FUNCTIONAL ASPECTS OF THE PNEUMATIC SYSTEM OF THE CALIFORNIA BROWN PELICAN

WITH THREE ILLUSTRATIONS

By FRANK RICHARDSON

This paper discusses the pneumatic system of the California Brown Pelican (*Pelecanus occidentalis californicus*). The system is of peculiar interest in the pelican because it is involved in this bird's striking adaptations for its special mode of feeding.

The term pneumatic system is used to include the air cavities in the bones and the complex series of small interconnected air cells between the skin and the muscular surface of the body. The internal air-sacs apparently have functions both in respiration and in a more purely pneumatic sense, although their functions may vary in different birds. Consequently, it is probably better to consider the internal air-sacs according to their function rather than to try to draw an arbitrary line between pneumatic and respiratory systems. Although I have here dealt primarily with the pneumatic system, the respiratory system is necessarily involved where the two systems have common

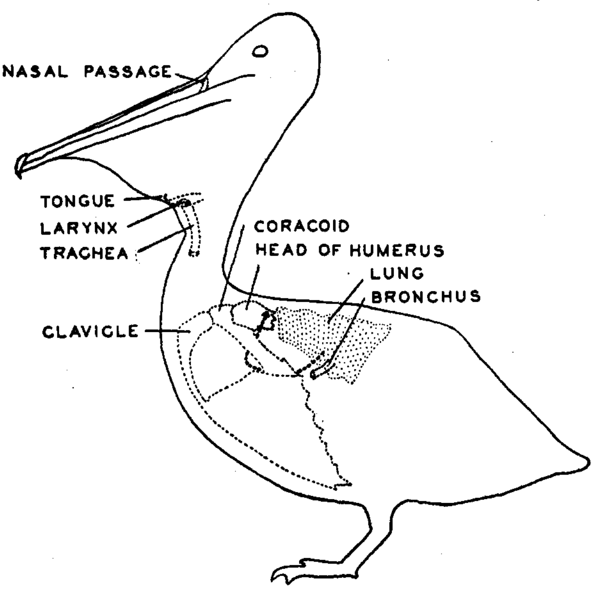

Fig 7. Outline of pelican showing location of certain parts of respiratory system. Heavy dotted line marks approximate course of air from lung to superficial air mattress.

passages, such as the nasal passages, trachea, and bronchi. The discussion in this paper traces the passage of air from its intake to its arrival in the superficial pneumatic system (see fig. 7), and concludes with a consideration of function.

The following account is based on dissection of two specimens only. With this limitation in mind, an attempt has been made to draw conclusions of a general nature not based on small and possibly variable anatomic details. The method of study has been the dissection of both freshly killed and preserved specimens, as well as observation of living birds. The most helpful adjunct to this method has been the blowing of air through the respiratory and pneumatic systems by means of a tube inserted into the trachea.

I gratefully acknowledge the stimulus of Dr. Loye H. Miller of the University of California at Los Angeles, under whom most of this work was done, and the advice of Dr. Alden H. Miller of the University of California at Berkeley in preparing this report.

External nares.—Macgillivray (A history of British birds, vol. 5, 1852, p. 378), Balthasar (Zeitschr. Anat. u. Entwickel., vol. 104, 1935, p. 614), and others have pointed out the usual complete closing of the external nares in cormorants. Owen (Proc. Zool. Soc. London, 1835, p. 9) mentioned this closure as being virtually complete in the pelican. Dissection disclosed the external bony opening to be effectively blocked by a flap of horny skin coming down from above. The close binding of this skin to the underlying bone and the lack of any skin muscles in this immediate region seem to preclude control of the opening of the external nares. It seems true, however, that though these horny flaps would effectively prevent appreciable ingress of water or air, their effect would be much less marked on the expulsion of air.

Internal nares.—The internal nares, though reduced to a slit approximately ten millimeters long, are not closed. Slight contraction of large muscles (M. pterygoideus internus) running along the sides of this slit probably could completely close it. However, a small amount of air under pressure could be blown into the internal nares and out the external, and it seems likely that though the nasal passage has lost its primary respiratory function, it can still be used to a very limited degree. Possible reasons for this loss of use are considered in an ensuing paragraph.

Larynx.—The extremely small size of the tongue and hyoid apparatus of the pelican has been mentioned or figured by various early anatomists, as for example Gadow and Selenka (Vögel, Anatomischer Theil, Bronn's Thier-reichs, vol. 6, 1891, p. 664 and fig. 41). The muscles causing contraction of the pouch, essential in straining water from the pouch when it contains fish, have been further studied by Kühnau (Anat. Anzeig., vol. 73, 1932, p. 322). The strong development of laryngeal muscles emphasizes the necessity of a strong and tight closure of the glottis to prevent the entrance of water which often fills the pouch and covers the larynx. Moreover, a pocket-like fold of skin, opening into the pouch, was found on both of the opposing edges of the glottis. These folds, because of their valve-like nature, insure a perfect exclusion of water from the trachea. Their pockets would catch any water entering the glottis, but allow passage of air leaving the glottis. Such valves were not found in the Brown Booby (*Sula leucogaster*), a pelicaniform bird with comparable diving habits but without a pouch.

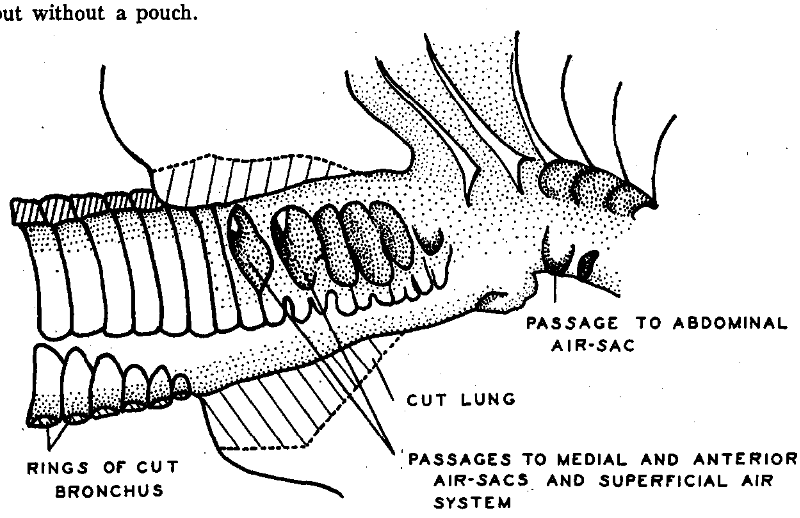

Fig 8. Left lung of pelican opened from lateral side to show entrance of bronchus into lung and passages to air-sacs.

Although the closing of the external nares is probably correlated with the pelican's surface plunging, the disuse of the nasal passage may be accounted for in part by other feeding adaptations, especially the great development of the pouch and the consequent wide separation of the larynx from the internal nares. Also, reduction of the internal nares may again be due to the need of excluding water from the nasal passage.

Bronchi and lungs.—The bronchi enter the ventromedial edges of the lungs. The semi-ring structure of each bronchus is continued, though becoming less and less complete, some two centimeters into the lung itself. Several large medial air passages are given off before the bronchus has penetrated even one centimeter (see fig. 8). These passages, the first to be given off, lead directly to air cavities chiefly anterior and medial to the lungs, which in turn lead to the superficial air system. The main air passage from each bronchus is through the lung to its outer surface and is there divided into superficial air passages covering over half of the outer surface of the lung but not leading to the ostia of the air-sacs. A direct but deeper passage (fig. 8) leads to the abdominal air-sacs.

Internal air-sacs.—The present study has made no direct contribution toward a more complete understanding of the rôle of air-sacs in respiration. However, dissections and artificial inflations have suggested another, though possibly incidental, function of the air-sacs of most birds, namely, the maintenance of body contours and the compensation for changes in size or position of the viscera. The maintenance of these contours is essential to most perfect flight. The feathers themselves are probably arranged and held most effectively in flight, and serve best as an insulating mat, when the skin beneath them is normally rounded out by underlying air cavities, as it may be especially in the abdominal region.

Superficial air cavities.—The superficial air mattress of the pelican is strikingly developed on all of the bird's ventral surface, including the neck and feathered parts of the head and extending out the wing even to the tip of the second digit. The only passage to this system of small interconnecting air cavities from an internal air-sac, and thus indirectly from the lungs, was found in the region just posterolateral to the head of the coracoid and below the head of the humerus (fig. 7). This passage is primarily between the M. coracobrachialis posterior and the M. subcoracoideus, following the nomenclature of Gadow (*op. cit.*, p. 211) and Howell (Auk, vol. 54, 1937, p. 374), and probably corresponds to the axillary diverticulum of an interclavicular air-sac figured by Müller (Smiths. Misc. Coll., vol. 50, 1908, fig. 11) in the pigeon. This sac is supplied with air fairly directly from the two medial ostia of the lung. These ostia receive air from the first two passages leaving the bronchus immediately after its penetration of the lung. After emerging between the above-mentioned muscles, the air passage continues over the ventral humeral head, past the pneumatic foramen and just medial to the insertion of the M. triceps, and then turns dorsally to pass under (medial to) the inserting tendon of the M. pectoralis before connecting with the superficial air cavities. These cavities thus receive air from the lungs rather directly, and probably by the above-mentioned passage only. This is also indicated by the frequently reported ability of a bird with a broken wing, especially if broken along the humerus, to continue breathing even though the trachea is closed. Breathing in this case may be primarily through the humerus itself, typically pneumatic in birds, especially since the primary pneumatic foramen of the humerus is located at a point along the passage to the superficial air system. Breathing could also be by way of superficial air cavities along the wing.

The above-mentioned passage for air from internal air-sacs to superficial ones has been found in just the same position in other birds. Gurney (The Gannet, 1913, p. 523) quoting C. B. Ticehurst on the gannet states: "'... Entrance (from within) to the large subcutaneous air-sacs is just outside the coracoid and close to the tendon of the pectoralis minor [M. coracobrachialis posterior], between that tendon and the nerves and vessels which supply the pectorals.'" Groebbels (Der Vogel, vol. 1, 1932, p. 58) implies that the presence of a Diverticulum humeri coming from the Diverticulum axillare of the interclavicular air-sacs is the usual condition in birds. The passage to the skin is apparently just a continuation of this route to the pneumatic foramen of the humerus.

Although there is just the one way for air to reach the superficial system from the lungs, there is sometimes a connection between the air cavities of the pharyngonasal system of the head region and the pulmonary cavities of the neck. Stresemann (Aves, *in* Kukenthal Handbuch der Zool., vol. 7, 1927-1934, p. 180) mentions that such a connection exists in only a few birds, including *Pelecanus* and *Sula*. In the present study only a very small amount of air could, by forceful lung pressure, be blown from the nasal passage of the pelican to the air mattress on the side of the neck just behind the head. This small amount of air does not seem significant, as the living bird would have no way, apparently, of forcing air in this way and could lose only very little through this channel.

Degree of inflation.—The term inflation is here used to denote the filling of the superficial air system. Actually the filling of internal air cavities, especially in the abdominal region, causes an initial but more limited visible inflation of the pelican. Figure 9 shows the degree of inflation possible under human lung pressure. Probably this inflation does not exceed that which may normally take place in the pelican, as inflation is limited to regions that for anatomical reasons permit it. This striking inflation was discovered by early workers. Milne-Edwards (Ann. Sci. Nat., Zool., ser. 5, vol.

3, 1865, p. 140) tells of an experiment to show the buoyancy of the inflated pelican in which a bird weighing 4.15 kg. was able to hold up 10.5 kg. without sinking. Assuming such an extensive inflation to be normal under certain conditions, we must, since air

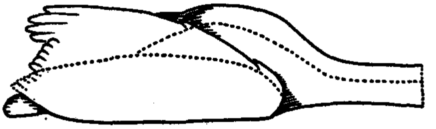

Fig. 9. Outlines of pelican showing degree of inflation. Dotted line, deflated bird; solid line, same bird inflated by human lung pressure. Outlines traced from photographs.

soon leaves the superficial air system when the pressure forcing it in is released, explain both the attainment and maintenance of such inflation.

Maintenance seems adequately explained by the tight and strong closure of the glottis. Attainment, that is, the problem of forcing air into the very large total space (considerably larger than the volume of the combined internal cavities alone) of the superficial air cavities, is not easily explained. Gurney (*op. cit.*, pp. 525–526) assumes that in the gannet the superficial air system can be filled by inhalation when flying (but not when standing), but offers no explanation. Though the present study cannot decide this question, a possible explanation is suggested, namely, that inflation is attained by a series of abdominal contractions which force air from the large abdominal air-sacs, each expulsion of air taking place while the glottis is closed. Thus air is forced to the superficial system since it is the only alternative space. Each expulsion would be followed by quick inhalation of air through the glottis. Such inhalation would be possible since air leaves the inflated superficial air cavities, after pressure is removed, much more slowly than air is inhaled through the glottis.

Observation of living pelicans has not proved just when inflation does occur, as differences in size cannot well be judged. However, plunging pelicans have never been seen to go more than partly below the surface. In fact they typically hit the water very heavily, only to float very high almost at once. This indicates inflation before the dive and suggests that inflation is a protection to the bird in striking the water. This correlation of a well developed superficial air mattress in pelecaniform birds with the habit of plunging for food has been mentioned by Stresemann (*op. cit.*, p. 801). He states that the booby and tropic-bird, which are plungers, are alike in the highly developed pneumaticity of the skin, and that this is an adaptation which lessens the force of the impact with the water. He further states that this adaptation is also found in the pelicans, though less marked, where plunging is again encountered, and that in contrast to this the pneumaticity of the true divers, *Phalacrocorax* and *Anhinga*, is greatly reduced. (See also Macgillivray, *op. cit.*, p. 419.) The validity of this correlation is borne out by a comparison of the California Brown Pelican and Brandt Cormorant. Superficial air cavities are little developed in this latter, deep-diving bird.

Other explanations have been offered for the pneumaticity of the pelican. It was once thought that the pelican is especially pneumatic to help it carry heavy loads in its pouch! The suggestion that such pneumaticity gives a desirable buoyancy in the water seems entirely possible, however, and need not negate the validity of the correlation of plunging with pneumaticity.

It should be emphasized that the above conclusions or inferences should be applied only with much caution to birds other than pelicans. The skin of the screamers

(Anhimidae), for instance, is highly pneumatic and although the reason for this is unknown, it certainly is not the one that holds for the pelican. In the light of this present study, then, the desirability of considering the parts of the respiratory and pneumatic systems in adaptation to different living habits becomes apparent.

Berkeley, California, November 24, 1938.

OBSERVATIONS ON THE NESTING OF THE ALLEN HUMMINGBIRD

WITH FOUR ILLUSTRATIONS

By ROBERT T. ORR

The Allen Hummingbird (*Selasphorus alleni*) is one of our common summer residents in the San Francisco Bay region, usually arriving before the middle of February and remaining in some numbers until the early part of September. From the first day of the arrival of the species to the end of the nesting season its presence is continually forced to human attention through the noise made in flight, by the shrill sound of the courtship dives, and by the constant noisy clashes of belligerent individuals objecting to intrusions upon one another's territories.

Strangely enough, despite the abundance of this diminutive avian representative, we know surprisingly little concerning its nesting activities and the behavior of the young. For this reason the writer kept rather careful notes on an Allen Hummingbird's nest that was situated within three feet of one of the windows of the California Academy of Sciences in Golden Gate Park, San Francisco, during the summer of 1938.

Allen Hummingbirds were first noted this year on February 15. On this day they were numerous in the vicinity of the Academy buildings and many males were seen and heard diving. By the first week in March at least three different females were seen to make regular trips to a box containing some old cotton placed on the roof of the North American Mammal Hall. Sometimes a skirmish would result when two birds arrived at the same time, but this did not often occur. It was not, however, until after the first broods had been raised that the writer's attention was called to a nest which was nearly completed. The structure was almost finished, with the exception of the inside lining, when first discovered on May 6. It was located on the northeast side of an exotic tree, *Eugenia paniculata*, at a height of 5 feet 3 inches above the ground. The nest was on a terminal twig that was drooping at an angle of approximately 45°. Two smaller twigs branched off above the base of the nest and penetrated the lower, central portion, giving it firm support. The outer part of the nest was formed of plant fiber covered largely with lichens and small strips of bark with moss adhering.

On May 6 the female was regularly seen carrying material to line the inside of the nest. This continued for the ensuing few days. On May 10 some cotton was placed on a window sill not far from the nest and this was also used as lining, in addition to plant down. The first egg was laid some time during the morning of May 11. The second egg was deposited the following morning and incubation began immediately. At 1:00 p.m. on May 12, the female was purposely frightened off the nest in order to photograph it. During the 20 minutes following, while preparations were being made to take the picture, she remained in the immediate vicinity, often within 3 or 4 feet of the writer. Three times during this period she was seen to chase away a male of this species. Within half a minute after the window from which the photographs were taken was closed she returned and settled on the nest.