AUTHOR CONTRIBUTIONS

F.J.S. conceived the study and reanalyzed the data. F.J.S. and L.M.C. interpreted the analyses and wrote the article.

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Response to Serrano and Chiappe

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In the recent study in *Current Biology* by Pei and colleagues[1], we used two proxies — wing loading and specific lift — to reconstruct powered flight potential across the vaned feathered fossil pennaraptorans. The results recovered multiple origins of powered flight. We respectfully disagree with the criticism raised by Serrano and Chiappe[2] that wing loading and specific lift, used in sequence, fail to discriminate between powered flight and gliding. We will explain this in reference to our original conservative approach.

We agree that wing loading alone does not distinguish between obligate gliders (i.e. gravity-powered, non-flapping flight) and powered flyers. Used alone, wing loading only distinguishes between flying (i.e. obligate gliders plus powered flyers) and non-flying taxa. However, the second stage of our work was a flapping flight power analysis that generated conservative specific lift estimates for flapping wings. Such an analysis explicitly and specifically tests for powered flight potential. To account for uncertainties in estimating performance, muscle power was allowed to vary over a considerable range (Po,m from 225 to 287 Wkg^{-1}). Our analysis specifically estimated the ability of the fossil taxa to achieve a positive rate of climb, using flapping flight, following a hind limb propelled launch. These behaviours define a powered flyer. Our specific lift analysis explicitly models powered flight, not fixed wing flight. There remains the potential to detect obligate gliders among 'marginal' taxa that we recovered as not capable of powered flight. This could be the case for taxa that were arboreal or scansorial, as shown for scansoriopterygids[3].

Serrano and Chiappe[2] note that wing loading lacks a direct or simple relationship to powered flight, citing Pennycuick[4]. While correct, it is important to note that this does not mean such a relationship is absent. The same study[4], and others[5–7], has demonstrated that wing loading does have a relationship to flapping flight performance. This relationship is complex and indirect, but still important to flapping flight performance analysis. Pennycuick[4] identifies this most directly in his demonstration of how flapping frequency, wing shape, and body mass are interrelated. Powered flyers have a wider range of wing loadings than obligate gliders because they generate additional airspeed (and vorticity) over the wings by flapping. This means that the maximum wing loading for powered flight is higher than for obligate gliding flight[8], up to ~2.5 gcm^{-2}; this is why we used this threshold to distinguish between flying and non-flying taxa. Total lift depends directly on wing area (first power) and the square of the airspeed over the wings. The squared influence of airspeed gives higher flapping frequency a major performance boost. However, for a given wing shape, power potential and body size, there is a limit on flapping frequency. Consequently, total wing area in any flapping flyer has a minimum value, below which, thrust and weight support will be insufficient for powered flight. This places a ceiling on wing loading for powered flight, over a given power, range of motion, and maximum lift coefficient, all of which we accounted for in our specific lift analysis.

Serrano and Chiappe[2] raise concerns about the muscle power estimates we made for non-avialan paravian taxa, and our use of a model modified from Marden[9]. They note that our estimates of specific lift are sensitive to the estimates of available power. We have justified our use of Marden's model[9] for fossil pennaraptorans in our paper[1] and elsewhere[5–7]. We expand in this regard below to provide a more complete understanding of our methodology.

We acknowledge that specific lift calculations are sensitive to estimates of available muscle power. For this reason, we chose the most conservative estimates for the flight muscles (flight mass ratio of 10% and maximum muscle mass-specific power output of

225–287 Wkg^{-1}). Marden's model deals with climb out immediately after launch, which is a rapid action, so our estimates reflect this in relating to burst flight. They are within the expected range for the combination of aerobic and anaerobic muscle action during a burst type action and well below (49–60%) of the maximum power output measured for extant avians (460 Wkg^{-1})[10]. Aerobic power output is lower in living birds at ~175 Wkg^{-1} and aerobic muscle dominates during endurance activities. During climb out, as we have modelled, birds utilise some fraction of anaerobic muscle for short-duration power[10]. We have not examined whether these taxa could sustain flight for long time periods, which is beyond the scope of our paper. We only examined whether powered flight was potentially available to the taxa examined, meaning that they could take off and achieve a positive rate of climb. The power outputs we used, with a maximum of 287 Wkg^{-1}, limit the modelled animals to mostly aerobic power and/or relatively low-grade anaerobic muscle, avoiding the use of maximum crown-group estimates.

Serrano and Chiappe[2] highlight the lack of forward speed in Marden's model. Marden's model does not include forward speed because, during climb out and other slow-flight phases, the translational speed relative to flapping speed is quite low. Our model specifically evaluates climb out immediately after launch in a conservative fashion. For both obligate gliders and powered flyers, launch is powered by the walking limbs, and this provides some initial forward speed. Any underestimation of forward speed we make is for all taxa, meaning that more taxa would be identified with powered flight potential than that already found. As we estimate the ability to achieve a positive rate of climb by flapping, this does not compromise our ability to distinguish powered flyers from obligate gliders.

Contrary to the assertion of Serrano and Chiappe[2], Marden's model does discriminate between flyers that can achieve climb out after launch and those that cannot. However, it does not discriminate between standing launch and running launch. Flight muscle ratio has little to do with launch performance in most birds. This is because launch is hind limb driven, and flight muscle ratio does not predict standing vs running launch utilisation in extant birds. Observational and mechanical data indicate that running launch is primarily an adaptation of anatids and diving waterfowl. They regularly take-off from water with shortened hind limbs with a position and range of motion adapted to swimming that precludes powerful leaping.

The very large forelimbs of *Rahonavis* are suggested by an unusually long ulna that is longer than the femur and tibia. When originally described, *Rahonavis* was inferred as a powered flyer. Our conservative wingspan estimate for *Rahonavis* uses measurements from the dromaeosaurid *Microraptor*. If *Rahonavis* was a fossil bird, the ulna should be proportionally longer than the other forelimb long bones and the entire forelimb should be longer compared to dromaeosaurids. Depending on the power value used, the minimum wing length needed for *Rahonavis* to pass the specific lift threshold is 360–480 mm, only necessitating primary feathers that are a few millimetres to under 16 cm long. These primary feather estimates are conservative compared with the longer primaries of similar-sized paravians, e.g. 20+ cm in *Microraptor* and *Jeholornis*. *Rahonavis* was therefore reasonably modelled based on available data. Our performance estimates for *Microraptor* also support multiple origins of powered theropod flight.

AUTHOR CONTRIBUTIONS

Conceptualization: M.P., M.B.H. and T.A.D.; Methodology: M.P., M.B.H. and T.A.D.; Validation: M.P., M.B.H. and T.A.D.; Formal Analysis: M.P., M.B.H., T.A.D. and H.C.E.L.; Investigation: M.P., M.B.H., T.A.D. and H.C.E.L.; Resources: M.P., M.B.H. and T.A.D.; Writing — Original Draft: M.P., M.B.H., T.A.D. and H.C.E.L.; Writing — Review and Editing: M.P., M.B.H., T.A.D., H.C.E.L., R.P., T.G.K., M.A.N., S.L.B. and X.X.; Supervision: M.P.; Project Administration: M.P.; Funding Acquisition: M.P.

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