

How Birds Breathe: Correlation of Radiographic with Anatomical and Pathological Studies

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INTRODUCTION

The avian respiratory system differs markedly in structure from that found in mammals (4, 6, 11). Rather than an expansile lung as an "end organ," semirigid lungs are placed dorsally in the nonmobile portion of the bony thorax interposed between two large air-sac systems (4, 11). This particular structural arrangement and the efficient gas exchange in birds has led to a number of theories regarding the relative movement of inspired gas blood circulation within the avian respiratory system (8, 9). Many invasive or semi-invasive studies have been obtained to assess the flow of air through this system and to establish the mechanism of gas exchange (1, 8, 9). A number of these experiments have been reconstruction of postmortem findings or have studied the bird under unphysiological circumstances. The present study utilized radiological imaging technics to document air pathways during quiet respiration and simulated flying. Anatomical and pathological reconstruction of these images in our postmortem specimens was employed to determine potential pathways and mechanisms by which birds breathe and for comparison with mammalian respiration. This study is presented to emphasize the facility of these radiological technics to examine basic physiological phenomena in a nontraumatic and nondestructive manner.

MATERIALS AND METHODS

Approximately 25 birds (flying, semiflying, and flightless) were used for this study including ducks

(*Anas platyrhynchos*), the homing pigeon (*Columba livia*), the domestic chicken (*Gallus domesticus*), and the common rhea (*Rhea americana*). Before any studies were undertaken the birds were given a dissociative anesthetic agent, *i.e.*, ketamine hydrochloride⁶ or a combination of tiletamine HCL and zolazepam.⁷ Care was taken to prevent any pain or trauma to the bird.

Survey radiographs were obtained by pulsing the radiographic exposure to depict various phases of quiet respiration. The birds were then stimulated during fluoroscopic observation, and subsequent radiographs were obtained (Fig. 1 A, B). To achieve greater detail in certain anatomical areas, magnification radiographs were taken using a 0.3 mm focal spot x-ray tube.⁸ Air-gap radiographic magnification was employed to improve depiction of structural detail. Contrast medium studies of the respiratory system using 5 μ particles of powered tantalum⁹ as well as tracheograms and bronchograms in various projections outlined the pathways of air flow (Fig. 2A). Later liquid radiopaque material¹⁰ was used to fill the respiratory system and to delineate potential pathways of air movement between the bronchi and air sacs (Fig. 2B).

Pulmonary angiograms employing catheterization of the right heart and injection of 10–12 ml of a water soluble radiopaque contrast medium were obtained. The arterial, capillary, and venous phases of the pulmonary angiogram were correlated with histological studies and radiographic contrast injection of the respiratory tree. Perfusion lung scans with intravenous injection of technetium ^{99m}labeled albumin microspheres (1–2mc 15–30 μ in diameter)¹¹ were em-

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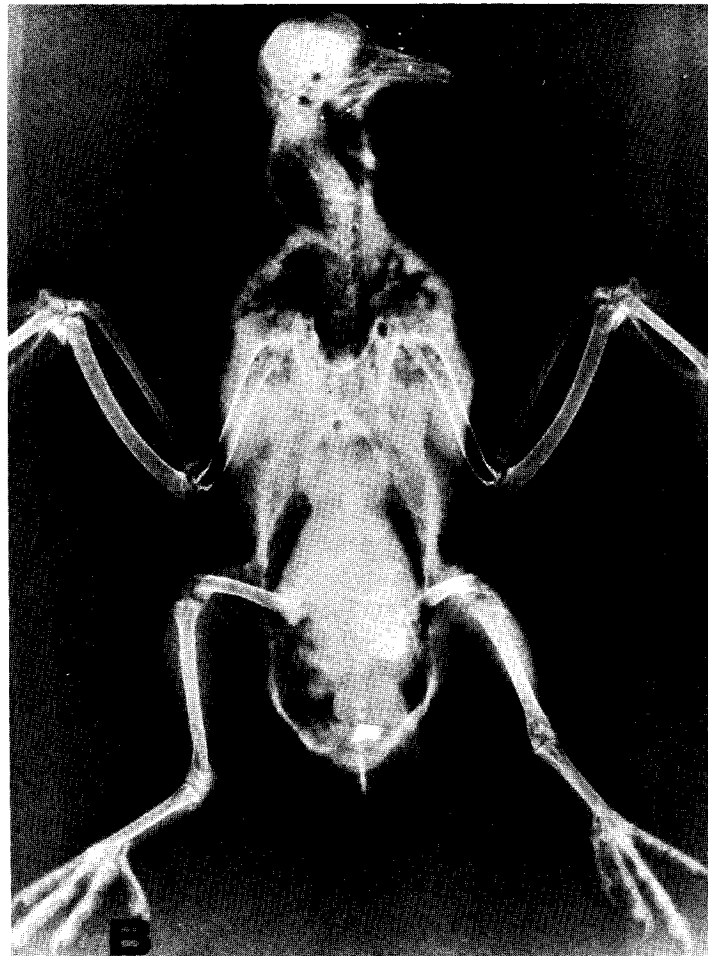


Fig. 1A. Radiograph of a bird lying supine during quiet respiration. This exposure is made with the radiographic tube employing the 1.0 mm focal spot oriented anteriorly or ventrally and the radiographic film-screen combination posteriorly. The lungs are seen as paired structures lateral to the centrally positioned heart. Anterior air sacs (broad arrows) which are mainly located ventrally in the upper thoracic and cervical region are only partially filled with air. The inferior (abdominal or caudal) air sacs (large thin arrows) are also filled with air rendering them radiolucent. B. Anteroposterior (ventrodorsal) radiograph in a bird following stimulation. The air sacs in the thoracic and cervical regions are expanded due to increased amounts of air and are more radiolucent than they appear at rest.

ployed. The distribution of the microspheres was imaged either on a rectilinear scanner¹² or a scintillation camera of the Anger type.¹³

To study the distribution of inspired air the birds were placed prone on a table under the scintillation camera with wing movement unrestricted. A collar at the neck base and surgical ties at the junction of legs and feet were employed as restraints. The bird was able to move its wings in such a manner as to simulate flying. They were able to raise themselves slightly above the soft polystyrene pad upon which they were placed.

Radioactive ¹³³Xe gas was delivered to the respiratory tree by both a single bolus injection or by continuous breathing from a bag. The birds were then allowed to breathe room air. The phases of the inhala-

tion study are referred to as "wash-in, equilibration, and "wash-out" images (5). The camera allowed simultaneous imaging and recording of the distribution or radioactivity. Images at 0.5 to 2.0 second intervals were obtained first while the bird was breathing room air (wash-out). If "equilibration" images (consisting of this equilibration image in multiple views) were obtained, correction could be made for volume differences of the various areas and anatomical overlap of air containing structures. Counts of radioactivity from the entire field of interest were placed on magnetic tape and stored in a computer memory for later retrieval and area analysis.

Single injection of a high specific activity xenon bolus was utilized to obtain statistically significant counts in the various regions of interest. This was also used to determine the initial distribution of air from an approximated single inspiration. To study position effect upon gas distribution, the radioxenon lung scans were also obtained with the bird lying su-

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¹³ Nuclear Chicago Corporation, 2000 Nuclear Drive, Des Plaines, IL 60018.

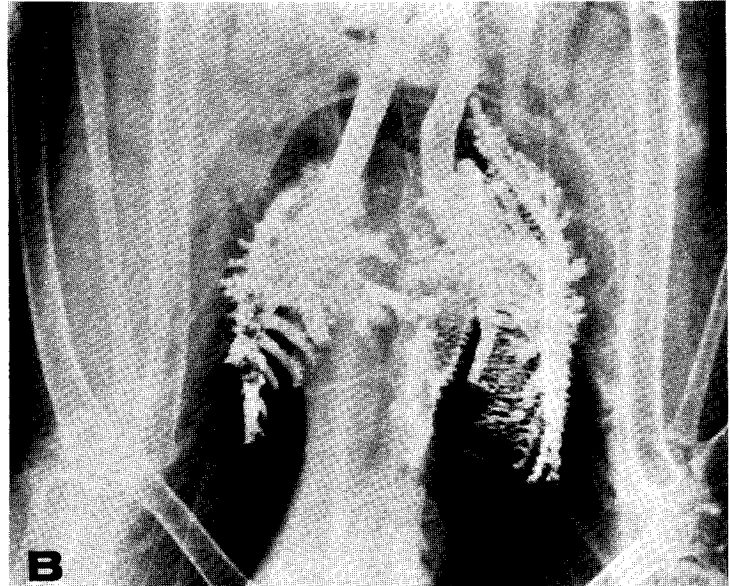


Fig. 2A. Tracheogram and bronchogram in a duck (*Anas platyrhynchos*) using powdered tantalum as the contrast medium and magnification radiography employing the 0.3 mm focal spot tube. Contrast medium delineates the trachea, syrinx, and primary bronchi. The secondary and parabronchi are not well visualized although they do contain a small amount of the tantalum. No contrast material has entered the air sacs. B. Tracheo-bronchogram employing oily Dionosil as the contrast medium. Filling of the secondary and tertiary bronchi (parabronchi) are seen. When oriented "end-on" the tertiary bronchi are imaged as rounded structures oriented in such a manner as to accept air flow from any direction in the secondary bronchi.

pine under anesthesia, resting prone directly on its thorax and abdomen, and in the lateral position.

RESULTS

Chest radiographs demonstrate the anatomical relations of the air sacs and lungs. Analysis of this data in the resting bird did not reveal any arrangement other than that usually described from anatomical studies (2, 3, 6). The lungs are seen as relatively radiodense structures lying between two air sac systems. The anterior air sac system consists of the cervical, intraclavicular, and anterior thoracic divisions. The posterior air sac system is formed by the posterior thoracic and abdominal divisions (Fig. 1A). The ventral and cephalic extension of the posterior air sacs appears slightly more prominent in some groups of birds than reconstruction from anatomical specimens would suggest. Following stimulation, the anterior sac was distended to a much greater extent than in the resting bird. Extensive filling of the cervical air sacs in the paraspinal region was noted with continuous stimulation (Fig. 1B).

In the tracheograms, tantalum dust impacted on the tracheal mucosa as well as the primary and secondary bronchi (Fig. 2A). Parabronchi were not well delineated, but the angle of the orifices of the parabronchi with the secondary bronchi suggest that flow from the larger bronchi to the parabronchi and not

the posterior air sacs would be favored. Filling of the primary and secondary bronchi with liquid contrast material from the trachea resulted in flow of the radiopaque material to the parabronchi prior to filling of any of the air sacs (Figure 2B). Recognizing that gas and fluid flow are not comparable, this observation only establishes the anatomical relationships.

The parabronchi were well delineated by liquid contrast material. They appear as bulbous terminal openings in some projections (Fig. 2B, 3A). These structures have an irregular outline suggesting that the ramifications that end in air capillaries are being filled with contrast medium. Even with radiographic magnification, these small structures were not seen well. We observed flow of the liquid contrast medium in the bird's lung during fluoroscopy. Primary and secondary bronchi filled first followed by the parabronchi. As the most distal parabronchi filled with contrast medium, entry into the posterior air sacs through a large communication with the primary bronchus on the inferior (caudal) aspect of the lung was seen. Continued infusion of the contrast medium resulted in almost total opacification of the lung area and greater filling of the air sacs (Fig. 3B). The air sac filling occurred from much smaller communications on the lung surface. The amount of contrast required to fill the air sacs (15–30 ml) was large. Even this resulted in only partial filling of proximal

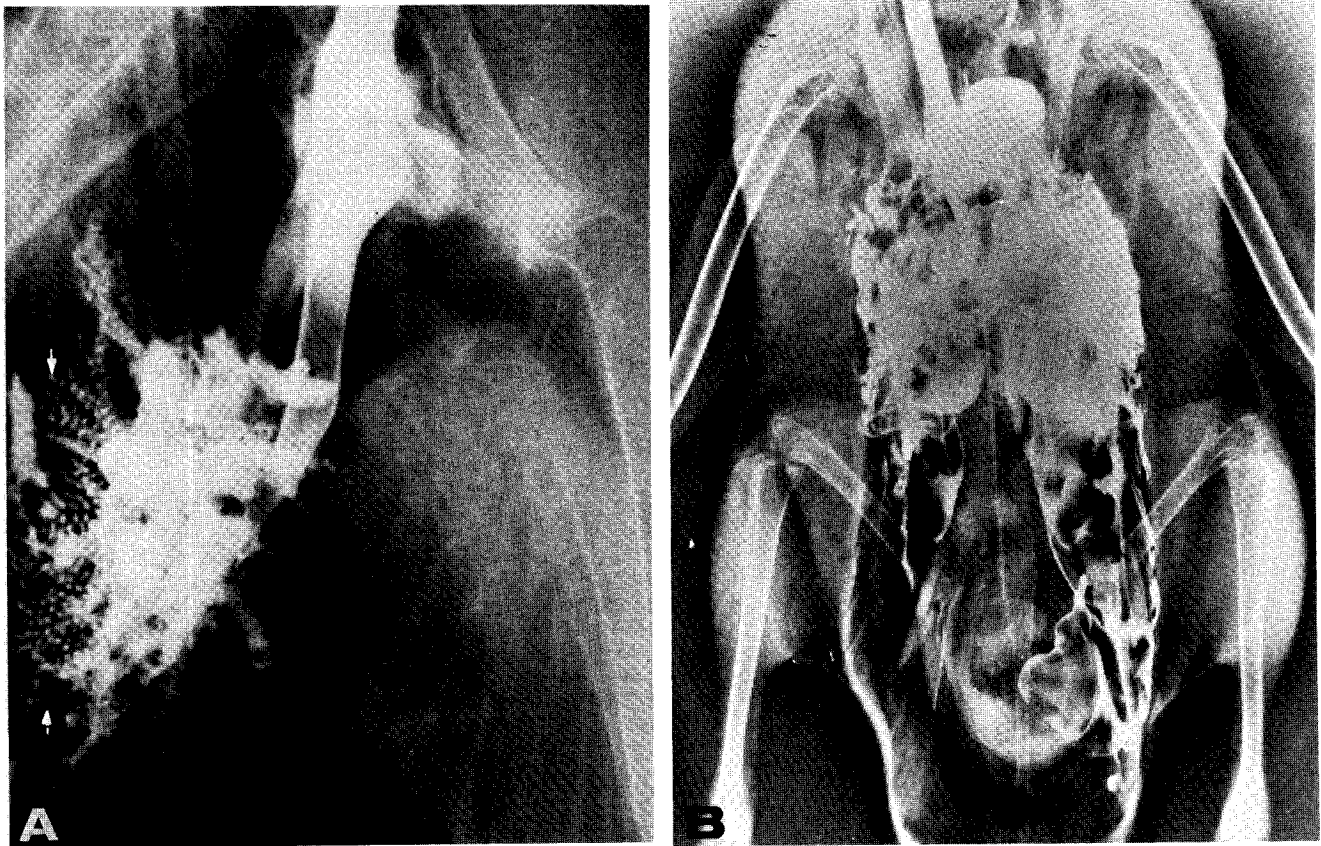


Fig. 3A. Lateral view of bronchogram. Oily Dionosil was used as contrast medium. The dorsal location of the lung structure is noted. The trachea, primary and secondary bronchi are well delineated with the contrast. The parabranchi appear as rounded structures arising from the secondary bronchi (arrows). B. Radiograph of continued infusion of oily contrast medium into the trachea of bird lying supine at rest. There has been almost complete filling of the bronchi with the Dionosil. In addition, the inferior (abdominal) air sacs contain contrast medium and some is identified in the superior (thoracic) air sac system. The contrast medium entered the air sacs only after filling of the bronchi was almost complete.

air sacs. If we wished to visualize the air sacs adequately, contrast had to be placed directly into them.

Pulmonary angiograms demonstrated the extensive vascular pattern of the birds' lungs. In the arterial phase (Fig. 4A), the central vessels tapered rapidly at the lung periphery. No extensive circumferential or surface network of vessels was visualized. In the capillary phases of the angiogram, the "pulmonary parenchymal" phase (Fig. 4B), contrast medium almost totally opacified the lung. Only small central circular relatively radiolucent areas were present when compared with the surrounding contrast medium. Contrast medium persisted in the precapillary arterioles, blood capillaries, and small draining venous structures (venules). Comparing the findings on the angiograms with those on the contrast-medium bronchograms, the radiolucent areas correspond in location and configuration to the parabranchi. The capillary blush surrounding these bronchi was more extensive than in angiograms of mammals. This demonstrates a much greater surface area of blood-air interface for gas exchange.

Perfusion lung scans reveal uniform distribution of pulmonary blood flow. The location of the radioac-

tive microspheres was entirely in the lung parenchyma. No bypass of the lungs or large arteriovenous communications were demonstrated, and microspheres were present in the lung area. The 15–30 μ particles were lodged in the short pulmonary arterioles or blood capillaries which surround the air capillaries.

Complete inhalation lung scans (Fig. 5 A, B, C) and single breath (bolus injection) lung scans were obtained to assess the initial distribution of inspired air and the filling of various portions of the respiratory system during the breathing cycle. The initial phase of respiration shows the greatest amount of radioactivity distributed to the lung area (Fig. 5A). By 6–9 seconds enough radioactivity was contained within the posterior (caudal) air sacs to create a recognizable image (Fig. 5B). Later during the washout phase (20–30 seconds) radioactivity within the air sacs and lungs approached uniformity (Fig. 5C).

Regional computation of radioactivity movement in each area by computer manipulation and analysis was used to evaluate the sequence of regional movement of the radioactive gas through the respiratory system. Comparing the distribution of radioxenon

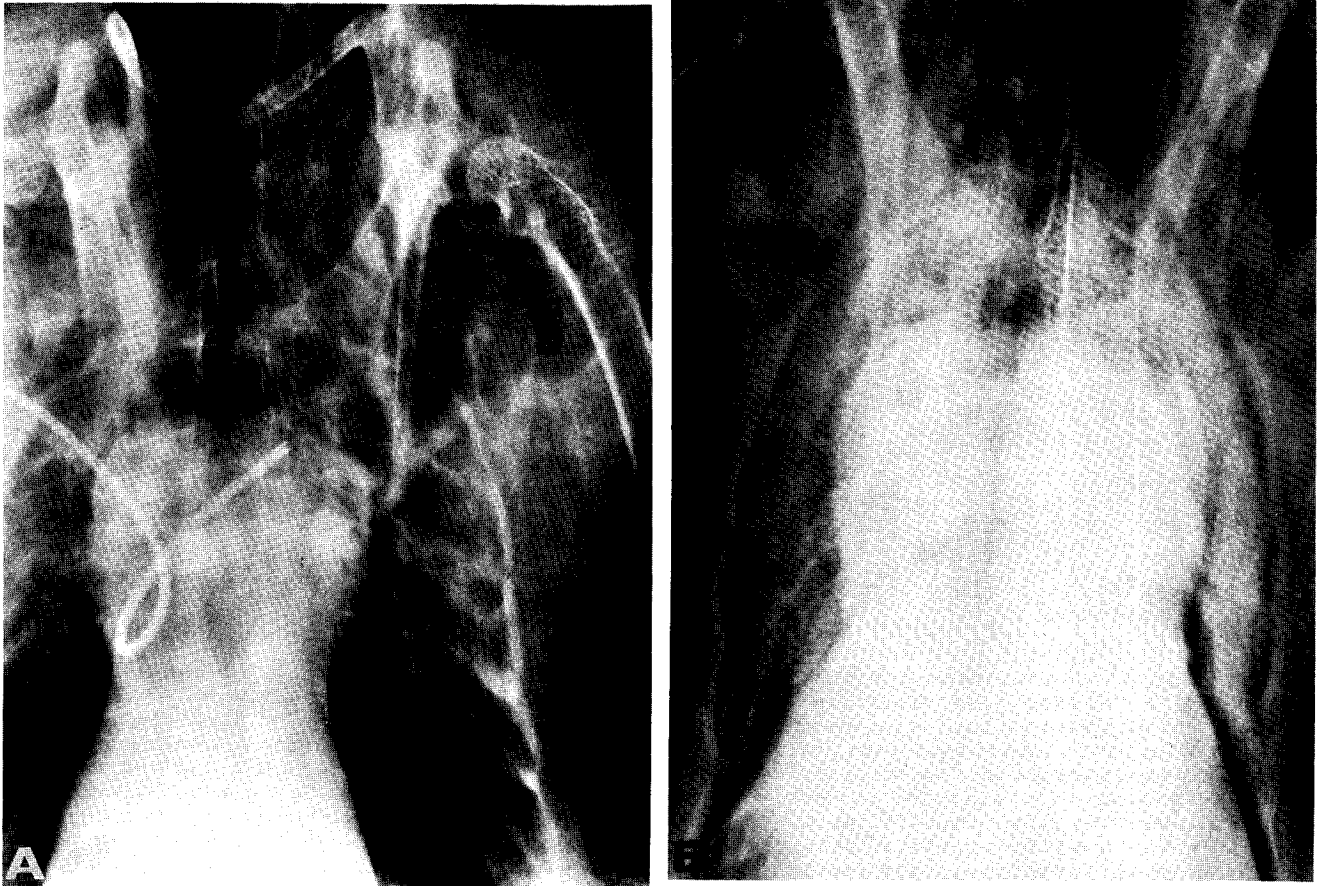


Fig. 4A. Pulmonary angiogram (late arterial phase). The catheter has been advanced from the right atrium into the pulmonary outflow tract and contrast medium (Renografin) injected during sequential radiographic exposures. Small pulmonary vessels are filled with contrast medium during this phase although both pulmonary arterial and venous structures are delineated. B. In the capillary (parenchymal phase) the catheter has been removed yet contrast medium persists in the small pulmonary vessels. The opacification of the lung with the contrast medium is dense and almost homogeneous. This appearance emphasizes the uniform vascularity of the avian lung. Comparing this image and the bronchogram, the small-rounded central areas of radiolucency on the angiogram correspond to the opacified parabronchi on the bronchogram.

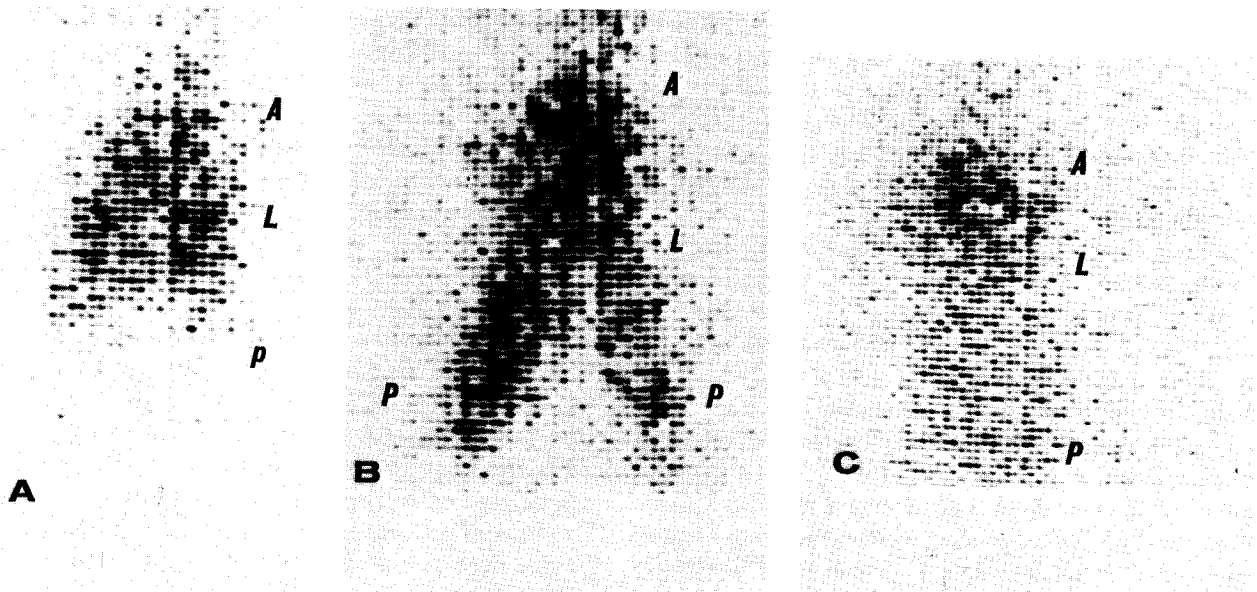


Fig. 5. Inhalation lung scan (posterior view, bird lying prone, ^{133}Xe as gas A = anterior sacs, L = lungs, P = posterior sacs). (5A) On the initial images after inhalation of 15 mCi ^{133}Xe the radioactive gas appears confined to the area of the lungs (L). (5B) Later, the posterior air sacs are filled as well (P). In the wash-out phase of the study, the anterior air sacs fill (A). Except in the late phase of the study (5C) the amount of radioactive gas in the lungs appear as great or greater than that contained in the air sacs. The radioactivity appears initially to be almost totally confined to the lungs (5A).

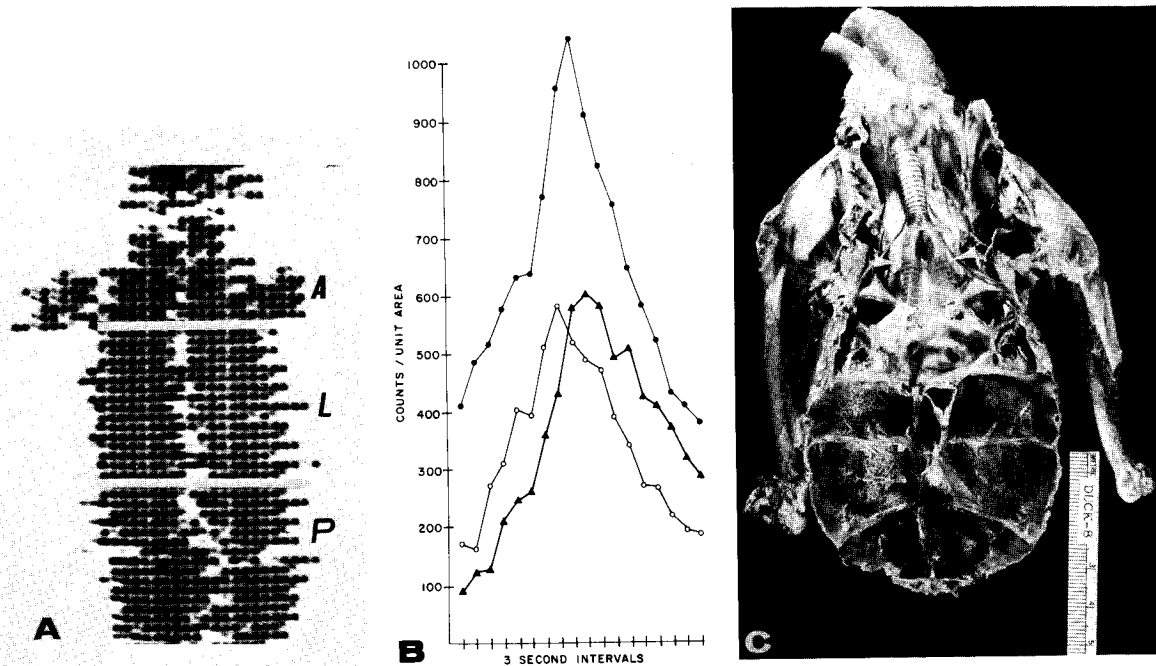


Fig. 6A. Photograph made from the video monitor of the image display and analysis system. On this reconstruction of the anatomical areas outlined with radioactivity on the equilibration image, specific locations can be selected by the electronic light pen and the amount of radio-activity per area computed for each time period. Thus, using this method various anatomical areas can be compared with regard to the time course and amount of radioactivity contained therein. The anterior air sacs (A) were arbitrarily selected as the most superior location of radioactivity. In the mid-zone, the lungs (L) were outlined to correspond to the general anatomical configuration as the (posterior) air sac system (P) was delineated. B. Graph of the radioactivity distribution (counts per unit area) versus time from the injection of single bolus of ^{133}Xe with the bird prone flapping its wings vigorously to simulate flying. The greatest amount of radioactivity is distributed to the lungs (closed circles). Entry of the radioactive gas into the posterior air sacs (open circles) is followed by movement into the anterior air sacs (triangles). This suggests that filling of the lungs only slightly precedes that of the air sacs and that they fill and empty at approximately the same rates. C. Coronal section through an anatomical specimen of a duck. The extensive air sac system in the anterior (thoracic and cervical) area is visualized as is the most (cranial) portion of the posterior air sac system. The lungs are seen through the thin (cranial) extension of the posterior thoracic air sacs. The most (caudal) portion of the abdominal air sacs is not seen in this anatomical specimen. The long primary bronchi (arrows) and trachea are surrounded by the multi-compartmental anterior air sac system.

gas at different time periods, the relative movement of air within the avian respiratory system could be depicted. The bolus injection (single breath) studies with an injection of 10–20 mCi xenon during inspiration showed that the bolus of radioactivity was initially distributed in greatest part to the area represented by the lungs (Fig. 6). Following this, radioactivity is present in the area of the posterior (caudal) air sacs and then in the anterior (cranial) air sac region (Fig. 6).

Data was accumulated in the computer on image frames at 0.5 second intervals. Even though a large bolus of radioactivity (10–20 mCi ^{133}Xe gas) was used, the frames were summed and analyzed at 3 second intervals. We recognized that the bird may have taken 2–4 breaths during this time period.

The relative distribution of the xenon gas changed with differences in the bird's activity. With stimulation of wing movement a greater relative distribution of inspired gas initially entered into the lungs than at quiet rest. Serial images and graphs of radioactivity distribution showed increased xenon gas in the lung area in the early phases with subsequent filling of the abdominal (caudal) and thoracic (cranial) air sacs (Figs. 5, 6). Radioactivity within the lung area re-

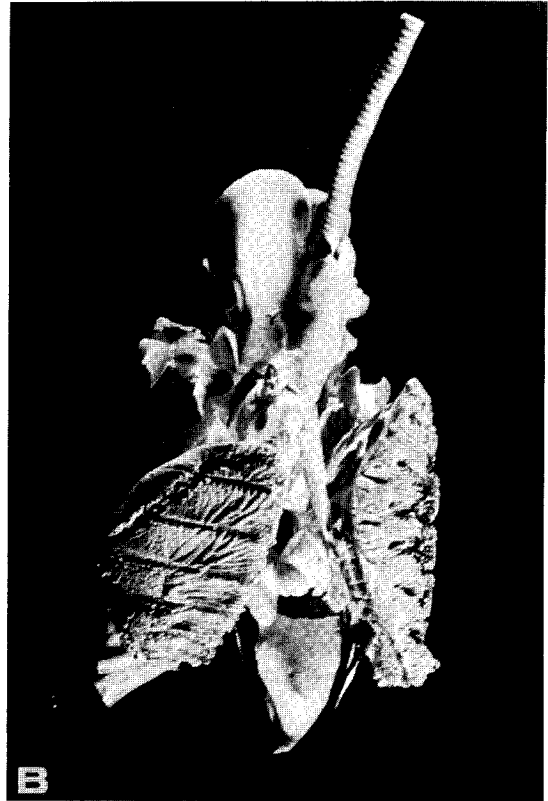
mained greater than that in the air sacs or other anatomical areas so long as radioactive gas was being inspired (Figs. 5 A, B, 6). In the later phases the bird breathed entirely room air and the lungs appeared to empty of radioactivity at approximately the same rate as the air sacs. Although a large bolus of concentrated radioactive gas was injected into the airway tube, entry into the respiratory system was most likely as a stream of radioactive gas entering over several respirations (or as many as 10–20). The prolonged recording time (3 seconds) may have contributed to obscuring the time relation of lung filling and air sac emptying (or the converse).

Coronal sections through the necropsy specimen confirm that the lungs were in the same location as outlined on the computer image (Figs. 5, 6C). They lie dorsally in the midportion of the body. In this area the bony thoracic cage has very little movement associated with wing flapping or flying. A portion of the posterior (caudal) air sacs is seen to extend ventrally over the surface of the lungs. Ventral-dorsal depth of this extension is small. Using lateral views on the dynamic images, correction in the quantitative data was initially made for this overlap. Further experience, however, showed that the amount of radio-



A

Fig. 7A. A single lung removed at necropsy from a duck. The large primary and secondary bronchi are seen with multiple numbers of parabronchi arising from the secondary bronchi. Following removal from the thoracic cage the avian lung had the consistency of a sponge and very little decrease in volume occurred. Parabronchi are seen as cylindrical structures when viewed in their long axis, but as rounded or hexagonal spaces when oriented so that they are observed "end-on." If one compares this appearance to that noted on the pulmonary angiogram, the very vascular nature of the lung parenchyma is again demonstrated. B. Injection of the entire respiratory tree of a duck with a silastic or silicone rubber preparation. The elongated trachea and primary bronchi are well visualized on the ventral aspect. Both the anterior and posterior air sac systems are partially filled. Filling of the parabronchi is noted as these appear as long, somewhat irregular cylindrical structures. The anatomical relationships and orientation of the lungs to the air sac system is clearly depicted by this method.



B

activity in this area was so small that it did not alter the counts significantly during any portion of the study. The lungs were inexpandible and did not collapse when removed from the thorax (Fig. 7A). They appeared as pyramidal shaped structures consisting of many irregular tubules of approximately equal length. The injection of the respiratory tree with a silastic mixture revealed the cylindrical parabronchi. There was some filling of the posterior (caudal) air sacs through the large orifice communicating with the primary bronchus (Fig. 7B).

From each lung there is a single large orifice leading from a primary bronchus into the abdominal air sac. Smaller orifices are also noted which predispose a directional gas and air flow from bronchus into air sac. Surrounding these large openings are smaller orifices whose angle of inclination favor air flow from the posterior air sacs into the lung. Pressure differences could cause the lining membrane of the air sac to rest directly against the lung to close the communications. In all species, the abdominal air sacs appeared to be largest, and the posterior air sacs were greater in volume than the lungs. The increased amount of radioactivity observed in the lungs was not due to a greater volume.

Histologically, a striking finding was marked large vascularity in the parabronchial area. Rather than a single vessel surrounded by a supporting structure

(as in the mammalian system) there was marked interlacing and interdigitation of vascular structures (Fig. 8A). Short arterioles have branches in all directions giving rise to blood capillaries. Parabronchi have communication with each other and multiple branches to form many air capillaries. These air and blood capillaries surround the parabronchi with an intricate network through which gas exchange is facilitated. Upon injection of the vascular portion of the lung with a modified injection medium, almost total opacification was seen (Fig. 8B, C).

In summary, these data accumulated in birds *in vivo* during active respiration and during simulated flying demonstrate that the lung has a large blood gas interface, is the area of greatest initial air distribution, and contains the greatest amount of inspired air during the entire respiratory cycle.

Discussion

Because of the increased facility for gas exchange and the unique anatomical arrangement, the avian respiratory system has proved a fascinating area for basic physiological research and anatomical-histological studies. Birds are able to oxygenate blood at altitudes and in states of physiological stress that would not be tolerated by mammals (8, 9). Some of

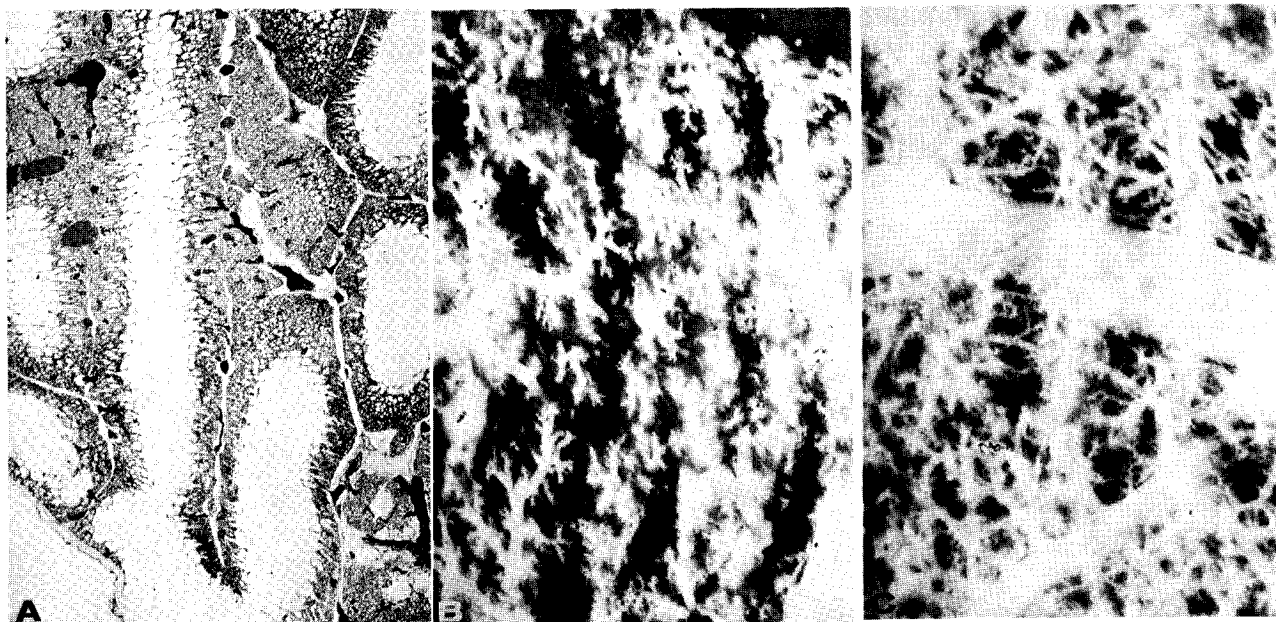


Fig. 8A. Histological section of the avian lung showing the long cylindrical parabronchi with the extensive vascular communications surrounding the air space. The multiple interdigitations of the blood and air capillaries are seen. In comparison to the circumstance in mammals, there is a markedly increased surface area for gas exchange. B. Injection of the venous portion of the avian pulmonary circulation again emphasizes and demonstrates the large vascular network as does the arterial injection C. Correlation of the histological appearance with that of the injection of both the arterial and venous supply as well as the airway graphically depicts the increased surface area to affect respiration.

the anatomical relationships have been documented for over 300 years, but there is no universal agreement as to the exact mechanism by which birds breathe (8, 9, 10).

Excellent descriptions of the anatomical relations are available and the characteristics of various exchange membranes have been documented by histological and ultrastructural analysis (3, 7). Semi-invasive and invasive physiological studies have determined the movement of air within the avian respiratory system (2, 8, 10). In general, these studies have been obtained on a bird that was either anesthetized or restrained in such a manner that it could not simulate normal flying motion. While these studies have provided significant basic data regarding the manner in which birds breathe, they must be subject to interpretation and qualification in that they produce anatomical and physiologic alterations themselves. We employed noninvasive and relatively noninvasive imaging technics which when subjected to quantification and subsequent anatomical and histological correlation could provide a more physiological and accurate method to study avian respiration.

There are two general theories of airway movement. The "cross current" model of avian respiration proposes a bellows mechanism by which nonexpansile lungs are interposed between the two air sac systems. Multidirectional air flow is possible depending upon the bird's activity. A number of pathways of movement of inspired gas in the parabronchial and air capillaries of the lung could be utilized

depending upon different physiological circumstances. This concept is the most widely held description of air movement in the avian respiratory tree (3, 7). In contrast there is a proposed "counter current" mechanism of avian respiration by which air flows in a single direction opposite to that of the blood in the pulmonary vascular tree (2, 9). The increased facility for gas exchange according to this theory is explained by the more efficient physical arrangement. The oxygen rich air lies adjacent to that portion of the blood with which it can more effectively exchange.

Survey radiographic studies demonstrated that the anterior air sacs were filled to a greater extent when the bird was stimulated. There was no definite relationship noted between the amount of filling of the posterior and anterior air sac regions. Since some investigators believe that the upper air sacs fill in response to the emptying first of the posterior air sacs and subsequently the lungs, we would have expected the volume of the two air sac systems to be inversely related. Fluoroscopic examination also failed to confirm this.

Tantalum particles impact upon the lining surface of the airways and give excellent "double contrast" images by which not only the size, but the internal characteristics of the pathways can be seen. We were able to achieve filling of the primary and secondary bronchi, but very little filling of the parabronchi was noted on even the large birds such as the rhea. This lack of filling probably represents a combina-

tion of the small diameter of the parabronchi and increased airway resistance in this area. The angle of origin of the parabronchi from the secondary bronchi would predispose air flow in the direction of the air sacs. Since there was lack of filling of the abdominal air sacs from the large orifices at the ends of the primary bronchi, this potential communication for air movement does not appear to be favored. When liquid contrast studies were obtained either in the recumbent or prone position, the parabronchi filled before there was any flow of the contrast medium into the air sacs. Only until we achieved almost complete filling of the pathways of air flow in the lung was there contrast medium movement into the air sacs.

Pulmonary angiograms showed uniform distribution of arterial blood flow to the lungs and no significant vascular communications between blood supply to the air sacs. In the capillary phase of the pulmonary angiogram, the entire lung appeared to be almost totally opacified with contrast medium. Correlation of these areas with those opacified on the conventional bronchogram showed that the space which was surrounded by the contrast on the angiogram was most probably occupied by the parabronchus. The serial radiographic exposures obtained on the angiogram demonstrate prolonged retention of the contrast material within this highly vascular network. The spherical radiolucencies appeared to become slightly smaller and the borders somewhat indistinct suggesting that there is even greater filling of the small vessels surrounding the parabronchi with the injected contrast medium. Histological studies show that these irregularities probably represent the indistinct delineation of the interdigitations of the air and blood capillaries surrounding the parabronchus. In comparing this with the type of configuration one notes in pulmonary angiography of mammals, there is an increase in vascular-respiratory interface for exchange in birds. Calculations from other studies estimate that on a unit volume basis the vascular-respiratory interface of birds is approximately ten times that of mammals. Perfusion lung scans in both the recumbent and prone positions demonstrated uniform distribution of pulmonary blood flow to the lungs (5). The horizontal orientation of the long axis of the lungs in birds would favor a more uniform distribution of normal pulmonary blood flow than in mammals that stand upright.

The major advantage of the methodology utilized to determine distribution of radioactive gases is that it is not invasive and allows study of the bird in normal physiological circumstances of rest and activity. These studies showed delivery of the greatest amount of radiopharmaceutical to the region of the lungs. The slope of the initial input function into the area of the lungs is greater than that for the abdominal

(caudal) or anterior air sac system. However, because of the bird's respiratory rate and the fact that we recorded at 0.5 second intervals, greater initial distribution of radioactivity could only be inferred by correlation with early images on the xenon scans. These data do correlate with the anatomy depicted by the radiographs and with movement of air-flow suggested by reconstruction of the three dimensional study *in vivo*. In the conventional inhalation lung scans, a greater concentration of radioactivity is seen initially over the lungs with more radioactivity present in the abdominal region (posterior or caudal sacs) than in the thoracic (anterior or cranial sacs). From the images displayed on a viewing monitor, electronic cursors were placed both over the entire anatomical regions (anterior or cranial air sacs, lungs, and posterior or caudal air sacs) and also selected areas of equal area within the fields of those regions.

The conventional xenon scan revealed there was movement of the ^{133}Xe gas into the area of the posterior air sacs after the lungs filled with radioactivity. Almost simultaneously the anterior (cranial) air sacs showed some radioactivity. On the later phases, the radioactivity of the abdominal air sacs approached that of the lungs and there was a rather homogeneous distribution of radioactivity in the entire respiratory system on the very late phases of the washout portion of the lung scan. We found that the distribution of radioactive gas was significantly affected by position, anesthesia, and level of physical activity. A greater amount of xenon gas was delivered initially and throughout the cycle to the lungs when the bird simulated flying than under any other condition. We believe that the wing movement causes volume changes in the upper portion (abdominal) of the posterior (caudal) air sac to cause greater air flow to the lung area. Analysis of the radioactivity curves with continuous recording and imaging suggests that the lungs are preferentially filled with air during periods of vigorous physical activity. The posterior air sacs appear to have a significant function in air movement. While the anterior (cranial) air sacs seem to have much more of a reservoir function and may serve only for heat and water dissipation. This also occurs to some extent in the posterior (caudal) air sacs and probably within the diverticula that are known to pass into the hollow bones. The movement of radioactive xenon gas in association with the anatomical findings would suggest that on inspiration the greatest amount of air enters the lungs directly, but some goes to the air sacs.

The histological study of the specimens reveal the marked increase in the surface area at the interface between the terminal respiratory unit (air capillary) and the blood (capillary). Although the surface area was not calculated, we believe that from the appear-

ance it would represent a multiple of that which exists in the mammalian system. It is probably this anatomical difference and not that of a countercurrent of air flow which mainly account for the increased facility for gas exchange in the avian respiratory system. We believe that the *in vivo* radiographic technic affords an excellent opportunity to study the fundamental mechanisms of avian respiration. When correlated with the data from previous studies and concurrent physiological and pathological analysis an accurate representation of how birds breathe can be obtained.

SUMMARY

The avian respiratory system was studied *in vivo* utilizing imaging technics. These data were correlated with anatomical and pathological specimens. Inspired air appeared initially to be distributed preferentially to the lungs and later to the posterior and finally the anterior air sacs. Pulmonary blood flow was uniform. Movement of radioactive gas suggested that the air sacs serve to move air into and out of the lungs. The increased facility for gas exchange when compared with mammals seems to be due to the increased surface area of the air-blood interface. The distribution of inspired gas changed depending upon the position and activity of the bird.

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REFERENCES

1. Biggs, P. M., and King, A. S.: A New Experimental Approach to the Problem of the Air Pathway within the Avian Lung. *J. Physiol.* 138:282, (1957).
2. Bretz, W. L., and Schmidt-Nielsen, K.: Bird Respiration: Flow Patterns in the Duck Lung. *J. Exp. Biol.* 54:103, (1971).
3. Duncker, H. R.: Structure of Avian Respiratory Tract. *Respir. Physiol.* 22:1, (1974).
4. Hazelhoff, E. H.: Structure and Function of the Lung of Birds. *Poult. Sci.* 30:3, (1951).
5. James, A. E., et al.: Lung Scan in Congestive Heart Failure. "Nuclear Cardiology," Strauss, H. W., Pitt, B., and James, A. E. (ed.). V. Mosby Co., St. Louis, M. (1974).
6. King, A. S.: Structural and Functional Aspects of the Avian Lungs and Air Sacs. *Int. Rev. of General and Exp. Zool.*, Vol. 2 Academic Press, New York, 1966.
7. Salt, G. W., and Zeuthen, E. The Respiratory System. "Biology and Comp. Phys. of Birds." A. J. Marshall, (ed.), pp. 363, (1960-61).
8. Scheid, P., and Piiper, J.: Avian Lungs: Effects of Reversal Parabronchial Air Flow in Ducks. *Respir. Physiol.* 16:304, (1972).
9. Schmidt-Nielsen, K.: How Birds Breathe. *Sci. Am.* 225:72, (1971).
10. Shepard, R. H.: Path Taken by Gases Through the Respiratory System of Chickens. *J. Appl. Physiol.* 14:733, (1959).
11. Zeuthen, E. The Ventilation of the Respiratory Tract in Birds. *K. danske Vidensk. Selsk. Biol. Medd.* 17:1, (1942).

ZUSAMMENFASSUNG

Das Atmungssystem in lebenden Voegeln wurde unter der Anwendung von Abbildungsmethoden untersucht. Diese Daten wurden dann mit anatomischen und pathologischen Proben verglichen. Eingeatmete Luft schien zuerst vorzugsweise in die Lungen zu fluessen und dann zu den auesseren und schliesslich zu den inneren Luftsaecken. Blutfluss in der Lunge war gleichmaessig. Die Bewegung von radioaktivem Gas zeigte an, dass die Luftsaecke wahrscheinlich dazu dienen, die Luft zu und von den Lungen zu bewegen. Der erhoehte Gasaustausch—im Vergleich zu Saeugetieren—beruht anscheinend auf der groesseren Flaechen der Luft-Blut-Grenze. Die Verteilung des eingeatmeten Gases wechselte je nach Lage und Taetigkeit des Vogels.

RÉSUMÉ

Le système respiratoire des oiseaux a été étudié *in vivo* par l'utilisation de techniques de projection. On a comparé les résultats de ces recherches avec des échantillons anatomiques et pathologiques. L'air aspiré a commencé par se montrer tout d'abord réparti de manière préférentielle dans les poumons et ensuite dans les sacs aériens postérieurs et finalement dans les sacs aériens antérieurs. L'écoulement sanguin pulmonaire était constant. L'observation de gaz à éléments radioactifs a indiqué que les sacs aériens servent à faire entrer l'air dans les poumons et à l'en chasser. En comparaison avec ce qui se passe chez les mammifères, la plus grande capacité de remplacement de gaz paraît due à la plus grande surface de contact air-sang. La répartition de l'air aspiré changeait selon les attitudes et les activités de l'oiseau.