Ancient *Argentavis* soars again

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Approximately 6 million years ago, in what is now Argentina, an enormous bird ranged across the region from the Andes Mountains to the pampas. Imagine a bird that has a condor-like body, weighs as much as a person, and has a wingspan nearly that of a small airplane. Imagine further that this bird has a 55-cm-long skull with a massive, eagle-like beak large enough to swallow a rabbit whole. *Argentavis magnificens*, the giant teratorn, fits this description. In addition to the general fascination stimulated by any huge (but safely extinct) carnivore, the fossils of this bird present paleontologists with a number of questions. Did it fly? If so, was it a flapper like a goose or a soarer like its relatives, the condors? Some of the questions about the flight in this huge bird have now been answered by computer models described in this issue of PNAS by Chatterjee *et al.* (1). Thanks to this work, we now have a clearer picture of the flight abilities of this extinct creature.

Argentavis is a member of Teratornithidae, a family of large, extinct birds. Although only partial skeletons of *Argentavis* have been found, they are very similar in general plan and proportion to *Teratornis merriami*, a smaller teratorn well known from >100 specimens collected at the Rancho La Brea tar pits in southern California (2). Earlier estimates put the mass of *Argentavis* at ≈80 kg (3), but Chatterjee *et al.* (1) used a more sophisticated multivariate analysis to arrive at an estimated body mass of 70 kg. A good estimate of mass is critical because overall weight has a crucial effect on flight characteristics like airspeed.

Too Big to Fly?

Argentavis was so large, researchers have long been intrigued about its flight capabilities. Large birds run up against a scaling problem because, as body size increases, weight increases faster than muscle power output, the former being a function of volume and the latter being related to cross-sectional area (4), so very large birds have proportionately less powerful flight muscles (5). Flight requires a lot of power, and *Argentavis* is so big that biologists have been puzzled about how it could have flown. The anatomical evidence that *Argentavis* flew is, however, quite powerful. It had air-filled bones, it had strong, appropriately spaced attachment points for secondary feathers in its wing bones, and its wing bones were long and robust, features not found in flightless birds (3).

Chatterjee *et al*. (1) developed a pair of computer models to analyze the flight of *Argentavis*. These models use a stream-tube method, an approach developed to simplify analyses of helicopter performance (6). Using a method developed for helicopters makes sense because, as various biomechanics researchers have pointed out, flying animals have more in common with helicopters than with fixed-wing airplanes (7, 8). Birds, in common with helicopters, use the same structures to produce both lift and thrust (wings for birds and rotors for helicopters), as opposed to separate wings (for lift) and engines (for thrust) in conventional airplanes. Chatterjee *et al.* developed two models, one to analyze the power requirements of continuous, level, flapping flight, and the other to simulate various flight maneuvers of *Argentavis*.

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To flesh out their model of flight power, Chatterjee *et al.* (1) first needed to estimate the power available from the flight muscles of *Argentavis*, which they based on the mass of the flight muscles. In living birds, the proportion of the body mass devoted to flight muscles is surprisingly constant over the whole range of body sizes, with the main downstroke muscles making up ≈15.5% of the total body mass (9). Using this muscle mass, Chatterjee *et al.* used data on the metabolic rates and power output of modern birds (10) to estimate the power *Argentavis* had available for flight. The power analysis model also incorporated wing dimensions, but no specimen of *Argentavis* has a complete wing skeleton, so they scaled up the dimensions of the skeleton of *T. merriami* to fill in the missing parts. [*T. merriami*, although only approximately one-fifth of the body mass and with wings only approximately half the span of *Argentavis* (3), was still a huge bird, ≈33% heavier than a California condor.] This procedure gave *Argentavis* a wingspan of 7 m and a wing area of 8 m^2 (1).

Using their estimates of body mass and dimensions as parameters in the power model, Chatterjee *et al.* (1) generated a U-shaped power curve, typical of flying animals and airplanes, with a minimum power requirement of ≈600 W for sustained, level flapping flight. Their estimate of the maximum sustainable aerobic power available from *Argentavis*'s muscles was only 170 W, meaning that *Argentavis* was incapable of sustained flapping flight. How, then, did it fly?

Argentavis, like modern condors and vultures, would have been a soaring bird. Soaring birds maintain a shallow glide, 3° or 4°, and take advantage of rising air to stay aloft without flapping. The two main sources of rising air available to land birds are thermals and ridge lift. A thermal occurs when uneven heating of terrain causes a mass of air to become warmer than the surrounding air. This mass of warm air rises, and if a thermal rises faster than the sinking speed of a soaring bird in the warm air mass, the bird is carried up by the thermal. Soaring birds typically circle upward in thermals and glide downward between thermals, sometimes covering enormous distances in the process (11). Ridge lift occurs when wind blows up the slope of any inclined terrain, such as a hill or mountain. If the vertical component of the wind speed is greater than a soaring bird's sinking speed, then the bird can soar across the face of the slope, or slope soar, indefinitely without losing altitude. If the slope is extensive, such as a long ridge or mountain chain, a soarer can also cover great distances by using ridge lift (8).

Challenging Takeoff

Perhaps the most intriguing result of this work comes from the flight maneuver simulation model of Chatterjee *et al.* (1), which shows that both takeoff and landing would have been problematic for *Argentavis*. Because its power output was less than one-third of the minimum

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needed for flapping flight, the model suggests that *Argentavis* could not have taken off from level ground in still air, even with a long takeoff run to gain speed like a taxiing airplane. Chatterjee *et al.* describe two possible takeoff methods. The first is to leap from a tall perch, in which the bird would need to drop ≈20 m to build up enough speed to level out in still air or ≈12 m in a 5 m/s headwind. The other method is to run down a slope, like a person launching a hang glider. Their model simulated various conditions and found that *Argentavis* could get airborne by running down a 10° slope for ≈30 m in still air or 10 m with a 5 m/s headwind (1).

The simulation model also suggests that landing on a level surface may have been challenging for *Argentavis*. Its slowest glide speed would have been ≈18 m/s (below which it would stall and lose its lift), far too fast to touchdown safely. By using its wings for aerodynamic braking, the simulated bird was able to slow to ≈6 m/s before touching down, which is still unsafe: A touchdown speed of 5 m/s is considered marginally safe at best for an animal this size (12). By gliding into a 5 m/s headwind and then braking, the simulated *Argentavis* was able to bring its ground speed at touchdown to <5 m/s.

Pampas Paradox

With a body built for soaring, and the modern example of the Andean condor demonstrating its feasibility, one might expect *Argentavis* to have spent its time slope soaring in the Andes. Some fossils of *Argentavis* have indeed been found in the Andean foothills. Others, however, have been found far to the southeast, on the Argentine pampas. How could a bird incapable of taking off from level ground have made a successful living on the pampas?

The modern pampas are a very windy place (3), and they were probably equally windy, although hotter and drier, at the time of *Argentavis* (1). By restricting their visits to the pampas to periods of predictably strong and numerous thermals and strong winds (probably summers), these huge birds should have been able to fly over the pampas. Based on leg and pelvis geometry, *Argentavis* would have been a much more agile walker than other large soaring birds like condors, and apparently was capable of extensive walking, although it was not much of a runner (3). This ability would have come in handy if *Argentavis* ever found itself grounded on level terrain. The big bird may have been accustomed to lengthy hikes to find the necessary slope to permit a takeoff.

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Some questions about flight in *Argentavis* remain unanswered. Could a burst of a few seconds of anaerobic power have given these huge birds enough power to take off without slopes or headwinds? Could they have landed on narrow ledges on cliffs or mountains, of the type favored by condors? How common were the large thermals they would have required? And going beyond *Argentavis*, can this approach tell us anything about flight in other, very large, extinct flying animals? What about the other teratorns, for example, or the pterosaurs, extinct flying relatives of the dinosaurs? As big as *Argentavis* was, even larger flying animals once lived. Among Cretaceous pterosaurs, *Pteranodon* had a wingspan that was approximately the same as *Argentavis*, although it probably weighed a bit less; another pterosaur, *Quetzalcoatlus*, had a wingspan >50% greater than *Argentavis*, making *Quetzalcoatlus* the largest known flying creature. Can we learn anything about power requirements and flight performance in pterosaurs using similar computer models? If takeoff was very difficult for *Argentavis*, how much more difficult would it have been for *Quetzalcoatlus*? Would knowing *Quetzalcoatlus*'s flight power requirements shed any light on whether it had an ectothermic or endothermic metabolism? This type of quantitative, biomechanical approach to studies of extinct animals has given us surprisingly detailed insight into how they may have lived, and an approach similar to that of Chatterjee *et al.* (1) applied to other extinct flyers should be equally enlightening.

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