	26.1

*Change in minute volume obtained by subtracting individual bird mean minute volume during pretreatment period from minute volume at times 1,5,...30. Mean change and standard error of the mean change are shown with $\bar{X}$ and SE.

APPENDIX TABLE 34

RESPIRATORY MINUTE VOLUME ($ML \cdot MIN^{-1}$)

AFTER 0.05% H_2S TREATMENT

WITH MEANS ($\bar{X}$), AND STANDARD ERROR (SE)

BIRD No.	TIME (MIN) 1	5	10	15	20	25	30
1	464.3	473.2	473.0	483.6	468.2	435.1	454.7
	-88.2*	-79.3	-79.5	-68.9	-85.3	-117.4	-97.8
2	567.6	612.1	645.0	579.6	620.4	626.2	636.3
	-113.5	-69.0	-36.1	-101.5	-60.7	-54.9	-44.8
3	420.2	423.7	447.2	425.7	454.5	412.3	449.0
	-235.7	-232.2	-208.7	-230.5	-201.4	-243.6	-206.9
4	170.0	183.2	162.2	173.4	171.8	169.2	178.4
	-44.5	-31.3	-52.3	-41.1	-42.7	-45.3	-36.1
5	156.1	147.2	158.4	151.7	144.0	167.3	155.6
	-87.3	-96.2	-85.0	-91.7	-99.4	-76.1	-87.8
6	583.8	558.0	582.1	632.0	572.6	591.7	586.8
	-62.5	-88.3	-64.2	-14.3	-73.7	-54.6	-59.5
7	680.4	674.8	681.6	677.0	691.7	665.6	693.4
	40.7	35.1	41.9	37.3	52.0	25.9	53.7
8	520.7	483.3	477.7	474.0	497.7	484.4	546.0
	-19.8	-57.2	-62.8	-66.5	-42.8	-56.1	5.5
9	517.3	529.6	509.3	534.7	514.8	522.0	510.7
	-88.1	-75.8	-96.1	-70.7	-90.6	-83.4	-94.7
10	614.6	604.2	629.2	612.7	626.0	624.4	615.9
	-19.2	-29.6	-4.6	-21.1	-7.8	-9.4	-17.9
$\bar{X}$	469.5	468.9	576.6	474.4	476.2	469.8	482.7
*	-71.8	-72.4	-64.7	-66.9	-65.1	-71.5	-58.6
SE	56.2	55.8	58.4	57.5	58.2	56.9	58.0
*	23.2	21.6	20.6	22.4	20.8	22.8	22.3

*Change in minute volume obtained by subtracting individual bird mean minute volume during pretreatment period from minute volume at times 1,5,...30. Mean change and standard error of the mean change are shown with $\bar{X}$ and SE.

APPENDIX TABLE 35

RESPIRATORY MINUTE VOLUME ($ML \cdot MIN^{-1}$)

BEFORE 0.2% H_2S TREATMENT

WITH MEANS ($\bar{X}$), AND STANDARD ERROR (SE)

BIRD No.	TIME (MIN) 1	5	10	15	20	25	30	$\bar{X}$
1	336.2	348.1	356.3	381.0	383.4	404.9	432.5	377.6
2	423.6	387.2	410.7	425.8	455.3	435.1	427.8	423.6
3	1123.2	1096.2	1138.7	1120.8	1045.8	998.8	999.5	1074.7
4	435.7	370.8	379.6	414.4	432.2	418.5	496.5	408.2
5	469.7	482.1	470.8	430.9	452.9	452.9	415.4	453.5
6	446.0	416.9	410.4	393.8	409.2	393.8	389.9	408.6
7	688.5	636.2	660.2	629.7	629.3	601.9	614.4	637.2
8	440.3	464.5	499.8	551.2	544.5	545.3	534.6	509.9
9	535.2	492.9	488.0	522.1	514.8	521.8	507.2	511.7
10	397.4	376.2	391.4	422.8	405.6	391.2	392.0	396.7
$\bar{X}$	520.6	507.1	520.6	529.3	526.2	516.4	521.0	516.2
SE	74.2	70.8	74.1	70.4	62.3	58.2	57.8	67.4

APPENDIX TABLE 36

RESPIRATORY MINUTE VOLUME ($ML \cdot MIN^{-1}$)

DURING 0.2% H_2S TREATMENT

WITH MEANS ($\bar{X}$), AND STANDARD ERROR (SE)

BIRD No.	TIME (MIN) 1	5	10	15	20	25	30
1	580.4	547.9	403.1	385.9	406.3	419.6	563.9
	202.9*	80.4	25.6	8.4	28.8	42.1	186.4
2	452.6	508.4	345.8	543.8	413.4	479.2	581.9
	29.0	84.8	-77.8	120.2	-10.2	55.6	158.3
3	860.5	1139.2	1188.8	892.1	697.5	652.1	387.9
	-214.2	64.5	190.1	-182.6	-377.2	-422.6	-686.8
4	372.4	679.0	258.0	191.1	897.4	688.5	580.1
	-35.8	270.8	-150.2	-217.1	489.2	280.3	171.9
5	294.0	472.0	233.0	407.9	405.0	304.9	376.6
	-159.5	18.5	-220.5	34.4	-48.5	-148.6	-76.9
6	614.6	447.2	314.6	437.0	394.0	444.7	510.4
	206.0	38.6	-94.0	28.4	-14.6	36.1	101.8
7	500.9	728.4	790.6	800.1	868.8	1945.4	1055.4
	-136.3	91.2	153.4	162.9	231.6	408.2	418.2
8	925.2	866.4	937.5	768.0	859.3	383.7	424.2
	415.3	356.5	427.6	258.1	349.4	-126.2	-85.7
9	812.0	479.4	444.1	474.4	466.3	499.4	535.1
	300.3	-32.3	-67.6	-37.3	-45.5	-12.3	23.4
10	499.5	635.7	792.0	558.8	526.6	279.4	329.8
	102.8	239.0	395.3	362.1	129.9	-117.3	-66.9
$\bar{X}$	591.2	641.4	570.2	574.9	593.5	519.7	534.5
*	71.0	121.2	50.1	53.8	73.3	-0.5	14.4
SE	67.2	70.9	104.4	70.2	67.8	71.7	64.8
*	66.6	39.4	70.0	57.2	76.5	73.2	92.1

*Change in minute volume obtained by subtracting individual bird mean minute volume during pretreatment period from minute volume at times 1,5,...30. Mean change and standard error of the mean change are shown with $\bar{X}$ and SE.

APPENDIX TABLE 37

RESPIRATORY MINUTE VOLUME ($ML \cdot MIN^{-1}$)

AFTER 0.2% H_2S TREATMENT

WITH MEANS ($\bar{X}$), AND STANDARD ERROR (SE)

BIRD No.	TIME (MIN) 1	5	10	15	20	25	30
1	518.9	677.1	569.2	577.4	533.3	235.0	511.8
	141.4*	299.6	191.7	199.9	155.8	-142.5	134.3
2	420.8	440.0	456.0	458.6	428.8	591.5	506.6
	-2.8	16.4	32.4	35.0	5.2	167.9	83.0
3	1064.2	915.8	1135.2	1104.6	1024.4	981.5	844.1
	-10.5	-158.9	60.5	29.9	-50.3	-93.2	-230.6
4	364.9	426.3	507.9	468.0	416.5	453.9	429.3
	-43.3	18.1	99.7	59.8	8.3	45.7	21.1
5	598.5	667.8	379.1	328.4	354.0	377.4	315.8
	145.0	214.3	-74.4	-125.1	-99.5	-116.1	-137.7
6	883.0	442.8	478.0	452.7	442.4	432.5	432.3
	474.4	34.2	69.4	44.1	38.8	23.9	23.7
7	1238.3	1001.0	984.1	960.4	887.9	857.7	770.1
	601.1	363.8	346.9	323.2	250.7	220.5	132.9
8	944.3	1124.8	1091.5	1016.7	833.3	913.2	860.8
	434.4	614.9	581.6	506.8	323.4	403.3	350.9
9	618.0	660.1	665.7	683.6	643.2	532.8	527.0
	106.3	148.4	154.0	171.9	131.5	21.1	15.3
10	712.5	679.7	692.6	695.3	695.0	709.2	637.8
	315.8	283.0	295.9	298.6	298.3	312.5	241.1
$\bar{X}$	736.3	703.5	695.9	674.5	625.9	604.5	541.0
*	216.2	183.4	175.8	154.4	105.7	84.3	63.4
SE	90.9	76.8	87.6	85.2	72.7	80.2	51.9
*	71.7	69.9	59.9	58.2	47.2	58.9	53.5

*Change in minute volume obtained by subtracting individual bird mean minute volume during pretreatment period from minute volume at times 1,5,...30. Mean change and standard error of the mean change are shown with $\bar{X}$ and SE.

APPENDIX TABLE 38

RESPIRATORY MINUTE VOLUME ($ML \cdot MIN^{-1}$)

BEFORE 0.3% H_2S TREATMENT

WITH MEANS ($\overline{X}$), AND STANDARD ERROR (SE)

BIRD No.	TIME (MIN) 1	5	10	15	20	25	30	$\overline{X}$
1	357.0	433.8	441.0	518.6	449.6	409.2	446.8	436.6
2	539.0	486.2	386.9	480.4	520.8	403.2	492.3	472.7
3	504.0	371.3	335.0	382.0	420.4	425.9	300.6	419.9
4	406.0	388.6	396.0	391.3	394.0	437.1	399.8	401.8
5	405.6	300.0	319.7	310.2	331.7	245.8	301.6	323.5
$\overline{X}$	442.3	396.0	375.7	416.5	423.3	394.2	428.2	410.9
SE	34.0	31.2	21.9	37.2	31.2	25.3	36.4	24.8

APPENDIX TABLE 39

RESPIRATORY MINUTE VOLUME ($ML \cdot MIN^{-1}$)

DURING 0.3% H_2S TREATMENT

WITH MEANS ($\bar{X}$), AND STANDARD ERROR (SE)

BIRD No.	TIME (MIN) 1	5	10	15	20	25	30
1	527.0	430.9	414.0	387.0	619.5	327.5	276.8
	90.4*	-5.7	-22.6	-49.6	182.9	-109.1	-159.8
2	966.7	1040.2	664.4	564.7	494.8	463.7	399.3
	494.0	568.5	191.7	92.0	22.1	-9.0	-73.5
3	550.0	548.0	33.5	30.0	530.2	430.9	342.0
	130.1	128.1	-397.4	-389.9	110.3	11.0	-77.9
4	932.8	583.2	484.1	346.4	403.2	341.9	319.8
	531.0	181.4	82.3	-45.4	1.4	-59.9	-82.0
5	499.2	162.5	100.1	70.2	162.8	314.5	328.0
	175.7	-161.0	-223.4	-253.3	-160.7	-9.0	4.5
$\bar{X}$	695.1	553.2	337.0	281.7	442.1	375.7	333.2
*	294.2	142.3	-73.9	-129.2	31.2	-35.2	-77.7
SE	104.4	142.6	120.2	101.2	78.0	30.0	19.8
*	94.2	121.7	105.8	85.2	57.8	21.8	25.9

*Change in minute volume obtained by subtracting individual bird mean minute volume during pretreatment period from minute volume at times 1,5,...30. Mean change and standard error of the mean change are shown with $\bar{X}$ and SE.

APPENDIX TABLE 40

RESPIRATORY MINUTE VOLUME ($ML \cdot MIN^{-1}$)

AFTER 0.3% H_2S TREATMENT

WITH MEANS ($\bar{X}$), AND STANDARD ERROR (SE)

BIRD No.	TIME (MIN)						
	1	5	10	15	20	25	30
1	513.5	669.4	613.8	596.9	554.8	609.0	574.1
	76.9	232.8	177.2	160.3	118.2	172.4	137.5
2	583.1	544.0	457.9	411.6	388.8	385.9	306.6
	110.4	71.3	-14.8	-61.1	-83.9	-86.8	-166.7
3	539.4	766.7	856.4	742.6	713.6	685.9	683.6
	119.5	346.8	436.6	322.6	293.7	266.0	263.7
4	631.8	822.1	795.6	802.2	759.9	810.9	739.5
	230.0	420.3	393.8	400.4	358.1	409.1	337.7
5	195.5	616.8	498.0	383.5	474.6	374.7	343.8
	-128.0	293.3	174.5	60.0	51.5	51.9	20.3
$\bar{X}$	492.7	683.8	644.4	587.4	558.3	567.6	529.4
*	81.8	272.9	233.5	176.5	147.4	162.5	118.5
SE	77.0	50.1	79.1	84.5	79.8	84.7	87.8
*	58.3	59.0	82.1	84.0	80.3	85.3	89.4

*Change in minute volume obtained by subtracting individual bird mean minute volume during pretreatment period from minute volume at times 1,5,...30. Mean change and standard error of the mean change are shown with $\bar{X}$ and SE.

APPENDIX TABLE 41

RESPIRATORY MINUTE VOLUME ($ML \cdot MIN^{-1}$)

BEFORE 0.4% H_2S TREATMENT

WITH MEANS ($\bar{X}$), AND STANDARD ERROR (SE)

BIRD No.	TIME (MIN) 1	5	10	15	20	25	30	$\bar{X}$
1	628.3	647.5	760.7	749.4	710.7	695.6	750.2	706.1
2	458.6	400.2	502.3	430.4	446.9	414.8	484.9	448.3
3	468.6	398.8	422.2	379.4	376.4	417.4	391.0	407.7
4	506.3	499.3	468.3	471.9	411.2	381.9	431.2	445.7
5	395.5	421.1	453.6	458.4	456.4	468.0	453.1	443.7
$\bar{X}$	491.5	463.4	521.4	497.9	480.3	475.5	502.1	490.3
SE	38.6	46.9	61.2	64.8	59.3	56.7	63.9	59.5

APPENDIX TABLE 42

RESPIRATORY MINUTE VOLUME ($ML \cdot MIN^{-1}$)

DURING 0.4% H_2S TREATMENT

WITH MEANS ($\bar{X}$), AND STANDARD ERROR (SE)

BIRD No.	TIME (MIN) 1	5	10
1	988.8		
	282.7*		
2	695.6	121.5	
	247.3	-326.8	
3	552.4	164.2	67.8
	144.7	-243.5	-339.9
4	594.0		
	148.3		
5	494.3	551.7	366.5
	50.6	108.0	-77.2
$\bar{X}$	665.0	279.1	217.2
*	174.7	-154.1	-208.6
SE	87.4	136.8	149.4
*	41.1	133.2	131.4

*Change in minute volume obtained by subtracting individual bird mean minute volume during pretreatment period from minute volume at times 1,5,...30. Mean change and standard error of the mean change are shown with $\bar{X}$ and SE.

APPENDIX TABLE 43

DISCHARGE FREQUENCIES OF INTRAPULMONARY CO_2 RECEPTORS DURING STATIC CO_2 ADMINISTRATION

$F_{I_{CO_2}}$ %	DISCHARGE FREQUENCY (IMP·SEC^{-1})	$F_{I_{CO_2}}$ %	DISCHARGE FREQUENCY (IMP·SEC^{-1})	$F_{I_{CO_2}}$ %	DISCHARGE FREQUENCY (IMP·SEC^{-1})
UNIT 1:		UNIT 2:		UNIT 3:	
0.0	7.0	0.0	8.0	0.0	21.5
1.1	5.3	2.0	6.6	1.0	15.6
2.1	2.6	3.0	5.5	2.0	6.5
3.1	2.3	4.7	5.0	3.0	4.5
4.1	1.8	7.3	4.4	5.2	1.1
6.5	0.4	8.8	3.5	7.0	0.0
9.0	0.0				
UNIT 4:		UNIT 5:		UNIT 6:	
0.0	11.2	0.0	30.0	0.0	17.2
1.0	10.5	1.0	21.0	1.0	17.0
2.2	7.5	2.1	11.8	2.1	12.4
3.0	4.0	3.1	4.8	3.1	7.2
4.5	2.3	4.3	0.8	4.3	1.4
5.6	0.5	7.2	0.0	7.2	0.0
8.0	0.0				
UNIT 7:		UNIT 8:			
0.0	12.4	0.0	17.8		
1.0	15.0	1.9	14.3		
2.1	10.4	3.3	10.1		
3.1	7.0	4.2	7.7		
4.3	4.2	5.4	5.6		
7.2	1.2	9.2	1.0		
		10.0	0.0		

APPENDIX TABLE 44

CHANGE IN INTRAPULMONARY CO_2 RECEPTOR SENSITIVITY TO STATIC AIRWAY CO_2 DURING H_2S EXPOSURE

PRE H_2S EXPOSURE		DURING H_2S EXPOSURE	
$F_{I_{CO_2}}$ %	DISCHARGE FREQUENCY (IMP/SEC)	$F_{I_{CO_2}}$ %	DISCHARGE FREQUENCY (IMP/SEC)
UNIT 1: Data taken after 5 minutes of 0.035% H_2S exposure			
0.0	7.0	0.0	1.2
1.1	5.3	2.2	0.1
2.1	2.6	3.1	0.1
3.1	2.3	4.1	0.0
4.1	1.8	5.5	0.0
6.5	0.4	6.1	0.0
9.0	0.0		
UNIT 4: Data taken after 10 minutes of 0.050% H_2S exposure			
0.0	11.2	0.0	7.8
1.0	10.5	1.0	20.1
2.2	7.5	2.0	17.6
3.0	4.0	5.0	16.2
4.5	2.3		
5.6	0.5		
8.0	0.0		
UNIT 8: Data taken after 5 minutes of 0.045% H_2S exposure			
0.0	17.8	1.3	5.3
1.9	14.3	2.5	8.2
3.3	10.1	3.8	6.1
4.2	7.7	10.0	0.0
5.4	5.6		
9.2	1.0		
10.0	0.0		

HYDROGEN SULFIDE: EFFECTS ON AVIAN RESPIRATORY CONTROL AND INTRAPULMONARY CO_2 RECEPTORS

by

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AN ABSTRACT OF A MASTER'S THESIS

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ABSTRACT

The effect of hydrogen sulfide gas (H_2S) on spontaneous ventilation and intrapulmonary CO_2-sensitive receptors was studied in chickens. Two sets of experiments were conducted on White Leghorn type chickens (Babcock strain) anesthetized with phenobarbital sodium. In the first set of experiments, ten spontaneously breathing birds each were exposed to 0.0%, 0.05% or 0.2% H_2S; five each to 0.3% or 0.4% H_2S. Experiments consisted of three tandem 30 minute parts - pretreatment, treatment, post-treatment - during which tidal volume (V_T, ml per breath), frequency (f, breaths$\cdot$min^{-1}) and minute volume ($\dot{V}$, ml$\cdot$min^{-1}) were measured. Mean f, V_T and $\dot{V}$ for each bird during part 1 served as individual controls to evaluate the effect of H_2S on respiration. Birds receiving 0.0% and 0.05% H_2S displayed no significant alteration in respiration. At the higher concentrations, respiration increased within one minute and oscillated throughout the treatment period. During H_2S treatment and post-treatment V_T, f and $\dot{V}$ were mostly significantly different from values established during the pretreatment period. There was a concentration related, significant increase in variability within treatment groups while exposed to H_2S at the higher levels.

In the second set of experiments, birds were unidirectionally, artificially ventilated with warmed, humidified gas at a flow of 4 l/min into the trachea through the lungs and out incised thoracic and abdominal air sacs. Intrapulmonary CO_2 sensitive receptor afferents in the left vagus nerve were isolated at a midcervical location. Receptors were first identified and characterized as to their response to dynamic change in airway CO_2 concentration and to static airway CO_2 levels. Afferent receptor output along with vertical sternal movement were recorded. H_2S was delivered and effects

studied in six birds on eight receptors while a static airway CO_2 was maintained. Each of five birds received 0.035%, 0.045%, 0.050%, 0.052% or 0.055% H_2S. Two birds received 0.10% H_2S. Immediate pre-exposure data and acute exposure data were compared. In three cases, an effect on CO_2 sensitivity was demonstrated by comparing CO_2 sensitivity pre-exposure to sensitivity during H_2S exposure. The two birds receiving 0.1% H_2S died within five minutes of exposure while all others survived 30 minutes of exposure. All birds responded to H_2S with increased sternal movements after approximately 30 seconds of exposure. Sternal movements ceased within four minutes in all but one bird which continued to ten minutes. Receptor discharge increased in all cases within 30 seconds, peaked after approximately 40 seconds and continued at an elevated level for a variable length of time.

The paradoxical increase in respiratory vertical sternal movement and receptor discharge during H_2S treatment implied that some central action of H_2S is overriding the normally inhibitory influence of the intrapulmonary CO_2 receptors. The possibility that HS^- anion produced by the dissociation of H_2S at body pH may be inhibiting carbonic anhydrase within intrapulmonary CO_2 receptors to produce the increased firing is discussed.