



air sacs facilitate soaring

A recent study describes how an extension of the interclavicular air sac between the major flight muscles helps birds to soar.

PETER RYAN

Although flight is efficient in terms of the energetic cost per unit distance covered, powered flight is one of the most energetically expensive modes of locomotion per unit time. This means that birds require an effective respiratory system to deliver sufficient oxygen to power the flight muscles. Unlike mammals, where the lungs are blind structures and air flow in and out is tidal, birds have through-flow lungs connected to a series of air sacs.

The main role of the air sacs is to act as bellows, pushing air continuously through the lungs while the bird breathes in and out. Because air flow is unidirectional, a counter-current blood flow system ensures that as much oxygen as possible is harvested. As a result, gas exchange in birds is much more efficient than in mammals.

Interestingly, this adaptation is not confined to birds. Crocodiles and alligators have a similar system, although air flow is driven by a different mechanism. The avian air sac system probably evolved in theropod dinosaurs, the direct ancestors of modern birds. Various lines of evidence indicate that the

pterosaurs, the first flying vertebrates, also had a through-flow lung linked to a network of air sacs.

Birds typically have nine air sacs, many of which have non-ventilatory appendages termed diverticula that extend throughout much of a bird's body. In addition to facilitating gas exchange, air sacs influence heat exchange and moisture loss. They also play a role in vocalisations by regulating air flow across the syrinx and by creating resonance chambers. In some species, the air sacs and diverticula are used in displays. In the Marabou Stork, for instance, they inflate neck pouches that indicate social status. Subcutaneous air sacs also help to buffer the impact of plunge diving in gannets and some pelicans.

A recent paper by Emma Schachner and colleagues in *Nature* (doi: 10.1038/s41586-024-07485-y) describes a novel function for the subpectoral diverticulum, an extension of the interclavicular air sac that lies between the flight muscles in some birds. During flight, the wing's downstroke is powered by the pectoralis muscle, the larger of the two main flight muscles on the outside of a bird's breast. The supracoracoideus muscle, which lies along the breastbone under the pectoralis muscle, raises the wing during the recovery stroke.

When a bird is soaring or gliding, its wing muscles don't need to expand and contract, but the pectoralis muscle holds the wing at the correct angle to ensure effective flight. This requires an isometric contraction and incurs some energy expenditure. Soaring birds have slow muscle fibres deep in their pectoralis specifically for this role, and these use less energy than the fast muscle fibres used for powered flight.

The force exerted by the pectoralis muscle during soaring flight depends on the angle between the muscle and its insertion point on the humerus; the more vertical this angle, the less force required. Inflating the subpectoral diverticulum, which lies between the two flight muscles, increases the angle of attachment to the humerus, reducing the effort required by the pectoralis muscle while soaring.

As expected, a well-developed subpectoral diverticulum is only found in birds that regularly soar or glide, including eagles, hawks, vultures, storks, cranes, pelicans, gannets, frigatebirds, cormorants, albatrosses and petrels.

This is the first direct evidence that the air sac system can play a role in the mechanics of avian flight. It will be interesting to see whether it sparks further discoveries about this overlooked organ system.

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ABOVE Air sacs reduce the energy used to hold wings at the correct angle for soaring in birds like this Tristan Albatross.